

SYSTEMATICS OF *SYLVILAGUS* GRAY, 1867 (LAGOMORPHA: LEPORIDAE) FROM SOUTHWESTERN NORTH AMERICA

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A multivariate morphological analysis of 26 cranial, mandibular, and dental characters was carried out on five taxa of cottontails: *Sylvilagus floridanus chapmani* (J. A. Allen, 1899), *S. f. cognatus* (Nelson, 1907), *S. f. holzneri* (Mearns, 1896), *S. f. robustus* (Bailey, 1905), and *S. nuttallii pinetis* (J. A. Allen, 1894). Discrete characters of upper P2 and P3 and lower p3 were examined in the above taxa, *S. n. grangerii* (J. A. Allen, 1895), and *S. a. audubonii* in the context of cladistic analyses. In the latter series of analyses, particular attention was paid to inter- and intrapopulation variation in the *S. f. floridanus* (J. A. Allen, 1890) and *robustus* taxa and in *S. audubonii* (Baird, 1857). I describe dental variation among holotypes and topotypes of these three taxa. My principal objective was to assess whether or not *S. robustus* was a subspecies of *S. floridanus*. An analysis of variance indicated that *robustus* differed from other taxa in six characters (greatest length of skull, condylobasal length, breadth of rostrum, interbasiooccipital length, width of tympanic bullae, and mastoid breadth). Principal component analysis indicated ontogenetic differences between *robustus* and remaining taxa. Neighbor joining analysis in every case correctly classified each specimen examined to its predetermined taxon. Besides a large difference in size, several discrete differences in cranial and dental morphology separated *S. robustus* from the parapatric *S. f. chapmani* and from the nominal subspecies, *S. f. floridanus*; characters based on premolar enamel pattern in particular differentiated between *S. f. floridanus* and *robustus*. In phylogenetic analyses of 24 dental characters, *S. cognatus*, *S. robustus*, and *S. holzneri* were successive sister taxa to an unresolved clade consisting of two paraphyletic *S. nuttallii* "subspecies" and two subspecies of *S. floridanus* (sensu stricto). I propose that *Sylvilagus robustus* is a species distinct from *S. floridanus* and its subspecies, some of which probably also constitute distinct species. These results help clarify biogeographic problems inherent in the genus *Sylvilagus* under the current taxonomic framework.

Key words: *Sylvilagus*, cottontail rabbit, systematics, dentition

Texas is well known for a number of limital and endemic species of vertebrates and invertebrates. Among mammals, a number of these taxa occur west of the Pecos River (Schmidly, 1977), in an area known as the Trans-Pecos Texas. One of these Trans-Pecos species is the rare endemic Davis Mountains cottontail rabbit (*Sylvilagus floridanus robustus*), currently relegated (Hall, 1951) to a subspecies of the widespread eastern cottontail, *Sylvilagus floridanus*. The taxon *robustus* first was described from a series of specimens collected by Vernon Bailey in the Fort Davis area (Jeff Davis

Co., Texas), at an elevation of 6,000 feet (Bailey, 1905). Bailey described the animals as a subspecies of *Lepus* (sic.) *pinetis*; however, he noted that worthwhile comparisons could be undertaken among *robustus* and *L. p. pinetis* and *L. p. holzneri*. Currently, *pinetis* is considered a subspecies of *S. nuttallii*, while *holzneri* is considered a southwestern montane subspecies of *S. floridanus*. Of the taxa considered herein, only *chapmani*, *holzneri*, and *nuttallii* were described when Lagomorpha was revised by Lyon (1904). Of these, *chapmani* and *holzneri* were treated as subspecies of *S. flori-*

danus; *nuttallii* was considered a monotypic species and *pinetis* was not recognized as a subspecies separate or distinct from other geographic variants of *nuttallii*. In his description, Bailey (1905:159–160) noted that *robustus* is “similar to *Lepus pinetis holzneri* but larger, with relatively narrower braincase and conspicuously wider, more prominent postorbital processes.” Bailey largely reiterated these items verbatim in his commentary regarding cranial characters, adding that individuals in the species displayed “slightly larger bullæ, and conspicuously wider, more prominent postorbital processes.”

Shortly after the description of *robustus* as a subspecies of “*pinetis*” (= *nuttallii*), Nelson (1909) published a revision of rabbits of North America in which he elevated *robustus* to a species, placing it in the *floridanus* species group, with *S. floridanus* and its subspecies, *S. transitionalis*, and *S. cognatus*. Like *robustus*, *cognatus* currently is considered a subspecies of *floridanus*. Nelson (1909) provided no justification for this taxonomic scheme, although he did recognize the close relationship among species constituting the group. Although *S. nuttallii* also was recognized as a member of the *floridanus* group in the introductory remarks (Nelson, 1909:43), *nuttallii* was treated as a separate species group, with three subspecies, in the main body of the work (Nelson, 1909:199), thereby increasing confusion with respect to the systematics of these species of *Sylvilagus*.

The *robustus* taxon maintained its species rank until Hall and Kelson (1951) synonymized the taxon with *floridanus*. Their justification was based on the apparent intermediate nature of a specimen (Louisiana State University Museum of Natural Science No. 658) assigned to *robustus* by Davis and Robertson (1944) but that appeared intermediate in morphology between *S. f. cognatus* and *S. robustus* to Hall and Kelson (1951:56): “considering the intermediate nature of [the specimen . . .] it seems appropriate to us to use the name-combi-

nation *Sylvilagus floridanus robustus*.” Based on their treatment of these *Sylvilagus* taxa in this and succeeding works (Hall, 1951, 1981; Hall and Kelson, 1959), subsequent authors have continued to use without question this taxonomic scheme (Chapman et al., 1980, 1982; Hoffmann, 1993; Nowak and Paradiso, 1983). Indeed, Davis and Schmidly (1994:92) stated that “only nominal differences” distinguish *S. f. chapmani* from *robustus*; accordingly, those authors continued the treatment of *chapmani* and *robustus* as subspecies of *S. floridanus* (although W. B. Davis always maintained, personally, that *robustus* was distinct enough that it would be elevated to species rank—D. J. Schmidly, pers. comm.). *Sylvilagus floridanus nelsoni*, described by Baker (1955) from Coahuila, México (Baker, 1956) was synonymized with *S. f. robustus* by Raun (1965).

No subsequent analysis has been undertaken to determine the validity or justification of the assignment of *robustus* to *S. floridanus*. As a consequence, and given the stark difference in size between *robustus* and the purportedly parapatric *S. f. chapmani* (e.g., Hall, 1951, 1981; Davis, 1974), it is not surprising that *robustus*, following Nelson (1909), is accepted widely as a distinct species in the Trans-Pecos.

My purpose in this study was to assess the morphological basis of the assignment of *robustus* to *S. floridanus*, with the benefit of examination of most known *robustus* specimens, and to determine if *robustus* constitutes a species, as suggested by Nelson (1909). A second objective was to consider biogeographic relationships among taxa in light of any novel taxonomic schemes ensuing from phylogenetic analyses using currently designated subspecies of *Sylvilagus* as terminal taxa.

MATERIALS AND METHODS

I examined the holotypes of *robustus* and *holzneri*, and a series of *S. f. chapmani*, *S. f. cognatus*, *S. f. holzneri*, *S. f. robustus*, and *S. nuttallii pinetis* at the United States National

Museum (USNM). At the American Museum of Natural History (AMNH), I examined the holotypes of *S. f. floridanus* and *S. nuttallii grangerii*. Topotypes of *S. audubonii* were examined from the Museum of Vertebrate Zoology (MVZ). Because cottontails of the genus *Sylvilagus* tend to be relatively homogeneous morphologically, and the range of intraspecific phenotypic variation in the genus so broad as to overlap interspecifically, my initial analyses focused on morphometric analyses of continuously variable characters. However, subsequent analyses focused on dental characters, which were more useful in delineating species boundaries among *Sylvilagus* species.

Continuous characters.—Depending on the state of the cranium and mandible, 26 cranial and mandibular measurements were recorded from each specimen. Most of the measurements recorded were defined by White (1987); those that were not are defined below. Measurements (and acronyms) were: greatest length of cranium (GLS); condylopremaxillary length (CONDL); length and width of palatine foramina (LPALFOR, WPALFOR); palatal length (PALONG); length of basioccipital (BASIOC); width and anteroposterior diameter of auditory bulla (WIDBULL, ANT-BULL); width between auditory bullae (INTBD); width across occipital condyles (OCCOND); least postorbital constriction (POSTORB); breadth and height of rostrum (BROSTR, DEPROSTR; measured at plane of extremity of anterior zygomatic process); least alveolar length of I2-P2 diastema (I2P2); greatest alveolar length of P2-M3 toothrow (P2M3); length and breadth of p3 (LP3, WP3); least alveolar length of i-p3 diastema (IP3); mandibular height at m1 (MANDEP); greatest alveolar length of p3-m3 toothrow (P3M3); interbasioccipital (from posterior edge of palate to suture at anterior end of basioccipital of White, 1987; INTBOC); breadth of choana (CHOANA); greatest height (HBRAIN) and breadth of braincase (BBRAIN; taken at extremity of posterior zygomatic process); mastoid breadth (MASTOID); and zygomatic breadth (ZYGO).

Statistical analyses were performed using the Statistical Analysis System (SAS) software, version 6.03 (SAS Institute, 1988a, 1988b), generally following Ruedas (1995) and Ruedas and Bickham (1992). Significance in all analyses was set at $\alpha = 0.05$. Because of the restrictions imposed by a limited sample, all analyses were

carried out on males and females combined; no attempt was made to determine presence or extent of sexual dimorphism in any of the taxa examined, although sexual dimorphism does exist in continuous characters (measurements) in *Sylvilagus* (Orr, 1940) and, with small sample size, could affect results of future multivariate analyses (Reyment et al., 1984). Univariate statistics, including mean, standard error, moment statistics (skewness, g_1 , and kurtosis, g_2) and tests of normality were performed invoking the normal option of the UNIVARIATE procedure with the "normal" option, which tests for normality using the Shapiro-Wilk statistic, W , and provides the associated probability value. Significance of the moment statistics was calculated by hand (Sokal and Rohlf, 1981:174–175; vide Ruedas et al., 1994). Analysis of variance was carried out using the GLM procedure that accounts for unbalanced data; two means-separation procedures were used. The Student-Newman-Keuls (MEANS, option SNK) multiple range test was employed because of its widespread use in studies of this sort; however, this test does not control for Type I error under each partial null hypothesis. An alternative multiple range test is the Ryan-Einot-Gabriel-Welsh multiple F test (MEANS, option REGWF) that controls for Type I error (Day and Quinn, 1989; SAS Institute, 1988b); results of the latter test are presented.

Two multivariate analyses were undertaken. A principal component analysis (procedure PRINCOMP) was carried out on the correlation matrix of raw (untransformed) data to determine if any group separation occurred using measurements taken (except breadth of zygomatic arch and braincase, which were not recorded from the holotypes of *holzneri* and *robustus*). Such a posteriori grouping methods were preferred over a priori grouping methods (multiple range tests, canonical discriminant analysis) because there was no prior hypothesis as to the putative identity of specimens examined. The NEIGHBOR procedure was used to determine if individual specimens were classified correctly to species groups using nearest-neighbor classification based on Mahalanobis distances, setting the prior probability to be proportional to taxon sample sizes (statement PRIORS PROPORTIONAL).

Discrete characters.—Drawings of P2, P3, and p3 were made using a camera-lucida microscope. Among North American leporids, P2 and

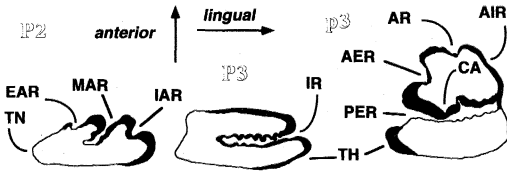


FIG. 1.—Camera lucida drawing of typical *Sylvilagus* P2, P3, and p3 (*S. f. floridanus* holotype, AMNH 1890/1155) showing structures and characters examined in the analysis of discrete characters. Abbreviations are: AR, anterior reentrant of p3; AER, anteroexternal reentrant of p3; AIR, anteroexternal reentrant of p3; CA, central angle of of p3; EAR, anteroexternal reentrant of P2; IAR, anteroexternal reentrant of P2; IR, internal reentrant of P3; MAR, main anterior reentrant of P2; PER, posteroexternal reentrant of p3; TN, thin enamel; TH, thick enamel. See Appendix I for additional characters and character states associated with these features.

particularly p3 generally are the most informative dental elements for taxonomic and systematic purposes (Dalquest, 1979; Dalquest et al., 1989; Hibbard, 1963; White, 1987, 1991; White and Morgan, 1995). White (1987) further noted that although P3 (among others) eventually might prove to be diagnostic, adequate descriptive work was lacking for that tooth. In the particular case of *S. f. floridanus* and *robustus*, P3 was diagnostically distinct, so was described and illustrated herein. Discrete characters (i.e., shape derived) were deemed the most important in this particular research; accordingly, resulting figures were oriented and scaled to the same size in linear dimensions to carry out size-independent comparisons of interspecific characters. Characters considered (Fig. 1; Table 1) are described in Appendix I; all are polarized with respect to the presumed plesiomorphic condition as exhibited by *Lepus californicus*, in the genus hypothesized sister to *Sylvilagus* (Halanych and Robinson, 1997; White, 1991; White and Morgan, 1995) in the absence of *Brachylagus*.

Cladistic characters were analysed using PAUP 3.1.1 for MacIntosh (Swofford, 1993), and PAUP*, version 4.0.0d54 (test version provided by D. L. Swofford) on a Silicon Graphics Challenge S workstation. Two series of analyses were carried out. The first included all taxa without *S. audubonii*, for which extent of population variation in morphological characters was not

TABLE 1.—Distribution of character states in the cladistic analysis. Characters are polarized in reference to the outgroup *Lepus californicus*.

Species	Character ^a																						
	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	xiii	xiv	xv	xvi	xvii	xviii	xix	xx	xxi	xxii	xxiii
<i>Sylvilagus holzneri</i>	0	0	1	0	0	0	0	0	2	0	0	1	0	0	1	0	1	0	2	0	1	0	0
<i>S. cognatus</i>	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	2	1	1	0	1
<i>S. robustus</i>	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	2	0	0	1	0	1
<i>S. fl. floridanus</i>	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1
<i>S. fl. chapmani</i>	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0
<i>S. nuttallii grangerii</i>	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	0	0	2
<i>S. n. pinetis</i>	2	1	0	0	0	2	1	2	1	1	1	0	0	0	0	1	0	2	1	0	1	1	1
<i>S. audubonii</i>	1	1	1	0	1	0	1	1	1	0	0	1	0	0	0	1	0	1	1	0	1	0	2
<i>Lepus californicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

^a Appendix I provides a description of the characters.

deemed to be adequately resolved; the second series of analyses included *S. audubonii*. In all cases, search criterion was set to maximum parsimony, and *Lepus californicus* designated as the outgroup. Characters were unordered because the sequence of multistate characters was indeterminate. All characters were equally weighted. Because of the small number of taxa involved, it was possible to invoke the alltrees option, which carried out an exhaustive search and generated a frequency distribution of tree lengths suitable for skewness and kurtosis statistics (hierarchical structure—Hillis, 1991; Hillis and Huelsenbeck, 1992; Huelsenbeck, 1991). Significance of the skewness statistic was evaluated using values calculated by Hillis (1991) and Hillis and Huelsenbeck (1992), and by hand using the method of Sokal and Rohlf (1981). Consensus trees were done using the majrule and le50 options, which resulted in the 50% majority-rule consensus tree (majrule), but also retained groups occurring on <50% of the trees if they are compatible with the groups already on the tree (le50). Bootstrap analysis used 10,000 replicates with the method set to branch-and-bound, the tree bisection-reconnection (tbr) branch swapping algorithm, addition sequence set to simple, and three trees held at each cycle of the addition procedure. Jackknife analyses used the same defaults.

RESULTS

Continuous characters.—Five characters were not significantly different among taxa examined (Table 2): length of palate (PALONG), width between auditory bullae (INTBD), width across occipital condyles (OCCOND), alveolar length of maxillary diastema (I2P2), and breadth of the choana (CHOANA). All other characters differed significantly and separated taxa to varying extent.

Separation of group means between *robustus* and all other taxa examined occurred in six characters ($P \leq 0.0001$). Characters were greatest length of skull (GLS), condylopremaxillary length (CONDL), breadth of rostrum (BROSTR), interbasioccipital length (INTBOC), width of auditory bullae (WIDBULL), and mastoid breadth (MASTOID). In each of those characters, *robus-*

tus had the highest mean. The Gulf Coastal *chapmani* usually displayed the lowest mean for each character, including significantly smaller measurements ($P \leq 0.0001$) than all other taxa examined in length of palatine foramina (LPALFOR), anteroposterior diameter of auditory bullae (ANTBULL), zygomatic breadth (ZYGO), and breadth of braincase (BBRAIN). Means for *pinetis* usually did not differ from *chapmani* and formed a group exclusive of the other taxa based on greatest length of skull, condylobasal length, and alveolar length of mandibular diastema. Means for *pinetis* only differed significantly from those of all other taxa in having the narrowest rostrum (BROSTR) and wider auditory bullae (WIDBULL) than all taxa but *robustus*.

Specimens identified as *pinetis* display discrete separation from other taxa (Fig. 2; Table 3). Remaining taxa, all currently classified as subspecies of *Sylvilagus floridanus*, display varying degrees of overlap. The orthogonal orientation of the primary principal component axes of each taxon's dispersion in multivariate space has been shown to be indicative of differing ontogenetic growth patterns (Voss and Marcus, 1992; Voss et al., 1990). A corollary of the foregoing is that different orientations of the primary axes are thereby good prima facie evidence of distinct specific status based on these ontogenetic differences (Brown et al., 1995). In the case of the taxa examined herein, it is clear that orientation of the primary axis of dispersion is distinct between *robustus* and all remaining taxa, to a lesser extent between *pinetis* and *chapmani* + *cognatus* + *holzneri*, and almost identical among the latter three taxa. Specimens of *chapmani* appear to display clinal variation from south to central to western Texas. This variation needs to be examined further with larger samples.

The degree of morphological conservatism among *Sylvilagus* taxa examined was underscored by the fact that the first three principal components only accounted for 69% of the variation (52.2%, 11.3%, and

TABLE 2.—Univariate descriptive statistics and results of the analysis of variance for unbalanced cell sizes. The mean \pm SD, the range, and the sample size in parentheses are presented for each species and character. Symbols superscripted by the character abbreviation indicate results of the Ryan-Einot-Gabriel-Welsh multiple F-test for each partial null hypothesis; n indicates no significant difference among means ($P > 0.05$), * $0.05 \geq P > 0.01$, * $0.01 \geq P > 0.001$, *** $P \leq 0.001$. Letters superscripted by means and standard deviation in each character indicate non-significant species groups as determined by the REGWF multiple range test, ranked by size class ($a > b > c > d$).

Character ^a	<i>S. f. chapmani</i>		<i>S. f. cognatus</i>	
GLS***	67.12 \pm 2.88 ^d	61.1–72.3 (17)	70.68 \pm 1.97 ^{b,c}	67.4–72.9 (6)
CONDL***	59.45 \pm 2.32 ^d	54.5–63.1 (16)	63.01 \pm 1.61 ^{b,c}	60.2–64.5 (6)
LPALFOR***	16.61 \pm 0.85 ^c	14.7–17.8 (19)	17.86 \pm 0.52 ^{a,b}	17.3–18.5 (6)
WPALFOR	6.34 \pm 0.46 ^b	5.4–7.3 (18)	6.77 \pm 0.21 ^{a,b}	6.4–7.0 (6)
PALONG ⁿ	6.01 \pm 0.46 ^a	5.3–7.0 (19)	6.12 \pm 0.24 ^a	5.8–6.4 (6)
BASIOC***	8.34 \pm 0.43 ^b	7.7–9.3 (18)	8.60 \pm 0.53 ^b	7.7–9.3 (6)
WIDBULL***	9.68 \pm 0.69 ^d	8.5–10.8 (18)	10.46 \pm 0.40 ^c	9.8–10.8 (6)
ANTBULL***	8.39 \pm 0.45 ^d	7.5–9.2 (18)	8.89 \pm 0.34 ^{c,d}	8.4–9.3 (6)
INTBD ⁿ	7.55 \pm 0.55 ^a	6.7–8.8 (18)	7.49 \pm 0.92 ^a	6.0–8.6 (6)
OCCOND ⁿ	12.63 \pm 0.77 ^a	11.1–13.8 (17)	12.85 \pm 0.83 ^a	11.4–13.8 (6)
POSTORB**	11.58 \pm 0.65 ^b	10.2–12.8 (18)	12.68 \pm 0.64 ^a	11.8–13.6 (6)
BROSTR***	17.44 \pm 1.40 ^b	14.2–19.5 (19)	17.59 \pm 0.77 ^b	16.6–18.5 (6)
I2P2***	18.37 \pm 1.05 ^b	16.3–20.0 (19)	19.79 \pm 0.64 ^{a,b}	18.9–20.3 (6)
P2M3 ⁿ	13.19 \pm 0.64 ^a	12.0–14.6 (18)	13.20 \pm 0.69 ^a	12.1–14.2 (6)
LP3*	3.02 \pm 0.18 ^{a,b}	2.7–3.4 (19)	3.05 \pm 0.12 ^{a,b}	3.0–3.2 (5)
WP3**	2.70 \pm 0.15 ^{a,b}	2.4–3.0 (19)	2.75 \pm 0.22 ^a	2.6–3.1 (5)
IP3***	14.18 \pm 0.82 ^c	12.6–15.4 (19)	15.73 \pm 1.19 ^{a,b}	14.6–17.8 (6)
MANDEP*	10.91 \pm 0.80 ^{a,b}	9.8–13.0 (18)	10.80 \pm 0.83 ^b	10.1–12.4 (6)
P3M3*	13.49 \pm 0.62 ^{a,b}	12.2–14.5 (18)	13.59 \pm 0.55 ^{a,b}	12.8–14.5 (6)
INTBOC***	19.76 \pm 1.13 ^{b,c}	17.9–22.1 (18)	20.76 \pm 0.66 ^{b,c}	19.8–21.6 (6)
CHOANA ⁿ	6.28 \pm 0.58 ^{a,b}	5.3–7.0 (18)	5.97 \pm 0.26 ^{a,b}	5.8–6.5 (6)
HBRAIN***	22.77 \pm 0.89 ^b	21.3–24.3 (17)	23.35 \pm 0.85 ^{a,b}	22.1–24.2 (6)
DEPROST*	15.06 \pm 1.06 ^{a,b}	13.5–17.9 (19)	14.34 \pm 0.91 ^b	12.8–15.5 (6)
MASTOID***	21.77 \pm 0.89 ^{b,c}	20.1–23.1 (17)	22.17 \pm 1.17 ^{b,c}	20.3–23.3 (6)
ZYGO***	33.38 \pm 1.09 ^b	31.1–35.4 (16)	35.36 \pm 0.78 ^a	34.1–36.1 (6)
BBRAIN***	25.39 \pm 0.83 ^b	23.9–26.8 (17)	26.72 \pm 0.91 ^a	25.3–27.8 (6)

^a Appendix 1 gives description of characters.

5.4%, respectively). Only by principal component 9 did total variation account for >90% (90.4%). Better separation might have been achieved by a more judicious selection of characters; however, such a procedure would have obscured the overall picture by unduly focusing on interspecific differences. There were no standout characters contributing to the first principal component (Table 3); greatest length of skull and condylobasal length (0.978 correlation) and interbasiooccipital length being possible exceptions. Principal component 2 displayed clear differences in magnitude of eigenvectors with respect to dimensions of tympanic bullæ and p3, as well as length of

upper molar toothrow. Breadths of the zygomatic arch and of braincase were not included in the principal component analysis because they were not recorded from holotypes of *robustus* and *holzneri*. The relative contribution of p3 in principal component (or other) analyses was not surprising given the utility of both size and morphology of this character in paleontological studies of Lagomorpha (White, 1987); in particular, marked differences in morphology and size of p3 are observed among archaolagine genera and species (White, 1987).

As in the case of the principal component analysis, the neighbor-joining procedure

TABLE 2.—*Extended.*

<i>S. f. holzneri</i>		<i>S. f. robustus</i>		<i>S. n. pinetis</i>	
72.12 ± 2.10 ^b	69.6–75.3 (8)	72.85 ± 2.66 ^a	68.7–78.9 (13)	68.15 ± 1.60 ^{c,d}	66.5–71.1 (10)
64.04 ± 2.27 ^b	59.8–67.1 (8)	68.10 ± 3.70 ^a	54.2–69.5 (13)	60.54 ± 1.86 ^{c,d}	57.9–63.6 (10)
18.46 ± 1.06 ^{a,b}	16.3–19.9 (9)	18.11 ± 0.94 ^a	16.7–20.3 (13)	17.69 ± 0.80 ^b	16.5–19.0 (10)
6.61 ± 0.33 ^{a,b}	6.2–7.0 (9)	6.70 ± 0.76 ^a	5.6–8.2 (13)	6.42 ± 0.29 ^b	6.2–7.1 (10)
5.89 ± 0.48 ^a	5.0–6.6 (9)	6.01 ± 0.66 ^a	5.2–7.6 (13)	5.71 ± 0.56 ^a	4.9–6.4 (10)
8.87 ± 0.56 ^{a,b}	7.9–9.5 (9)	9.24 ± 0.52 ^a	8.3–10.0 (13)	8.44 ± 0.32 ^b	7.8–8.8 (10)
11.23 ± 0.46 ^b	10.5–11.8 (8)	11.91 ± 0.50 ^a	11.1–13.2 (13)	11.82 ± 0.42 ^{a,b}	11.2–12.6 (10)
9.14 ± 0.14 ^c	8.5–10.2 (8)	10.36 ± 0.48 ^a	9.6–11.2 (13)	9.74 ± 0.22 ^b	9.4–10.1 (10)
7.51 ± 0.57 ^a	6.7–8.1 (9)	7.46 ± 0.65 ^a	6.0–8.4 (13)	6.86 ± 0.70 ^a	5.2–7.4 (10)
12.71 ± 0.50 ^a	12.0–13.5 (8)	13.36 ± 0.66 ^a	12.6–14.7 (13)	12.85 ± 0.42 ^a	12.5–13.9 (10)
12.40 ± 1.15 ^{a,b}	10.8–14.2 (8)	12.46 ± 0.85 ^a	10.7–13.9 (13)	11.53 ± 0.66 ^b	10.6–12.5 (10)
17.63 ± 1.01 ^b	16.5–19.9 (9)	19.04 ± 1.35 ^a	16.8–21.0 (13)	15.86 ± 0.87 ^c	14.6–17.4 (10)
20.34 ± 1.40 ^a	17.3–22.0 (9)	21.42 ± 1.03 ^a	18.8–22.8 (13)	18.86 ± 0.76 ^b	17.7–20.5 (10)
13.22 ± 0.60 ^a	11.8–13.8 (9)	13.42 ± 0.44 ^a	12.6–14.3 (13)	12.74 ± 0.68 ^a	11.8–14.1 (10)
3.08 ± 0.34 ^a	2.4–3.6 (9)	3.07 ± 0.25 ^a	2.8–3.8 (13)	2.76 ± 0.10 ^b	2.6–2.9 (10)
2.72 ± 0.10 ^a	2.6–2.9 (9)	2.89 ± 0.20 ^a	2.6–3.3 (13)	2.52 ± 0.14 ^b	2.2–2.7 (10)
15.82 ± 1.29 ^{a,b}	13.6–17.7 (9)	15.86 ± 1.00 ^a	14.7–18.0 (13)	14.88 ± 0.65 ^{b,c}	14.2–16.2 (9)
11.51 ± 0.53 ^{a,b}	10.6–12.1 (9)	11.41 ± 0.45 ^a	10.6–12.2 (13)	10.68 ± 0.31 ^b	10.2–11.0 (9)
13.33 ± 0.72 ^{a,b}	12.3–14.3 (9)	13.91 ± 0.49 ^a	13.0–14.8 (13)	12.88 ± 0.49 ^b	12.2–13.9 (9)
20.96 ± 1.03 ^b	19.3–22.6 (9)	21.04 ± 1.15 ^a	19.0–22.9 (13)	19.65 ± 0.61 ^c	18.9–20.8 (10)
6.37 ± 0.49 ^{a,b}	5.4–7.0 (9)	6.17 ± 0.60 ^a	5.1–6.8 (13)	5.91 ± 0.30 ^b	5.3–6.2 (10)
24.02 ± 0.70 ^a	23.2–25.2 (8)	24.24 ± 0.82 ^a	22.8–25.5 (13)	22.89 ± 0.61 ^b	22.1–23.8 (10)
15.29 ± 1.06 ^{a,b}	12.6–16.4 (9)	15.38 ± 0.92 ^a	14.2–17.3 (13)	14.51 ± 0.61 ^b	13.2–15.3 (10)
22.54 ± 0.82 ^b	21.7–23.7 (7)	23.10 ± 0.99 ^a	21.2–24.5 (13)	21.35 ± 0.27 ^c	20.9–21.8 (10)
35.43 ± 0.73 ^a	34.4–36.4 (5)	35.33 ± 0.84 ^a	34.2–36.8 (10)	34.98 ± 0.73 ^a	34.3–36.5 (10)
27.13 ± 0.99 ^a	25.2–28.0 (6)	26.96 ± 0.59 ^a	26.3–28.4 (12)	26.66 ± 0.77 ^a	25.3–27.9 (10)

based on Mahalanobis distances was carried out excluding breadth of zygomatic arch and braincase. Every individual was assigned correctly to its a priori determined taxon. Nelson (1909) expressed reservations about the assignation of USNM 127446 (female) to *cognatus*, referring the specimen to this taxon “with some hesitation,” and adding that upon eventual examination of a larger series, *cognatus* and *holzneri* might be shown to intergrade. The nearest neighbor analysis classified this specimen as *cognatus*. While examining crania in my study, I noted that USNM 95560 (male; MÉXICO: Chihuahua; Sierra Madre, near Guadalupe y Calvo) identified as *holzneri*, was close to the *robustus* ge-

stalt in general conformation. This specimen too was assigned to *holzneri* in the morphometric analysis; dental morphology, not scrutinized by me, needs to be examined closely in this specimen to incontrovertibly ascertain its taxonomic identity.

Discrete characters.—Discrete morphological characters of crania and mandibles were examined separately in the context of a comparison only between a limited number of specimens of *chapmani* and *robustus*. The two taxa differed in a number of characters. In the basisphenoid, *robustus* had two distinct foramina, while *chapmani* specimens have a single foramen. The two taxa differed in the shape of the interparietal (a highly variable character in *chap-*

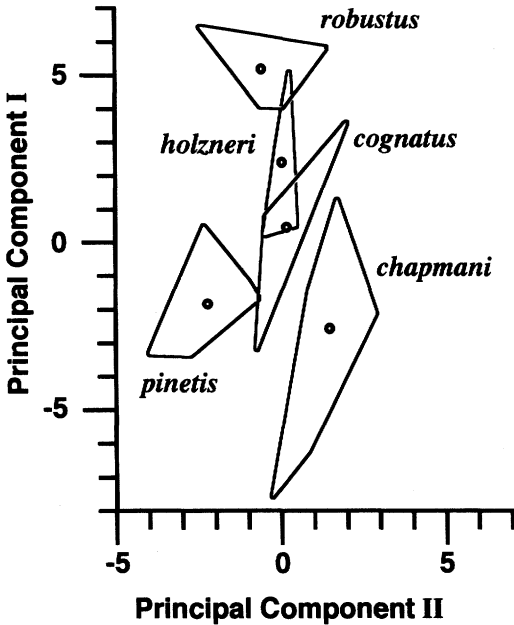


FIG. 2.—Graphical representation of the results of the principal component analysis (Table 2). The circle inside each polygon represents the centroid mean for that taxon (note that the mean for *cognatus* is located within the multivariate space of *holzneri*).

mani) and alisphenoid. *Sylvilagus robustus* lacked a tympanic process, which in *chapmani* was a distinct process originating at the base of the external auditory meatus, extending ventrally, ending in a point separated from the bulla, but level with the ventral aspect of the bulla. The foramina of the alisphenoid differed in size and conformation. The mental foramen was twice as long as high and located on the dorsad aspect of the mandible in *robustus*, but less than one-half again as long as high and usually on the labial aspect of the mandible in *chapmani*.

Discrete dental characters differed between *floridanus* and *robustus*, particularly in the holotypes (Fig. 3) but also in population samples (Fig. 4). In P2, the external anterior reentrant (EAR) tended to be particularly deep in *robustus* but shallow in *floridanus*; in general, it appeared that the trend for the EAR was to be deeper in *ro-*

TABLE 3.—Values for the first through third eigenvectors from the principal component analysis carried out on the correlation matrix of the cranial and mandibular data of specimens of *Sylvilagus*. The first four principal components together account for 73.4% of the variation (52.2%, 11.3%, 5.4%, and 4.6%, respectively). Results of the principal component analysis are graphically summarized in Fig. 2.

Character ^a	Principal component		
	1	2	3
GLS	0.272485	-0.091402	0.001892
CONDL	0.269917	-0.076634	0.011218
LPALFOR	0.243578	-0.181208	-0.007065
WPALFOR	0.177589	-0.095207	-0.033070
PALONG	0.041248	0.289915	-0.397311
BASIOC	0.227203	0.015315	0.089097
ANTBULL	0.166804	-0.415675	0.009829
WIDBULL	0.188319	-0.351482	-0.164859
INTBD	0.020424	0.243862	0.673324
OCCOND	0.192113	0.015547	-0.223151
POSTORB	0.145161	-0.074365	-0.194020
BROSTR	0.203124	0.112003	0.066613
I2P2	0.255481	-0.126630	0.112422
P2M3	0.197038	0.339229	-0.097644
LP3	0.186281	0.302220	-0.021652
WP3	0.165397	0.363453	-0.210805
IP3	0.231046	-0.150767	0.107571
MANDEP	0.161228	0.034871	-0.076835
P3M3	0.207900	0.254191	0.074470
INTBOC	0.262451	-0.021757	0.098446
CHOANA	0.192556	0.005205	0.388118
HBRAIN	0.245674	-0.044073	-0.099598
DEPROST	0.194033	0.195095	0.002583
MASTOID	0.230326	0.043187	-0.007735

^a Appendix I gives descriptions of characters.

bustus and shallow to imperceptible in *floridanus*; however, some *robustus* also had a shallow EAR. There also was some overlap in depth and acuteness of angles in the internal anterior reentrant (IAR) of P2 with *robustus* generally displaying deep IAR with acute angles and *floridanus* displaying shallow IARs with open angles. The most marked difference in P2 between the two taxa was in the conformation of the main anterior reentrant (MAR). The holotype of *robustus* displayed a highly complex and convoluted MAR (Fig. 3), particularly in the caudal surface, with thin enamel constituting the walls. In contrast, the holotype

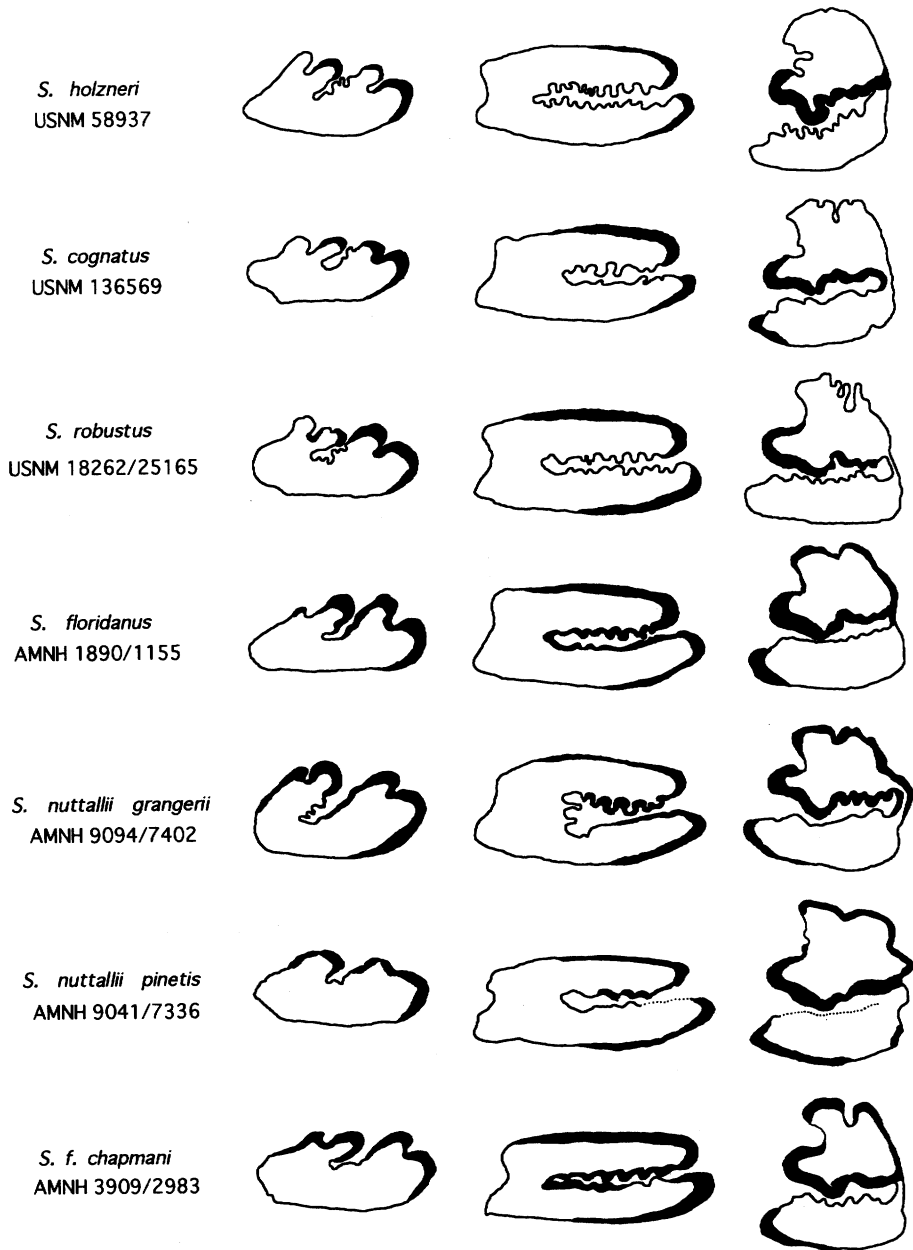


FIG. 3.—Camera lucida drawings of P2 (left column), P3 (center), and p3 (right) of the holotypes of the taxa considered in this paper. Drawings not to scale.

of *floridanus* (Fig. 3) had a smooth-walled and simple MAR, with thick enamel running almost to the terminal lacuna of the reentrant in both anterior and posterior walls of the MAR. While there was variation among specimens of the two taxa in

the thickness of the enamel forming the walls (Fig. 4), *robustus* specimens always had highly complex and convoluted caudad walls to the MAR. One illustrated specimen of *robustus* (ASNHC 545) had a highly crenelated caudad aspect to the MAR; how-

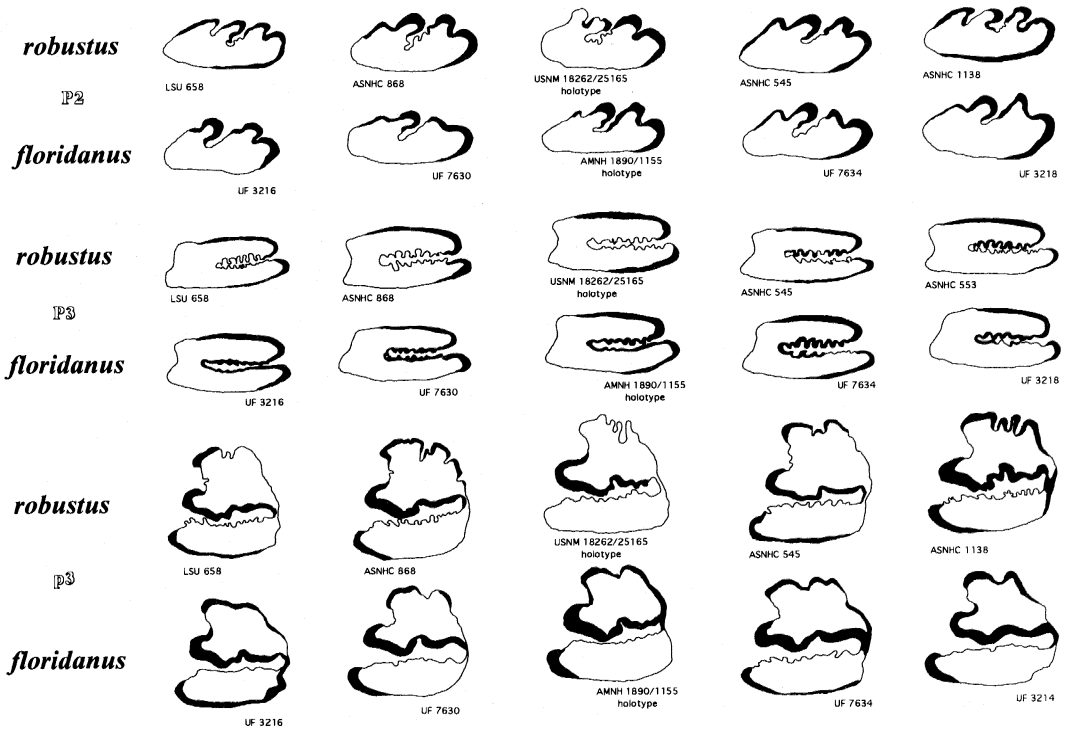


FIG. 4.—Camera lucida drawings of the teeth of a population sample of *Sylvilagus robustus* (top row in each pair) and *S. floridanus* (bottom row in each pair). Middle column shows holotypes of each of the two taxa (*S. f. floridanus* and *S. robustus*). Bottom row specimens of the rightmost diads fall within the range of *S. f. mallurus* in Florida, but show no discernible differences from *S. f. floridanus*. Top two rows: P2; middle rows: P3; bottom rows: p3. Drawings not to scale.

ever, those were so shallow as to be almost invisible in the illustration; crenulations were present nonetheless, in stark contrast to the inevitably smooth caudad aspects of the MAR in *floridanus* sensu stricto, including subspecies *S. f. floridanus* and *S. f. chapmani*.

In P3, there was a trend for *floridanus* to have a smoother, less crenelated internal reentrant (IR), in contrast to a highly crenelated IR in *robustus*, although the variation in this particular character overlapped between the two taxa: for example, *floridanus* UF 7634 displayed a high degree of crenelation in the walls of the IR (Fig. 4). A difference that was diagnostic between the two taxa in the specimens examined, however, was the thickness and distribution of enamel along the walls of the IR of P3. In *robustus*, the anterior wall of the IR typi-

cally was composed of thin enamel; if there was thick enamel present, this was either discontinuous (e.g., ASNHC 545), or continuous with the thick enamel forming the anterior wall of the tooth (in contact with P2), but not continuing to the full extent of the IR (ASNHC 553); the terminal lacuna of the IR inevitably was walled by thin enamel. In contrast, the IR of *floridanus* was homogeneously walled by thick enamel (although in some specimens there were slight gaps in the caudad wall of the IR—e.g., UF 3218, 7634). The thick enamel invariably surrounded the end of the IR, so that the terminal lacuna was thick-walled throughout.

Variation in S. audubonii.—Populational variation among *S. a. audubonii* was examined because this species also was known to occur in the Davis Mountains and

potentially could be conflated with *robustus*. Indeed, the *S. audubonii* from the Davis Mountains are darker than specimens from the High Plains or other areas of the range of this species, although quite typical in all other aspects of their morphology, including dental morphology. Most particularly, however, there exist a number of uncertainties surrounding the taxonomy and identification of *audubonii*. Poole and Schantz (1942:216) stated that the skull of the holotype had been lost; however, R. D. Fisher located the skull in the USNM collection in 1974, and it remains associated with the skin today (A. L. Gardner, pers. comm.). There also is some confusion regarding the exact type locality, compounded by the fact that the type only was designated by Poole and Schantz (1942:216), rather than by Baird himself in the 1857 description. Baird's description was based on five specimens from three distinct localities in California: Presidio, San Francisco, and San Diego. Only the specimen from San Francisco (USNM 1163) had the skull number in the description (skull number 2045). Further, it was that skull that was illustrated in Baird (1857: plate LVIII), thereby causing Poole and Schantz (1942:216) to comment that "as this specimen seems to be mentioned more particularly than any other specimen, it seems well to take it as the type." Indeed, specimens from San Diego enumerated in Baird's description (USNM 1591, 1594, and 1596) subsequently were placed in *Lepus floridanus sanctidiegi* [= *Sylvilagus audubonii sanctidiegi*] by Miller (1899).

Confusion also surrounds the date of publication of Baird's description. Although cited as 1858 in most works (Hall, 1951, 1981; Hoffmann, 1993), it also has been cited as 1857 (Nelson, 1909). Baird's work itself bears a publication date of 1857; inside, the letter of transmittal to the publisher bears the date of 7 April 1857, and the preface is dated 20 July 1857. However, a copy in the USNM bears a handwritten note beneath the 1857 publication date of 14 July

1858. This latter date is that preferred by Miller and Kellog (1955), but the 1857 date also is listed, albeit in parentheses. It is possible, but unlikely, that 5 months elapsed between the writing of the preface and the publication date; furthermore, the work was reviewed in the *Annals and Magazine of Natural History*, third series, volume 1, number 5, published in May 1858 (p. 369, Bibliographic Notices), adding further credence to the 1857 publication date (A. L. Gardner, pers. comm.). Accordingly, and in view of the lack of evidence to the contrary, I have opted herein to use 1857 as the date of publication for Baird's description, in accordance with Art. 21(c) (ii) of the International Code of Zoological Nomenclature (Ride et al., 1985), to be corrected (Art. 21(d)) should evidence to contrary be found.

Teeth of *S. a. audubonii* from near the type locality for that species were distinct from those of remaining taxa examined. In particular, p3 of *audubonii* (Fig. 5) were characterized by a highly reflected central angle in the posteroexternal reentrant, producing anterolingually a large lacuna with highly convoluted borders that angled back in a posterolingual direction. In this respect alone, *audubonii* strongly contrasted with specimens of all other taxa examined. The central angle may be so reflected as to be continuous across the posteroexternal reentrant (e.g., MVZ 102706). In addition, the posteroexternal reentrant had a very delicate lingual border, to the extent that in some individuals, it was open, essentially resulting in a bilophid tooth (e.g., MVZ 18443), or, if bisected by a connection between anterior and posterior lophs, essentially creating separate posteroexternal and posterointernal reentrants (MVZ 102706, left; terminology of White, 1987). The anterior reentrant of p3 was neither as complex as in *robustus* nor as shallow as in *S. f. floridanus*, instead tending to be single and deep. In P2, the main anterior reentrant tended to be deeper than those of other species, and although it may have been con-

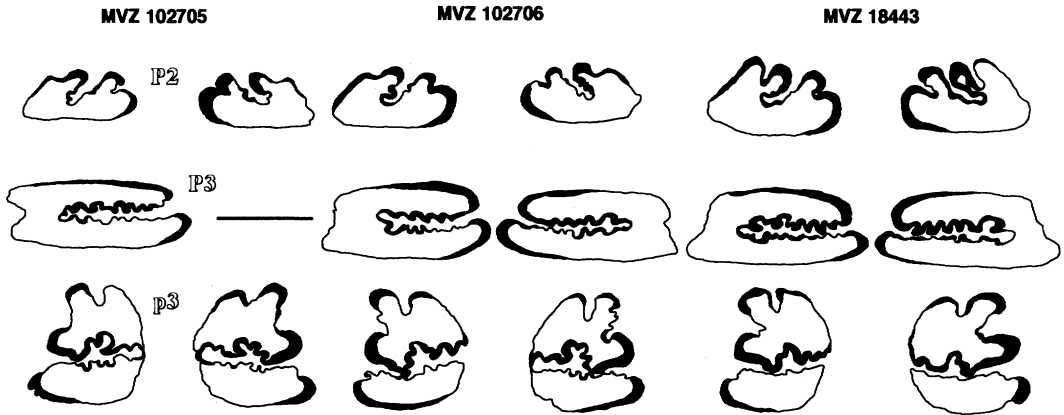


FIG. 5.—Sample of three near topotypes of *Sylvilagus a. audubonii* (exact type locality is unknown beyond “San Francisco,” in San Mateo Co. [Baird, 1857]). The three illustrated specimens are from adjacent Alameda (left and center) and Contra Costa (right) counties. Both left and right teeth are illustrated because the original description does not provide any detail as to possible characters defining *S. audubonii*. Drawings not to scale.

stituted by either smooth or complex enamel borders, the trend appeared to be towards some degree of crenelation. Conformation of enamel in the internal reentrant of P3 also differed from all other species examined. While the internal reentrant tended to be constituted by thin enamel in most species of *Sylvilagus* examined, *S. floridanus* had thick enamel throughout. In *S. audubonii*, the cranial wall of the internal reentrant was invariably constituted by thick enamel that did not extend through the entire extent of the caudal wall; rather, the thick enamel extended halfway through the caudal wall (continuously with that of the cranial wall), or was discontinuously distributed on the caudal wall of the internal reentrant (e.g., MVZ 18443, right).

Phylogenetic analyses.—Insofar as phylogenetic signal is concerned, Hillis (1991) stated that for eight taxa, the data should be informative (signal > noise) if the g_1 (skewness) statistic was more than $|0.34|$. For my data, the g_1 statistic was -0.474 . That value fell between $0.05 > P > 0.01$ for eight taxa and 10–50 binary state characters as calculated by Hillis and Huelsenbeck (1992); testing (using the method of Sokal and Rohlf, 1981) the significance of the depar-

ture from normality of the distribution of the universe of trees generated by PAUP* resulted in $P \lll 0.001$. Finally, there was no evidence of sexual dimorphism in discrete characters among the taxa examined. Consequently, and notwithstanding the fact that Hillis’ analyses referred explicitly to DNA data, I am confident that the dental variation that I analysed cladistically is suitably informative regarding the phylogenetic history of the southwestern North American *Sylvilagus*.

Four equally parsimonious trees were resolved in an exhaustive search of the tree space for the data set without *Sylvilagus audubonii* (Fig. 6). In each case, *S. holzneri* was the most basal taxon of the *Sylvilagus* examined from the North American Southwest and usually was succeeded by *robustus* and *cognatus*. The 50% majority rule consensus tree (Fig. 7) supported that topology in all cases, as it did the sister taxon arrangement of *S. f. floridanus* with *S. f. chapmani*. However, less support was obtained for the relative topology of *S. nuttallii pinetis* and *S. n. grangerii*, as reflected by results of the bootstrap analysis, which was unresolved for those nodes. Phylogenetic analyses all agree, however, that *S.*

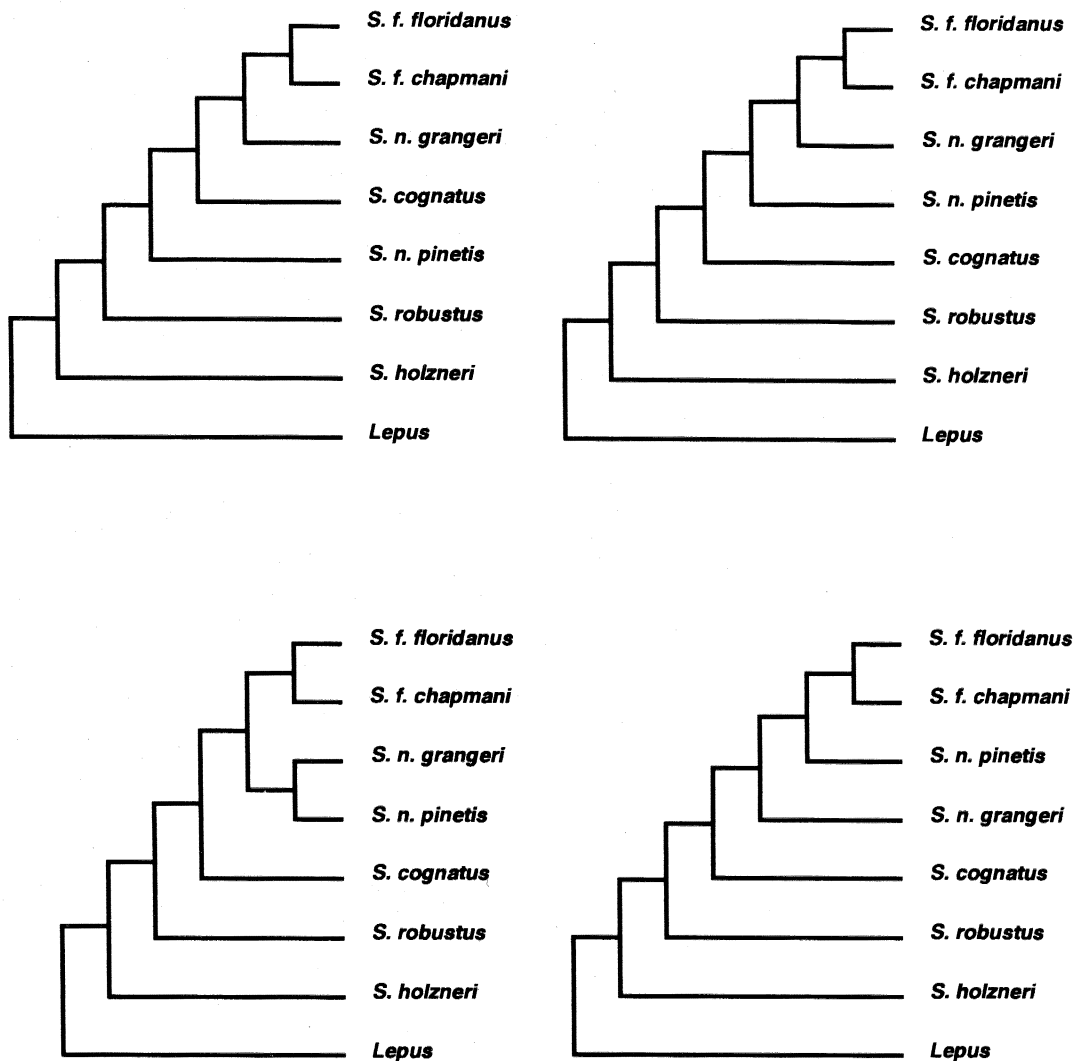


FIG. 6.—The four equally most parsimonious trees (of 10,395 evaluated) for the data from Table 1, as elucidated by the PAUP* program (version 4.0.0d54; D. L. Swofford, in litt.). For each tree illustrated, tree length is 43, consistency index (CI) is 0.6512, homoplasy index (HI) is 0.3488. *Sylvilagus audubonii* was not included as only a small number of individuals were examined for population variation.

nuttallii was paraphyletic, with the two subspecies examined contained in that taxon not being sister taxa. Also, with respect to *cognatus*, and using characters described in the foregoing section, the jackknife analysis failed to resolve a topology among *cognatus*, the two *floridanus* subspecies, and the two *nuttallii* subspecies, although the bootstrap analysis displayed (for *cognatus*) the

same percent support as the 50% majority-rule consensus tree for the successive topology (*holzneri-robustus-cognatus*).

DISCUSSION

Results of phylogenetic analyses are particularly important with respect to the biogeographic history of the North American Southwest in general, and to the biogeo-

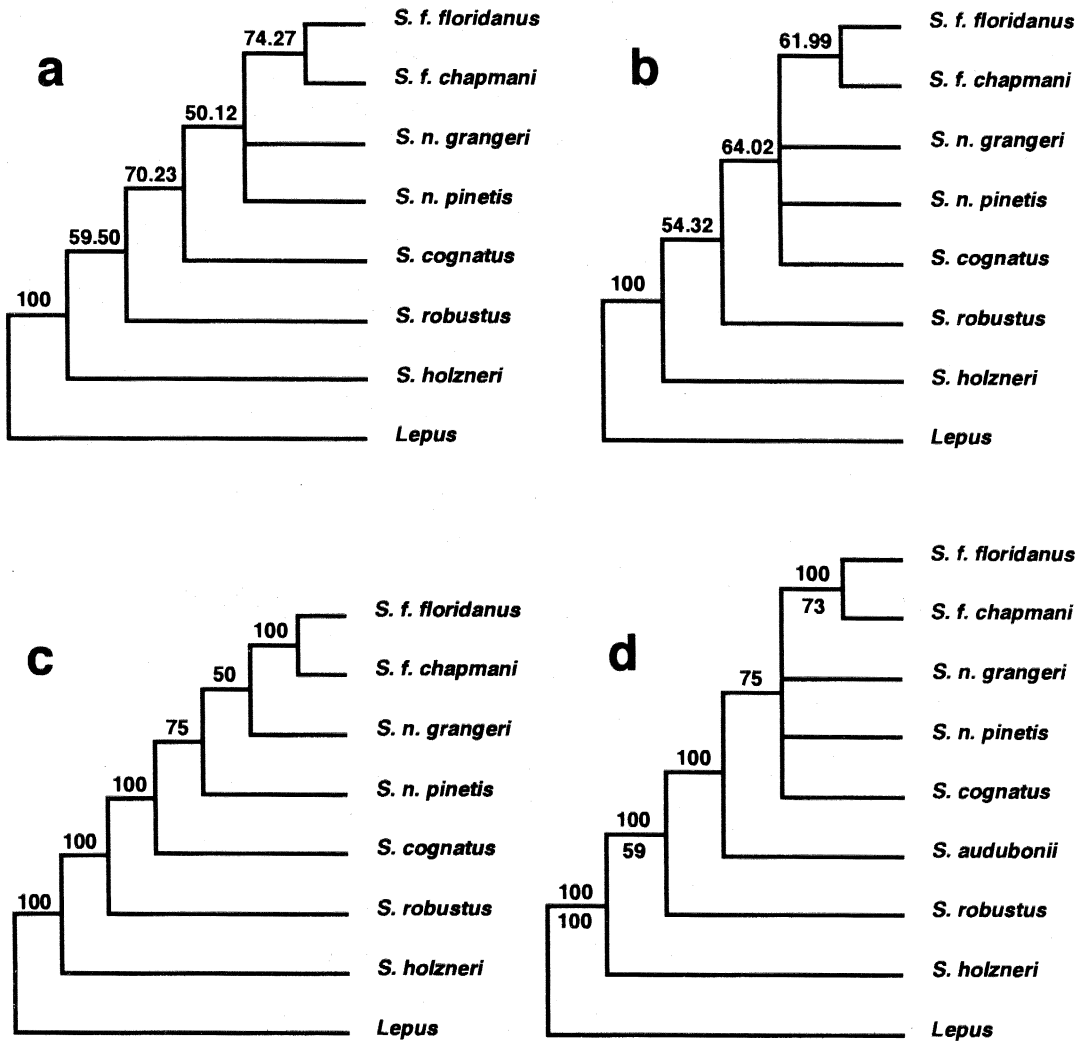


FIG. 7.—a) Results of the bootstrap analysis using the branch and bound method of PAUP* (version 4.0.0d54; D. L. Swofford, in litt.). Tree length is 45 steps; CI, 0.6222; HI, 0.3778. Numbers above each node represent the percent bootstrap support (of 10,000 replicates) for each branch. b) Results of the jackknife analysis. Tree length is 47 steps; CI, 0.5957; HI, 0.4043. Numbers above each node represent the percent jackknife support (of 10,000 replicates) for each branch. c) 50% majority-rule consensus tree of the four equally most parsimonious trees resulting from the analysis of discretely variable dental data of Table 1. d) Results of analyses including *S. audubonii*: numbers above branches show the 50% majority-rule consensus tree resulting from eight equally most parsimonious trees (all trees with the following statistics: length, 49; CI, 0.5714; HI, 0.4286). Numbers below the branches: results of the bootstrap analysis (% support for each branch out of 10,000 replicates) using the branch and bound method of PAUP*. Tree statistics as above. Branches below which no numbers are shown had less than 50% support in this analysis (within the unresolved tetratomy, the sequence *audubonii* to *cognatus* showed 36.10% support; *cognatus* to *grangerii*, 25.74%; and *grangerii* to *pinetis*, 28.53%. The *robustus*-*audubonii* branch exhibited 44.45% support).

graphic history of *Sylvilagus* in particular. Riddle and Honeycutt (1990:1) noted that before historical biogeographic relationships among any set of taxa can be elucidated, a number of important data must be available; in particular, there must be "recognizable patterns of allopatric divergence of phylogenetically operational taxa," and there must exist "phylogenetic hypotheses among endemically differentiated taxa" (Humphries and Parenti, 1986; Platnick and Nelson, 1978; Rosen, 1978). In the case of *Sylvilagus*, the potential for confusion in historical biogeography has been compounded by the fact that a large number of species have been subsumed in what are in effect supraspecific taxa, so that phylogenetically operational taxa have been effectively non-existent. The exact number of these obscured species remains to be elucidated, but the present work points to clear trends in future *Sylvilagus* systematics; *Sylvilagus floridanus* can not be allowed to exist as is currently understood. It is clear from my results that at least three of the subspecies (*cognatus*, *holzneri*, and *robustus*) traditionally ascribed to *S. floridanus* are of species rank. It also is quite likely that upon closer examination, many of the 24 currently recognized subspecies of *S. floridanus* also will need revision.

Clarifying the taxonomy of taxa subsumed in *S. floridanus* will aid in the elucidation the biogeography of the North American Southwest by apporting the use of another, extremely useful taxon. Riddle and Honeycutt (1990) and Riddle (1995) used molecular tools to study the biogeography of the North American Southwest using *Chaetodipus*, *Perognathus*, and *Onychomys*. Because of the ecological requirements of those taxa, their focus was on arid lands (sensu Brown, 1987; areas also defined and illustrated by Riddle, 1995:284–285). However, the *Sylvilagus* taxa examined herein (with the exception of *S. audubonii*) are exclusively montane endemics, restricted in Arizona and New Mexico to piñon-oak-juniper (*Pinus*, primarily *P. ed-*

ulis; *Quercus gambelii*, and *Juniperus*, primarily *J. monosperma*) woodlands (Rocky Mountain [Petran]-Madrean montane coniferous forest and Great Basin conifer woodlands—Brown, 1994a; Pase and Brown, 1994; lower montane coniferous forest—Dick-Peddie, 1993; Frey and Yates, 1996), and oak-juniper grasslands (*Quercus-Juniperus* and *Bouteloua*; coniferous and mixed woodland—Dick-Peddie, 1993). In contrast, in sub-Mogollón Arizona, southern New Mexico, and Trans-Pecos Texas, *Sylvilagus* species considered herein (except for *S. audubonii*) occur in Madrean evergreen woodland (Brown, 1994b), dominated by evergreen oaks (especially *Q. grisea*) and juniper (especially *J. deppeana*).

Changes in these biomes and ecological associations were significant in the last 1×10^5 years, and particularly marked over the last 2×10^4 years. However, these changes also mirrored prior changes of equal magnitude over greater time spans of 3×10^6 years (Webb and Bartlein, 1992). While these climatic changes and associated biotic migrations may not have influenced taxonomic divergence in some of the montane fauna (e.g., *Neotoma*—Sullivan, 1994), it is quite possible that the population structure of leporids did in fact lend itself to speciation. Sullivan (1994; following Brown, 1978, and Patterson, 1982) suggested that the most appropriate species for investigating biogeographic phenomena in the American Southwest would conform to the following suite of properties: widely distributed among sites under consideration, small in size (100–200 g?), occupy a low, herbivorous trophic level, and inhabit intermediate elevations, between 2000 and 2500 m. However, the evolutionary change in *Neotoma mexicana* was of a microevolutionary nature (Sullivan, 1994). Most likely, the slight amount of interspecific variation in this and other *Neotoma* species (both at the molecular and morphological levels) tends to mask potential biogeographically significant information. Thus, it is probable the populational parameters of more informa-

tive taxa, from a biogeographic perspective, will not be that the taxon under scrutiny is small in size, but rather that it is intermediate in size (500–2,000 g), of relatively low vagility, and in relatively low densities.

Leporids embody these attributes; species that are distinct from a morphological perspective often display high genetic identities. For example, *S. audubonii* and *S. floridanus* examined by Scribner and Warren (1986) displayed Nei's genetic identities on the order of 0.911, despite the fact that a high degree of populational and temporal structuring is apparent at least within and between isolated demes of the *S. floridanus* (Scribner and Chesser, 1993; Scribner and Warren, 1990; Scribner et al., 1983; Van den Bussche et al., 1987). Similar genetic identity values (Nei's $I = 0.9063$; $D = 0.0984$) were reported by Grillitsch et al. (1992) between *Lepus europaeus* and *L. timidus*, while Bonhomme et al. (1986) reported a Nei's of $D = 0.135$ between *L. europaeus* and *L. granatensis*. However, *L. castroviejoii* displayed greater genetic distances among its congeners: Bonhomme et al. (1986) reported Nei's D of 0.355 between *L. castroviejoii* and *L. europaeus* and 0.334 between *L. castroviejoii* and *L. granatensis*. *Sylvilagus*, in contrast to *Lepus*, appear to have decoupled genic from morphological evolution, because members of this genus are able to most effectively maintain intraspecific genetic cohesiveness by chromosomal, rather than genic, mechanisms of isolation (Robinson et al., 1983, 1984; Ruedas et al., 1989; Stock, 1976).

Notwithstanding the apparent decoupling of genic and morphological evolution in *Sylvilagus*, phylogenetic relationships hypothesized herein based on dental morphology generally agree with those derived from chromosomal and sequence-derived data. Robinson et al. (1984) proposed two alternative phylogenetic schemes based on chromosomal data. Although there was not much resolution in that data set (particularly in the basal relationships) and the taxa examined did not overlap completely with

those examined here, certain elements are congruent between studies. Based on their data, and those herein, *S. floridanus* sensu stricto represents, with *S. transitionalis* and *S. obscurus*, among the most derived of the *Sylvilagus* species. Robinson et al. (1983) did not specify subspecific taxonomy; their specimen was obtained from Allegany Co., Maryland, within the geographic range of *S. f. mallurus*, which, so far as I have been able to determine, is conspecific with *S. f. floridanus*. However, it is from a locality close to the reported range of *S. f. mearnsii*, which may be distinct from *S. f. floridanus* at the morphological level. In Robinson et al.'s (1983) study, a clade jointly formed by *S. aquaticus* and *S. palustris* obtained as the sister clade to *S. floridanus*. I did not examine these two species, because my focus was on Southwestern *Sylvilagus*. The succeeding sister clade was formed jointly by *S. audubonii* and *S. nuttallii*; this topology is somewhat congruent, in the absence of *S. aquaticus* and *S. palustris*, with the topology resulting from data derived from dental morphology.

A more recent study of phylogenetic relationships among *Sylvilagus* by Halanych and Robinson (1997) used sequence data derived from the mitochondrial 12S-rDNA gene obtained from the same specimens examined by Robinson et al. (1983, 1984). The sequence study resolved *S. obscurus* as the sister taxon to *S. floridanus* sensu stricto, a result congruent with dental morphology because *S. obscurus* and *S. transitionalis* have even more simplified dental morphology than *S. floridanus*. The study also confirmed the sister taxon placement of the *S. aquaticus*-*S. palustris* clade vis-à-vis *floridanus*-*obscurus*.

The principal disparity between chromosomal and sequence data and morphological data from my study concerns the relative relationships of *S. audubonii* and *S. nuttallii*. Dental morphology suggests that the *S. nuttalli* subspecies may be successive sister taxa to *S. floridanus* (but are not conclusive in that respect, as the position of *S.*

cognatus remains tentative). Remaining data resolve similarly in the absence of *S. audubonii*, but *S. audubonii* is resolved as the successive sister taxon to a *floridanus-nuttalli* clade, rather than sister to *S. nuttalli*, as chromosomal and molecular data show (Halanych and Robinson, 1997; Robinson et al., 1984). Upon additional and broader taxonomic sampling (that is, inclusion of individuals in all the nominate subspecies of *S. nuttalli*), both chromosomal and molecular data may result in topologies disparate from those currently resolved based on these data.

Ecological parameters contribute heavily to the utility of these taxa in biogeographic studies; montane *Sylvilagus* display a very rigid, demic population structure (Fa et al., 1992; Sullivan et al., 1989; Tefft and Chapman, 1987; Verts and Gehman, 1991). Besides having a population structure that predisposes them to fragmentation, population densities of populations of montane *Sylvilagus* are habitually low, perhaps in part because many of these populations are in areas where densities are maintained by such factors as low annual precipitation and consequent low productivity and food availability.

Thus, the biogeographic picture illustrated here presents itself as follows. The montane endemics considered herein for the southwestern United States appear to be Madrean in origin, based on results of the cladistic analysis, which identify the plesiomorphic *Sylvilagus* species as members of a southwestern biota and derived species as being those in the northeastern United States (*S. floridanus* sensu stricto and *S. transitionalis* and *obscurus*). However, *S. holzneri* and *S. robustus* are restricted to Madrean evergreen woodland, whereas *S. cognatus* and *S. nuttalli* are restricted to Madrean montane conifer forests (with the caveat that *S. nuttalli* is polytypic, likely consisting of at least two, and possibly three, evolutionarily and phylogenetically distinct species; the foregoing comments refer to *S. n. pinetis* only). *Sylvilagus audu-*

bonii appear morphologically homogeneous throughout their range, and most likely do constitute a singular evolutionary unit. The latter species tolerates a number of biotic communities and is found throughout Southwestern desert biomes.

A problem with application of my morphometric analyses is that unless large discrete differences occur, it is difficult to unequivocally establish categorical rank of specimens under question, or of the taxon that those specimens are said to represent. In my analysis, the appearance of a cline among some species (Fig. 2) is misleading. Although coastal *S. f. chapmani* are the smallest of taxa examined (and there is a size gradation in *chapmani*), remaining taxa follow no discernable intraspecific or intra-subspecific pattern of morphological dispersion.

Clearly, reproductive experiments could solve the species question; however, rarity of *robustus*, together with difficulties of obtaining live specimens, currently preclude this avenue of research. Because of the high degree of chromosomal variability among *Sylvilagus* species (in stark contrast to the confamilial *Lepus*), chromosomal data have been used successfully to elucidate species in the genus (Robinson et al. 1983, 1984; Ruedas and Elder, 1994; Ruedas et al., 1989; Stock 1976). Neither of these kinds of data currently are available for *robustus*.

Conservation implications.—The known range of *S. robustus* includes the Guadalupe Mountains of Texas and New Mexico, the Chisos and Davis mountains of Texas, and the Sierra de la Madera of Coahuila, México. The Guadalupe Mountains population was reduced severely as long as 45 years ago (Davis, 1940), when only ca. 50 individuals were thought to remain. Since then, they have become even more uncommon (Genoways et al., 1979). Indeed, no specimens are known from either the Chisos or the Guadalupe mountains within the last 30 years, although two possibly were seen in the Guadalupe mountains 20 years ago (Genoways et al., 1979), and only a single

specimen from the Davis Mountains in the past 20 years (MSB 82184), collected dead on the roadside by Linda Hedges, Texas Parks and Wildlife, on 5 March 1997. I was not successful in collecting specimens in the Davis Mountains in 8 years of active attempts, and saw only three individuals, in years of higher than average precipitation. The status of the Coahuila population from Sierra de la Madera is unknown. However, there are reports that there also exists a population in the Sierra del Carmen, Coahuila, and that this latter population is in good condition (G. Ceballos, in litt.). This area of Coahuila recently has been afforded protection as a wildlife refuge, which may afford some degree of protection in México for *S. robustus* in the area; further research needs to be carried out to ascertain whether the Sierra del Carmen population of *Sylvilagus* indeed is referable to *S. robustus*.

Thus, it appears from past and present research that the species occurred in historical times at low densities and population numbers, a circumstance which may have contributed to their probable extirpation from the Guadalupe Mountains, and almost certain extirpation from the Chisos Mountains. Since the Pleistocene, the species appears to have gone extinct in the Apache Mountains of Culberson Co., Texas, 65 km NNW of the Davis Mountains (Dalquest and Stangl, 1984, 1986). They remain in the Davis Mountains but clearly are imperiled by a number of natural and anthropogenic factors. Because they are not easily seen in dry years, it may be surmised that *S. robustus* are sensitive to precipitation patterns and drought—a pattern also seen in other montane *Sylvilagus*, such as *S. cognatus*. Grazing practices and brush clearing in the current known range of *S. robustus* may have further negative impact on populations of the species (Schmidly, 1977); increasing development, including urbanization, in the Davis Mountains certainly is having a negative effect by reducing available habitat.

The species currently is not listed as threatened or endangered by the Depart-

ment of the Interior's U. S. Fish and Wildlife Service (USFWS; 50 CFR 17.11, 31 October 1996), but was listed in the Federal Register (59(219):58982 et seq., 15 November 1994) with other candidate taxa for inclusion in a forthcoming list of endangered and threatened taxa, under Category 2: "Taxa for which information now in the possession of the Service indicates that proposing to list as endangered or threatened is possibly appropriate, but for which persuasive data on biological vulnerability and threat are not currently available . . ." (FR 59(219):58983). Category 2 since has been eliminated by USFWS (FR 61(40):7597, 28 February 1996): "The service remains concerned about these species, but further biological research and field study are needed to resolve the conservation status of these taxa." As far as state status is concerned, Texas Parks and Wildlife does not list the species as being of particular concern, although the Natural Heritage Program in Texas recognizes that *S. robustus* is rare or uncommon. Listing a species as federally endangered may result in detrimental repercussions to existing populations of *S. robustus* from local landowners, particularly in the part of Texas inhabited by the species; I therefore prefer at this time to consider state listing for the species, and red-book listing it as endangered by the International Union for the Conservation of Nature (IUCN). These recommendations are made pending the completion of more detailed studies that need to be undertaken of the biology of *S. robustus*, including assessments of population status and life history parameters, long-term ecological studies, and population genetic analyses.

Making conservation recommendations almost of necessity involves making subjective, rather than objective, assessments as to vulnerability. To obviate that subjectivity, the IUCN prepared a list of criteria that might be applied in conservation considerations (IUCN, 1994). By IUCN criteria, *S. robustus* is an endangered species, as the species has experienced: 1) a reduction

in population numbers due to a decline in area of occupancy, extent of occurrence and/or quality of habitat (criterion A1c); 2) the extent of occurrence of the species is estimated to be <5000 km² or their area of occupancy is estimated to be <500 km², and is severely fragmented and the number of mature individuals is subject to severe fluctuations, due to both natural and anthropogenic causes (criteria B1, B3d); and 3) the population is estimated to number well below 2500 individuals all of which are in a single subpopulation (criterion C2b).

Geologically, as far as the geographic range of *robustus*, the Davis Mountains occupy ca. 11,400 km² (Kier et al., 1977). The Madrean evergreen woodland and Petran montane conifer forest of the Davis and adjoining Cathedral and Puertacitas Mountains only cover ca. 2,530 km² of that geological formation (Brown, 1994c). However, because the Cathedral and Puertacitas Mountains are not biotically continuous with the Davis Mountains, the total contiguous Madrean evergreen woodland area in the Davis Mountains is actually closer to ca. 1,815 km². Finally, *robustus* are not known from <1,500 m in elevation, and have been reported to be more common >1,800 m (Bailey, 1905; Blair, 1940; Davis and Robertson, 1944). In the Davis Mountains, the approximate area above 1,675 m is 1,220 km² (Defense Mapping Agency, 1989). The intersection of the 1675 m contour with the Madrean evergreen woodland biotic zone yields a total potential habitable area of only ca. 730 km², which is a highly restricted contiguous range for a species such as *S. robustus* that persists in low population numbers.

Taxonomic recommendations.—A hypothesis may be advanced based on similarities and differences found in my analyses. The *robustus* specimens differed significantly from all other taxa in six of 26 characters (0.2307, rather than only 1 or 2 characters, or 0.05 proportion), as determined by the analysis of variance. Specimens of *robustus* were more distinct from

remaining subspecies of *S. floridanus* than the latter were from *S. n. pinetis*. Principal component analysis can be interpreted as indicating distinct differences in ontogenetic patterns between *robustus* and remaining taxa. Insofar as an examination of discretely variable dental characters, *robustus* invariably differed from *floridanus*; the nature and magnitude of those differences equaled or surpassed those between *floridanus* and recognised species of *Sylvilagus* such as *nuttalli* and *audubonii*. A more definitive solution to the question may have to await results of further analyses including studies of chromosomes and nuclear and mitochondrial DNA. Nevertheless, based on my results, and following Nelson (1909), *robustus* is a distinct species in the genus *Sylvilagus*, as follows:

Sylvilagus robustus (V. Bailey, 1905)

Synonyms:

- Lepus pinetis robustus* V. Bailey, 1905, North American Fauna 25:159; 24 October 1905.
Sylvilagus robustus Nelson, 1909, North American Fauna 29:42, 194; 31 August 1909.
Sylvilagus floridanus robustus Hall and Kelson, 1951, University of Kansas Publications, Museum of Natural History, 5(5):56; 1 October 1951.
Sylvilagus floridanus nelsoni Baker, 1955, University of Kansas Publications, Museum of Natural History, 7(13):611; 8 April 1955.

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APPENDIX I

Characters examined in the cladistic analysis

- i. P2, anteroexternal reentrant (EAR): deep (0), shallow (1), or absent (2).
- ii. P2, condition of enamel constituting the margin of the EAR: thin enamel (0) or thick enamel (1).
- iii. P2, main anterior reentrant (MAR): labial aspect enamel: thick enamel (0) or thin enamel (1).
- iv. P2, MAR labial aspect gross morphology: enamel smooth (0) or crenelated (1).
- v. P2, MAR lingual aspect enamel: enamel thin (0) or thick (1).
- vi. P2, MAR lingual aspect gross morphology: enamel crenelated (0) or smooth (1).
- vii. P2, anterointernal reentrant (IAR): deep (0), shallow (1), or absent (2).
- viii. P2, condition of enamel in IAR: thin enamel present in some portion of IAR (0) or thick enamel continuous throughout IAR (1).
- ix. p3, anterior reentrant (AR): multiple reentrants (0), one reentrant (1), or absent (2).
- x. p3, AR enamel: thick enamel absent (0), or present (1).
- xi. p3, anterointernal reentrant (AIR): absent (0), or present (1).
- xii. p3, anteroexternal reentrant (AER): one (0), or multiple reentrants (1).
- xiii. p3, AER enamel; margin thin (0) or thick (1).
- xiv. p3, posteroexternal reentrant (PER), condition of enamel: cranial wall of PER constituted by continuous layer of thick enamel (0), or thick enamel layer discontinuous (1).
- xv. p3, central angle (CA) of PER: reflected craniad relative to main axis of PER (0), vs. not highly reflected (1).

- xvi. p3, CA of PER: CA angled such that a lacuna is formed in the medial portion of the PER (0), vs. no lacuna formed by CA in PER (1).
- xvii. p3, condition of enamel in cranial wall of PER: enamel smooth (0) versus crenelated (1).
- xviii. p3, condition of enamel in caudal wall of PER; enamel crenelated (0) versus smooth (1).
- xix. P3, cranial wall of internal reentrant (IR), type and distribution of enamel: thick enamel throughout (0), thick enamel patchily distributed (1), thin enamel throughout (2).
- xx. P3, cranial wall of internal reentrant (IR), conformation of enamel: enamel surface crenelated or otherwise rugose (0), versus enamel surface smooth (1).
- xxi. P3, caudal wall of internal reentrant (IR), type of enamel: thick (0) versus thin enamel throughout (1).
- xxii. P3, caudal wall of internal reentrant (IR), conformation of enamel: enamel surface crenelated or otherwise rugose (0), versus enamel surface smooth (1).
- xxiii. P3, terminal lacuna of IR: absent (no expansion in labial terminus of IR; 0); lacuna present, with a smooth enamel surface, not greatly expanded (1); lacuna present, well developed, with rugose or otherwise crenelated surface to the enamel wall of the lacuna (2).

APPENDIX II

Specimens examined

Unless otherwise indicated, all specimen numbers are from United States National Museum (USNM); other abbreviations (after Hafner et al., 1997) include: AMNH: American Museum of Natural History; ASNHC: Angelo State University Natural History Collections; UF: University of Florida, Florida Museum of Natural History; LSUMZ: Louisiana State University Museum of Natural Science; MSB: Museum of Southwestern Biology, University of New Mexico; MVZ: University of California, Berkeley, Museum of Vertebrate Zoology; TTU: The Museum, Texas Tech University. Subspecific nomenclature in this section follows currently accepted taxonomy; abbreviations are: f, female; m, male; u, sex unknown; j, juvenile or subadult

(specimens in these age categories were examined but excluded from the analyses).

Sylvilagus audubonii audubonii (8).—CALIFORNIA: San Francisco Co.; San Francisco. Topotype: MVZ 7140, m. CALIFORNIA: Contra Costa Co.; 2 mi S. Walnut Cr.; 200 ft. MVZ 18440, m, 18441, uj, 18443, f. CALIFORNIA: Contra Costa Co.; 1.5 mi E. Albany. MVZ 46917, f. CALIFORNIA: Alameda Co.; 1 mi E. Tesla, Corral Hollow, 250 ft. MVZ 88007, m. CALIFORNIA: Alameda Co.; 2 mi E. Tesla, Corral Hollow. MVZ 102705, m; 102706, f.

Sylvilagus floridanus chapmani (22).—TEXAS: Nueces Co.; Corpus Christi. Topotypes: 43282–43283, 43285, 120196, 120198–120200, f; 43284, 43535, 120195, 120197, m. TEXAS: Mason Co.; Mason. 189172, 189175, f; 189173, 189176, m. TEXAS: 15 mi SW Junction. 313807, m. TEXAS: Victoria Co., no specific locality. 159247, f. TEXAS: Cameron Co.; Laguna Atascosa National Wildlife Refuge. 552594, f; 552595–552598, m.

Sylvilagus floridanus cognatus (7).—NEW MEXICO: Valencia Co.; Tajiique, near summit of Manzano Mountains, 10,000 ft. (restricted to the vicinity of Rea Ranch on the northeast side of Bosque Peak; 34°45'05.39"N, 106°25'18.04"W, 2,880 m by Frey et al., 1997). Holotype: 136569, u. NEW MEXICO: Santa Rosa. 127446, f. NEW MEXICO: Northeast slope Capitán Mountains. 128651, f. NEW MEXICO: Tajiique. 135755, u. NEW MEXICO: Manzano Mountains. 130958, f; 136567–136568, u.

Sylvilagus floridanus floridanus (5).—FLORIDA: Brevard Co.; San Sebastián River (near Micco), March 18, 1889 (nec "1899," of Lawrence, 1993). Holotype: AMNH 1890/1155, f. Brevard Co.; Cañaveral. UF 23788, u. Brevard Co.; 12 mi S Indiatlantic. UF 3216, u. Highlands Co.; Avon Park Game Management Area, 25 mi E. Ft. Kissimee. UF 7630, u; UF 7634, f.

Sylvilagus floridanus holzneri (12).—ARIZONA: Huachuca Mountains, Douglas Spruce Zone. Holotype: 58937, m. NEW MEXICO: Ánimas Mountains. 157123, f. NEW MEXICO: Burro Mountains. 157806–157807, m, 157808, jf. MÉXICO: Chihuahua; San Luis Mountains.

157126, f. MÉXICO: Chihuahua; Sierra Madre. 95560, m. MÉXICO: Chihuahua; Colonia García. 98257–98258, f; 98259, m. MÉXICO: Chihuahua; Majarachic. 265939–265940, ju.

Sylvilagus floridanus mallurus (2).—FLORIDA: Alachua Co.; Gainesville. UF 3214, f; 3218, m.

Sylvilagus floridanus robustus (14).—TEXAS: Jeff Davis County; Fort Davis, Davis Mountains, 6000 ft. Holotype: 18262/25165, f. TEXAS: Jeff Davis Co., Davis Mountains. Topotype: 109095, m. TEXAS: Jeff Davis County; Fort Davis, Davis Mountains, Finley's Ranch, 6000 ft. 25164, f. TEXAS: 35 mi South Marfa, Lloyd's. 25116, m. TEXAS: Chisos Mountains. 108695, f. TEXAS: Jeff Davis Co.; Davis Mts., Sawtooth Area, ASNHC 1135, f, 1138, m. TEXAS: Jeff Davis Co.; 1 mi W Rockpile Park, Loop 166. ASNHC 868, f. TEXAS: Jeff Davis Co.; 1 mi S Rockpile Park, Loop 166, elev. 1890 m. ASNHC 544, m, 545, f. TEXAS: Jeff Davis Co.; 2 mi SW Rockpile Park, Loop 166, elev. 1860–1890 m. ASNHC 549, 552, 553, m. TEXAS: Jeff Davis Co.; 2 mi NW Fort Davis. TTU 3876, m. TEXAS: Jeff Davis Co.; Hwy. 118 N, 6 mi. NW Ft. Davis, 30°36.486'N, 103°57.925'W, 1575m. MSB 82184, f. TEXAS: Culberson Co.; Guadalupe Mts. National Park, "The Bowl." LSUMZ 658, f. MÉXICO: Coahuila; 20 mi. S, 4 mi W Ocampo, 5300 ft. KU 57768–57769, f.

Sylvilagus nuttallii grangerii (1).—SOUTH DAKOTA: Custer C.; Hill City. Holotype: AMNH 9094/7402, f.

Sylvilagus nuttallii pinetis (13).—NEW MEXICO: Jemez Mountains. 147986, jm. NEW MEXICO: Tierra Amarilla. 133690, f, 134358, jf. NEW MEXICO: San Antonio Mountain. 133691, m. NEW MEXICO: Gallinas Mountains. 134900, f; 135157, u. NEW MEXICO: Copperton. 137755, f; 137756, m. NEW MEXICO: Chusca Mountains. 157820, 158546, f; 157819, m; 158601, jf. NEW MEXICO: Colfax Co.; Philmont Scout Ranch. 554392, jf. ARIZONA: Apache Co.; White Mountains, South of Mt. Ord. AMNH 9041/7336, m.

Lepus californicus (1).—NEW MEXICO: Torrance Co.; 22 mi S, 2 mi E (by road) junction of US Rte. 66 and NM Rte. 10. MSB 25851, m.