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Systematics of the mountain-inhabiting cottontails (*Sylvilagus*) from southwestern United States and northern Mexico (Mammalia: Lagomorpha: Leporidae)

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Abstract.—The skull morphology of four species of cottontails from the mountains and plateaus of southwestern United States and northern Mexico, currently recognized as *Sylvilagus nuttallii*, *S. cognatus*, *S. robustus*, and *S. holzneri* (=*S. floridanus holzneri*), was analyzed using multivariate statistics. Based on 26 or 30 measurements taken on each of 350 adult skulls, and formulation of 16 pooled samples, with each representing a different geographic population, the results show there are two species-level distinctions in skull type. Cottontails from southern Utah, northern and east-central Arizona, and northern New Mexico show morphological overlap among geographically adjacent samples and all have a highly arched skull. These are referable to *S. nuttallii*. Cottontails from central Arizona, central New Mexico, and western Texas southward along the Sierra Madre Occidental to Durango, Mexico, and Sierra Madre Oriental to central Coahuila, Mexico show morphological overlap among geographically adjacent samples and all have a relatively flat skull. These are referable to *S. holzneri*. Both *S. nuttallii* and *S. holzneri* are polytypic in the study area. *Sylvilagus n. pinetis* is restricted to the White Mountains of Arizona. Those north and west of the Colorado River in Arizona and Utah are referable to *S. n. nuttallii* and those from southeastern Utah, northeastern Arizona and northern New Mexico are referable to *S. n. grangeri*. The population of cottontails previously referred to *S. cognatus* from central New Mexico is indistinguishable from topotypical *S. holzneri* from southeastern Arizona as well as populations from southwestern New Mexico, Chihuahua, and Sonora, Mexico. Cottontails previously referred to *S. robustus*, from the Guadalupe Mountains of New Mexico and Texas, southward in the mountains of western Texas, and the Sierra Madre Oriental to central Coahuila, Mexico, average larger in overall size and, on average, have proportionately larger auditory bullae and are referable to *S. holzneri robustus*. The relationship of *S. holzneri* to other mountain/plateau-inhabiting taxa, outside the study area in central and southern Mexico remains to be resolved.

Keywords: cottontails, morphology, southwestern United States, *Sylvilagus*, systematics

When Nelson (1909) published his treatise on "The rabbits of North America" he recognized five species of cottontails in the

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southwestern United States, here defined as southern Utah, Arizona, New Mexico, and trans-Pecos Texas. These five species are *S. audubonii*, *S. nuttallii*, *S. floridanus*, *S. cognatus*, and *S. robustus*. Nelson (1909:200) also noted that intergradation may occur between *S. f. holzneri* and *S. n. pinetis* in Arizona. The five-species concept remained until Hall and Kelson (1951) considered both *S. cognatus* from New Mexico and *S. robustus* from trans-Pecos Texas, subspecies of *S. floridanus*. Hall and Kelson (1951:54) also pointed out that specimens referred by Nelson (1909:211) to *S. nuttallii* from northwestern Arizona (south of the Colorado River) were, in their opinion, referable to *S. floridanus*. Later, Findley et al. (1975:83), referring to the cottontails of New Mexico, wrote "Some or all of these populations may be a biological species distinct from the rest...". And, Hoffmeister (1986:127) in the "Mammals of Arizona" wrote "...the species are very much alike. A series of features is presented that will aid in distinguishing the species in Arizona." The three-species concept stood until Ruedas (1998:1369), using skull and dental morphology, informally proposed that *S. cognatus*, *S. robustus*, and S. *holzneri* are each distinct species, stating that "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." However, following this statement Ruedas (1998:1373) only formally proposed that *S. robustus* be recognized as a distinct species. In agreement with Ruedas (1998), Lee et al. (2010), using morphological and nuclear DNA data, concluded that the mountain-inhabiting *S. robustus* is a separate species from the geographically adjacent grassland and savanna-inhabiting *S. floridanus*. Frey (2004), citing Ruedas (1998), added *S. cognatus* and *S. holzneri* to a checklist of the mammals of New Mexico. Later, Hoffmann and Smith (2005) and Bradley et al. (2014), in the lists of recognized mammal species of the world and North America, respectively, both cited Ruedas (1998) for species recognition of *S. robustus*. And, for recognition of *S. cognatus* as a distinct species, Hoffmann and Smith (2005) cited Ruedas (1998) whereas Bradley et al. (2014) cited both Frey et al. (1997) and Ruedas (1998). Both authors did not follow Frey (2004) in recognition of *S. holzneri*. Given the above current taxonomy, the geographic distribution of *S. floridanus* is now bifurcated with the mountain-inhabiting *S. f. holzneri* occurring west of *S. cognatus* and *S. robustus* and *S. f. chapmani* and *S. f. alacer* (=*S. f. llanensis* of some authors), and other lowland forms of *S. floridanus*, occurring east of *S. cognatus* and *S. robustus*. Because of this recent confusion and conflicting statements on the taxonomic status of *Sylvilagus* in the southwestern United States and northern Mexico and because none of these studies conducted a comprehensive morphological analysis of all mountain populations in question, the purpose here is to provide that morphological analysis and compare the results with conclusions reached through other studies.

Materials and Methods

All cottontails were aged using the method described by Hoffmeister and Zimmerman (1967). Specimens considered as adults, and from which measurements were taken, were those individuals having both exoccipitals completely fused to the supraoccipital. In all cases the exoccipital-supraoccipital sutures were completely obliterated. A sample of 26 females and 24 males of *S. nuttallii* from central Oregon were measured (using the 26 skull measurements described below) to assess secondary sexual variation. Females averaged significantly larger in only 4 of 26 features; three (braincase breadth, breadth across nasals, and incisive foramen length) differed at the 0.05 level and one (nasal

length) at the 0.01 level. As examples, for greatest skull length, females averaged 64.79 mm and males 64.12 mm, bulla length 11.19 mm and 11.20 mm, and zygomatic breadth 32.67 mm and 32.59 mm, respectively. Since the differences between sexes are minor, sexes were combined in all analyses.

For the analysis of geographic variation, 26 skull measurements were initially taken to the nearest 0.05 mm using a dial and digital calipers. These measurements were taken as illustrated by Diersing (1981) and described by Diersing and Wilson (1980). After observing that some skulls differed in morphology that was not well reflected in the current data set of 26 measurements, an additional four measurements were taken on most cottontail skulls from southwestern United States where *S. nuttallii*, *S. holzneri*, and *S. cognatus* have complementary distributions. These four measurements are described as follows: 1) interparietal length is the greatest anteroposterior length of the interparietal; 2) interparietal breadth is the greatest breadth across the interparietal; 3) frontal curvature, distance "A" of Fig. 1, is measured using a glass slide positioned on top of the skull such that the slide rests both upon the nasals and the supraorbital processes. The measurement taken is the distance from the glass slide, and perpendicular to it, at the midline of the skull where the frontals meet the parietals; and 4) parietal curvature, distance "B" of Fig. 1, is measured using a glass slide positioned the same as in curvature of the frontal, except the slide is extended more posteriorly from its contact with the supraorbitals and nasals. The measurement is taken from the glass slide, and perpendicular to it, to the posterior point of the interparietal at the midline of the skull. The *a priori* grouping of skulls into 16 pooled samples is based on the current taxonomy of cottontails recognized by Hoffmann and Smith (2005) except the name *S. holzneri*, as informally proposed by Ruedas (1998), is used instead of *S. f. holzneri* to avoid confusion with the lowland forms of *S. floridanus*. In some cases, before assigning an individual to a specific pooled sample, exploratory comparisons were made of geographically adjacent specimens using univariate, bivariate, Principal Components Analysis (PCA), and Discriminant Function Analysis (DFA). As listed in Table 1, five of the 16 pooled samples are currently recognized as *S. nuttallii* (pooled samples 1–5), seven as *S. holzneri* (6–9 and 14–16), one as *S. cognatus* (10), and three as *S. robustus* (11–13). *Sylvilagus audubonii* was not included in the study and can be distinguished from all other species in having the dorsal tail hairs gray rather than rufous and by having larger auditory bullae. The statistical package, PAST, developed by Hammer et al. (2001), was used for all analyses. Geographic variation is assessed using Discriminant Function Analyses (DFA). Jackknife sampling and 95% confidence intervals were included with DFA to help understand the distinctiveness of pooled samples being compared (Lance et al. 2000). See Diersing and Wilson (2017) for application of DFA and jackknife sampling. The first DFA used 30 characters (includes interparietal breadth and length, frontal curvature and parietal curvature). These 30 measurements were available on 76 of 105 cottontails currently referred to *S. nuttallii* (combined into a single sample from samples 1–5) from Utah, Arizona, and New Mexico; 44 of 115 cottontails currently referred to *S. holzneri* from Arizona and New Mexico (representing two taxa; 24 from sample 6 currently referred to *S. h. hesperius* and 20 from samples 7–9 referred to *S. h. holzneri*); and 20 of 23 cottontails currently referred to *S. cognatus* (sample 10) from New Mexico. In all other DFAs, the integrity of the 16 pooled samples was maintained and DFA was used on 26 skull characters (did not include interparietal breadth and length, frontal curvature, and parietal curvature),

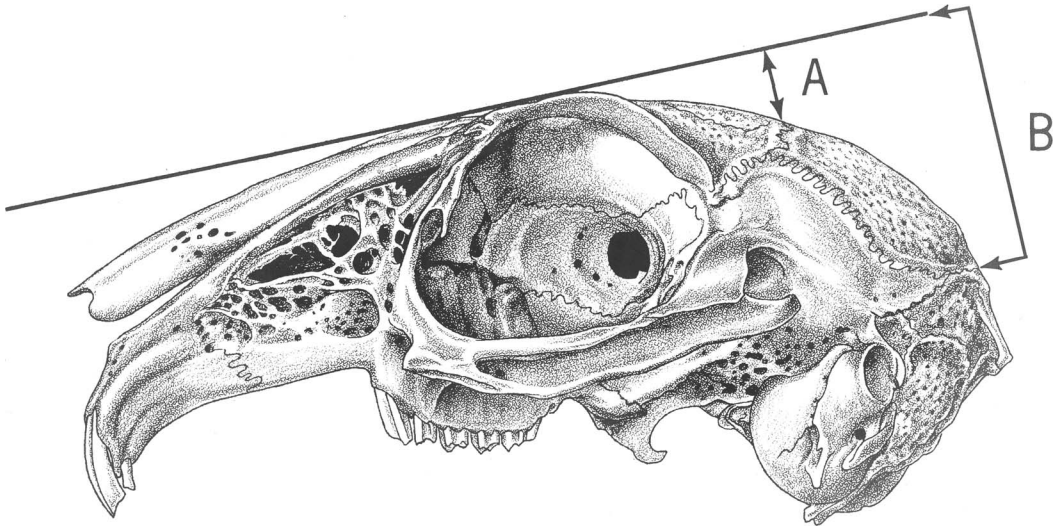

Fig. 1. Skull of *S. floridanus*, MSB 163198, from 3 mi W, 5 mi N Groom, Carson Co., Texas, illustrating 2 measurements: frontal curvature (A); and parietal curvature (B). The line over the skull represents a glass slide. Details for taking these measurements are provided under Materials and Methods.

each consisting of a few pooled samples within a small geographic region to ensure that detailed morphological differences among samples are fully elucidated. The list of specimens examined with new taxonomic assignments by pooled sample number is provided in Appendix I. Character loadings for each of the DFA's are provided in Appendix II. A table of measurements for each skull character, by pooled sample, is shown in Appendix III. Pooled samples were formed based on geographic proximity consistent with similarity of geographic features (mountain ranges, plateaus) and avoidance of potential barriers to dispersal (major rivers, deserts). Where this rule could not be followed, information from preliminary analyses, leading up to the final analysis, is provided in the Discussion section.

Museums where specimens were examined are: American Museum of Natural History (AMNH), New York; Philadelphia Academy of Natural Sciences (ANSP), Philadelphia; Angelo State Natural History Collection (ASNHC), San Angelo; Arizona State University, Mammal Collection (ASU), Tempe; Monte L. Bean Life Science Museum (BYU), Provo; California Academy of Sciences (CAS), San Francisco; California State University (CSULB), Long Beach; Dallas Museum of Natural History (DMNH), Dallas; Field Museum of Natural History (FMNH), Chicago; James Diersing Collection (JDC); University of Kansas Natural History Museum (KU), Lawrence; Louisiana State University, Museum of Natural Science (LSUMZ), Baton Rouge; Museum of Northern Arizona (MNA), Flagstaff; Museum of Southwestern Biology (MSB), Albuquerque; The Museum, (MSU), East Lansing; Museum of Vertebrate Zoology (MVZ), Berkeley; Midwestern State University (MWSU), Wichita Falls; Colorado Plateau Biodiversity Center, Northern Arizona University (NAU), Flagstaff; Texas Cooperative Wildlife Collection (TCWC), College Station; Texas Memorial Museum (TMM), Austin; Museum of Texas Tech University (TTU), Lubbock; Tulane University, Museum of Natural History Mammal Collection (TU), Belle Chasse; Museum of Natural History (UA),

Table 1.—A total of 350 cottontail skulls were examined. Each was assigned to 1 of 16 pooled samples. Species assignment was based on current taxonomy except *S. holzneri* is used instead of *S. floridanus holzneri*. The first Discriminant Function Analysis (DFA) was conducted using 30 skull characters and 3 combined samples. All other DFAs used 26 skull characters and the 16 pooled samples.

Pooled sample number	Sample size		Current taxonomy	Geographic location
	26 characters	30 characters		
1	21	$n = 76$ (samples	*S. nuttallii grangeri*	NW of the Colorado River, SW Utah and NW Arizona
2	19	1–5	*S. nuttallii pinetis* (type *pinetis*)	White Mountains, east-central Arizona
3	15	combined)	*S. nuttallii pinetis*	SE Utah, NE Arizona, NW New Mexico
4	22		*S. nuttallii pinetis*	north-central New Mexico west of the Rio Grande
5	28		*S. nuttallii pinetis*	NE New Mexico east of the Rio Grande
6	28	$n = 44$	*S. holzneri* (syn *hesperius*)	NW Arizona south of the Colorado River
7	24	(samples 6–9 combined)	*S. holzneri*	east-central Arizona from north-central Gila County and southern Navajo County south to Graham and Santa Catalina mountains
8	35		*S. holzneri* (type *holzneri*)	Huachuca and Santa Rita mountains of southeastern Arizona, northern Sonora, Mexico
9	28		*S. holzneri* (syn *rigidus*)	Chiricahua Mtns, Arizona, Hidalgo county, New Mexico, northern Chihuahua, Mexico
10	23	$n = 20$	*S. cognatus* (type *cognatus*)	New Mexico, Mt Taylor east to Santa Rosa, south to Sacramento Mtns, west to Grant County, New Mexico
11	25		*S. robustus* (type *robustus*)	Guadalupe and Davis mountains of New Mexico and Texas
12	12		*S. robustus*	Chisos Mountains, Texas
13	7		*S. robustus* (syn *nelsoni*)	northern and central Coahuila, Mexico
14	23		*S. holzneri*	eastern Sonora, Sinaloa, Chihuahua, Mexico
15	18		*S. holzneri* (syn *durangae*)	southern Chihuahua, northern Durango, Sinaloa Mexico
16	22		*S. holzneri*	southern Durango, Sinaloa, Mexico

Tucson; University of Michigan Museum of Zoology (UMMZ), Ann Arbor; National Museum of Natural History (USNM), Washington, D.C.; Natural History Museum of Utah (UMNH), Salt Lake City; Burke Museum of Natural History and Culture (UWBM), Seattle.

Results

Comparison of S. nuttallii, S. holzneri, *and* S. cognatus *along a zone of parapatry*.—A DFA was used to compare 140 skulls of three geographically adjacent species (Fig 2): 76 skulls currently referred to *S. nuttallii* from southern Utah, Arizona and New Mexico; 44 skulls referred to *S. holzneri* from Arizona and New Mexico (24 from sample 6 and 20 from samples 7–9); and 20 skulls referred to *S. cognatus* from New Mexico. All 30 cranial characters were used in the analysis. The first variate explained 86.88% of the total variation and widely separated all individuals of *S. nuttallii* from those identified as *S. holzneri* and *S. cognatus*. These two groups (*S. nuttallii* versus *S. holzneri*/*S. cognatus*) were separated beyond the 95% confidence limit and this separation was

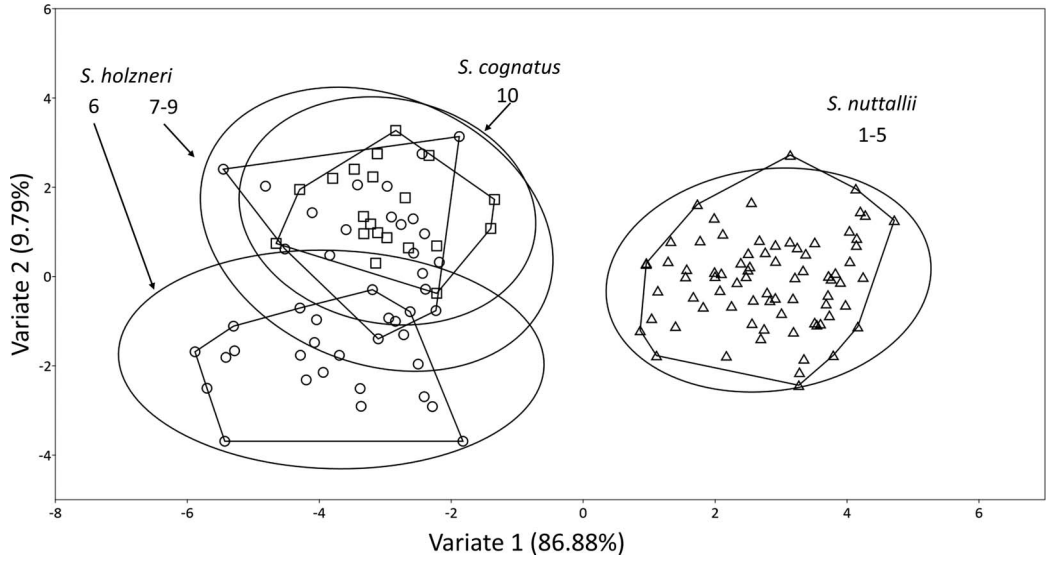

Fig. 2. A DFA comparing the skull morphology of three species of cottontails currently referred to *S. nuttallii* ($n = 76$), *S. holzneri* ($n = 44$), and *S. cognatus* ($n = 20$) from southern Utah, Arizona, and New Mexico. The *S. holzneri* group is subdivided into 2 taxa; 1) the small *S. h. hesperius* (sample 6) and large *S. h. holzneri* (samples 7–9). Data used for the analysis are the 30 skull measurements. The first variate explained 86.88% of the variation and the second variate explained an additional 9.79%. Each symbol represents the location of an individual for each species in the character space and each ellipse represents the 95% confidence limit. Character loadings are shown in Appendix IIa.

based primarily on differences in skull frontal curvature (0.42) and parietal curvature (0.59) contrasted against interparietal breadth (–0.25) and basal length of the skull (–0.21). Loadings for all characters are provided in Appendix IIa. None of the *S. nuttallii* was classified incorrectly and none jackknifed. Likewise, none of the *S. holzneri* and *S. cognatus* cottontails jackknifed into the *S. nuttallii* group**.** The second variate explained an additional 9.79% of the total variation and partially separated sample 6 of *S. holzneri* based on overall smaller size from the larger cottontails of samples 7–9 of *S. holzneri* and sample 10 of *S. cognatus*. The 95% confidence ellipse of sample 7–9 of *S. holzneri* completely overlaps the 95% confidence ellipse of sample 10 of *S. cognatus*. Three of 20 rabbits in the *S. cognatus* sample classified in the *S. holzneri* sample (7–9) and 12 (60%) jackknifed into the *S. holzneri* sample (grouped sample 7–9).

Comparison of samples 1–5 currently referred to S. nuttallii.—Using 26 skull characters, analyzed by DFA, geographic variation was described among pooled samples 1–5 currently referred to *S. nuttallii*. These samples represent the southern distribution of *S. nuttallii* in southern Utah, Arizona, and New Mexico. The DFA was conducted on 105 adult skulls grouped into five pooled samples (Fig. 3). The first variate explained 43.59% of the total variation and separated samples primarily on overall size contrasted slightly against bulla length. In general, cottontails increase in size from west to east with those from southwestern Utah and northwestern Arizona (sample 1) being the smallest in overall size, samples 2 and 3 from near the confluence of Utah, Arizona, and New Mexico being about intermediate in overall size and individuals comprising samples 4 and 5 from north-central and northeastern New Mexico being the largest. Geographically adjacent

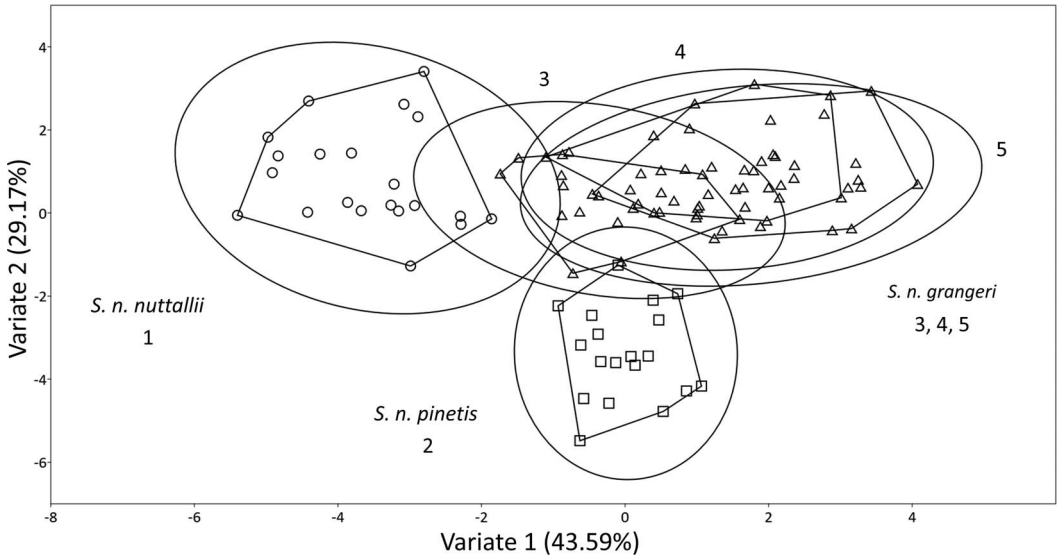

Fig. 3. A DFA showing geographic variation among five pooled samples currently referred to *S. nuttallii*. Data used in the analysis are 26 skull characters. The first variate separates samples based primarily on overall skull size (increasing in size from left to right). The second variate is a shape variate and largely separates sample 2 from all other samples. Each ellipse is a 95% confidence limit for that sample. Character loadings are shown in Appendix IIb.

samples show the greatest overlap in the character space and those samples being most distant from each other show the greatest separation in the character space. Variate 2, which explained an additional 29.17% of the total variation, separated most individuals of sample 2 from the White Mountains of Arizona from the other, more northern, samples (1, 3–5). Compared to other samples, cottontails from the White Mountains generally have shorter maxillary and mandibular toothrows (actually and relatively), slenderer mandibular ramus (as measured in ramus depth), smaller basioccipital (in length and breadth), smaller auditory bullae (bulla length), and slenderer rostrum (as measured in breadth across the nasals and rostrum depth). The ellipses are the 95% confidence interval around each sample. The ellipses of samples 4–5 broadly overlap each other. The ellipse of sample 3 overlaps all other samples but primarily those of samples 4 and 5. The ellipse of sample 1 is largely by itself, due to its small skull size, and the ellipse of sample 2 is largely by itself in the character space because of its shape differences; i.e., short toothrows and other unique features described above. All 21 individuals in sample 1 classified in that sample and only two jackknifed into other samples (3 and 5). Of the 19 individuals assigned to sample 2, 18 classified in that sample and two jackknifed into sample 5. Among samples 3–5, 60 of 65 classified correctly, but 22 of 65 jackknifed into some other sample. Loadings for all characters are provided in Appendix IIb.

Comparison of samples 6–10 currently referred to S. holzneri *and* S. cognatus.—A DFA was conducted on 138 individuals comprising five geographically adjacent samples 6–9 of *S. holzneri* from Arizona, southwestern New Mexico, and extreme northern portions of Sonora, and Chihuahua, Mexico and sample 10 of *S. cognatus* from New Mexico (Fig 4). The first variate explained 58.91% of the total variation and largely separated sample 6 from north-

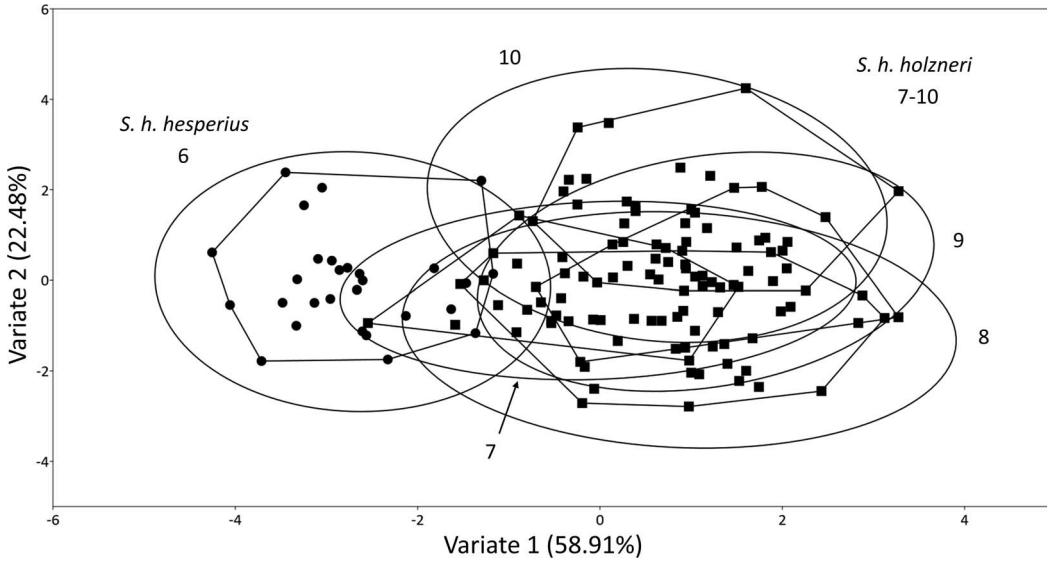

Fig. 4. A DFA comparing the skull morphology of geographically adjacent samples 6–9 currently referred to *S. holzneri* from Arizona and southwestern New Mexico and sample 10 currently referred to *S. cognatus* from central New Mexico. Each ellipse shows the 95% confidence for each sample. In general, cottontails in sample 6 are much smaller in overall size from all other samples (7–10). The second variate did little to further separate the five samples. Data used in the analysis are 26 skull characters. Character loadings are shown in Appendix IIc.

western Arizona from all other samples. The second variate explained an additional 22.48% of the total variation and partially separated samples 7–10 from each other. The ellipses in the figure show the 95% confidence limit for each pooled sample. In general, cottontails comprising sample 6 have a much smaller skull than cottontails forming the other samples. Morphological characters contributing most in the separation of sample 6 from the other samples are greatest skull length, basal length, mandible height, and mandible length. Only one character, palate length, was negatively correlated with overall skull size. Loadings for all characters are provided in Appendix IIc. For sample 6, all 28 cottontails were classified correctly and only three (11%) jackknifed into samples 7, 8, 9. Samples 7–10 all broadly overlap in the character space at the 95% confidence limit with geographically adjacent samples being most similar to each other. Sample 7, which is geographically adjacent to sample 6, shows the most overlap with sample 6 in the character space. Of the 23 individuals of *S. cognatus* from New Mexico (sample 10), five classified with samples of *S. holzneri* (samples 7, 8, and 9) and 14 of 23 (61%) jackknifed into samples of *S. holzneri* (7, 8, and, 9). Overall, samples 7–10 are remarkably similar in morphology.

Comparison of samples 8–13 currently referred to S. holzneri*,* S. cognatus*, and* S. robustus.—A detailed comparison was conducted on 130 individuals comprising six geographically adjacent samples 8–9 of *S. holzneri*, sample 10 of *S. cognatus*, and samples 11–13 of *S. robustus*. The *S. holzneri* samples are from southeastern Arizona, southwestern New Mexico, northeastern Sonora, and northern Chihuahua. The *S. cognatus* sample is from central New Mexico. The *S. robustus* samples are from the Guadalupe Mountains of New Mexico, mountains of western Texas, and northern half of

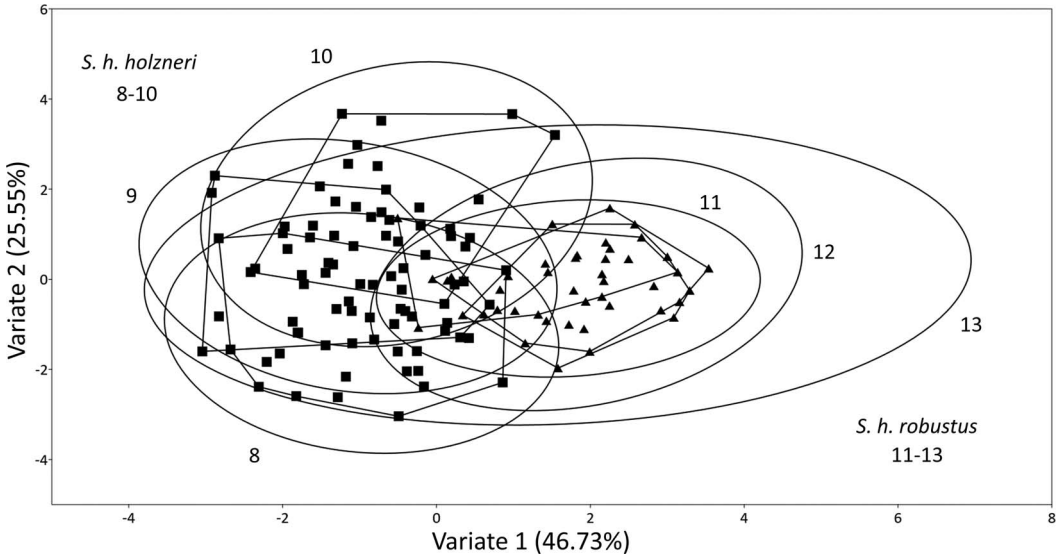

Fig. 5. A DFA analysis of geographically adjacent pooled samples 8–9 currently referred to *S. holzneri* from southeastern Arizona, southwestern New Mexico, and adjacent northern Mexico, sample 10 of *S. cognatus* from New Mexico, and samples 11–13 of *S. robustus* from extreme south-central New Mexico, mountains of Texas, and Sierra Madre Oriental to central Coahuila, Mexico. Based on current taxonomy, the first variate partially separated the six samples into two morphological groups: 1) samples 8–10 of *S. holzneri* and *S. cognatus* in one group; and 2) samples 11–13 of *S. robustus* in the other group. Each ellipse is the 95% confidence limit for each sample. Data used in the analysis are 26 skull characters. Character loadings are shown in Appendix IId.

Coahuila, Mexico. These six geographically adjacent samples are compared in a DFA. Figure 5 shows the first variate explained 46.73% of the total variation and partially separated samples 8–10 of *S. holzneri* and *S. cognatus* from samples 11–13 of *S. robustus*. The second variate explained an additional 25.55% of the total variation. The ellipses are the 95% confidence limit for each pooled sample. The second variate partially separated the *S. holzneri* and *S. cognatus* samples from each other, but did not farther separate the *S. robustus* samples each from the others. Characters that contributed the most to the separation of the samples on variate 1 were greatest skull length, bulla length, bullae breadth, shield-bullae depth, and skull depth. Compared to samples 8–10 of *S. holzneri* and *S. cognatus*, samples 11–13 of *S. robustus*, on average, have a slightly longer skull as measured in greatest skull length and larger auditory bullae, which is reflected in bulla length, bullae breadth, shield-bullae depth, and skull depth. Overall, geographically adjacent samples show the most overlap in the character space with 2 morphological groups being identifiable. One morphological group consists of samples 8–10 of *S. holzneri* and *S. cognatus* and the other group consists of samples 11–13 of *S. robustus*. Of these 2 morphological groups, 8 of 86 individuals of *S. holzneri* and *S. cognatus* classified in the *S. robustus* group and 18 of 86 (=21%) jackknifed into the *S. robustus* group. Of the *S. robustus* morphological group, four of 44 individuals classified in the other group and nine of 44 (=20%) jackknifed into the *S. holzneri* and *S. cognatus* group. Loadings for all characters are provided in Appendix IId.

Comparison of samples 8–9 and 14–16 currently referred to S. holzneri.—A DFA

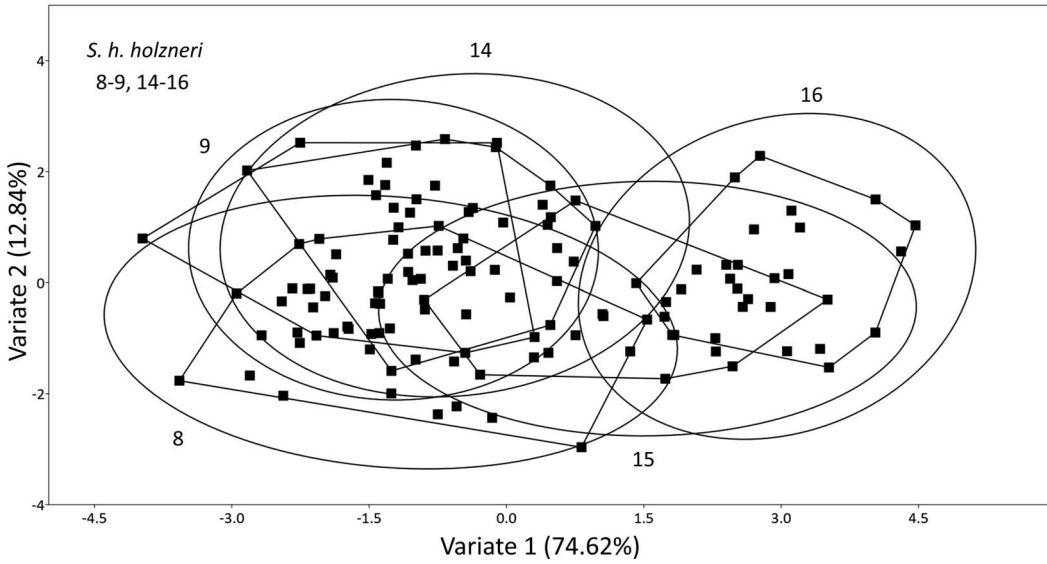

Fig. 6. A DFA of pooled samples 8–9, and 14–16 all currently referred to *S. holzneri* from southeastern Arizona, southwestern New Mexico, and the Sierra Madre Occidental of Sonora, Chihuahua, Sinaloa, and Durango, Mexico. Each ellipse is the 95% confidence limit for each sample. Data used in the analysis are 26 skull characters. Character loadings are shown in Appendix IIe.

analysis was conducted on 126 individuals forming pooled samples 8, 9, 14, 15, 16 from southern Arizona and southern New Mexico southward along the Sierra Madre Occidental through Sonora, Chihuahua, Sinaloa, and Durango (Fig. 6). These five pooled samples are geographically adjacent to each other. The ellipses are the 95% confidence limit for each pooled sample. The first variate explained 74.62% of the total variation and separated samples 8, 9, 14 from southern Arizona, southern New Mexico and Sonora and Chihuahua, Mexico from sample 16 from southern Durango with sample 15 from northern Durango bridging the morphological character space between the two groups. Characters that separated sample 16 from southern Durango from the other samples are related to overall size with cottontails from southern Durango being the largest. The second variate explained an additional 12.84% of the total variation but did little to further separate the samples. Geographically adjacent samples show the most overlap in the character space. And, those samples separated by the most distance are morphologically the most different. Although sample 16 from southern Durango seems distinctive in the character space, one of 22 classified into another sample and eight of 22 (36%) jackknifed into one of the other samples. Loadings for all characters are provided in Appendix IIe.

Discussion

Based on the results of the multivariate analyses, six morphological groups are identified. The taxonomy of these groups with their geographic distribution is shown in Fig. 7 and discussed below.

Comparison of S. nuttallii*,* S. holzneri*, and* S. cognatus.—The first DFA (Fig. 2) addresses the issue raised by several authors that some recognized species of cottontails in southern Utah, Arizona and New Mexico may not represent a biological species. This analysis included 30 morphological characters, four of which quantified, for the first time, skull curva-

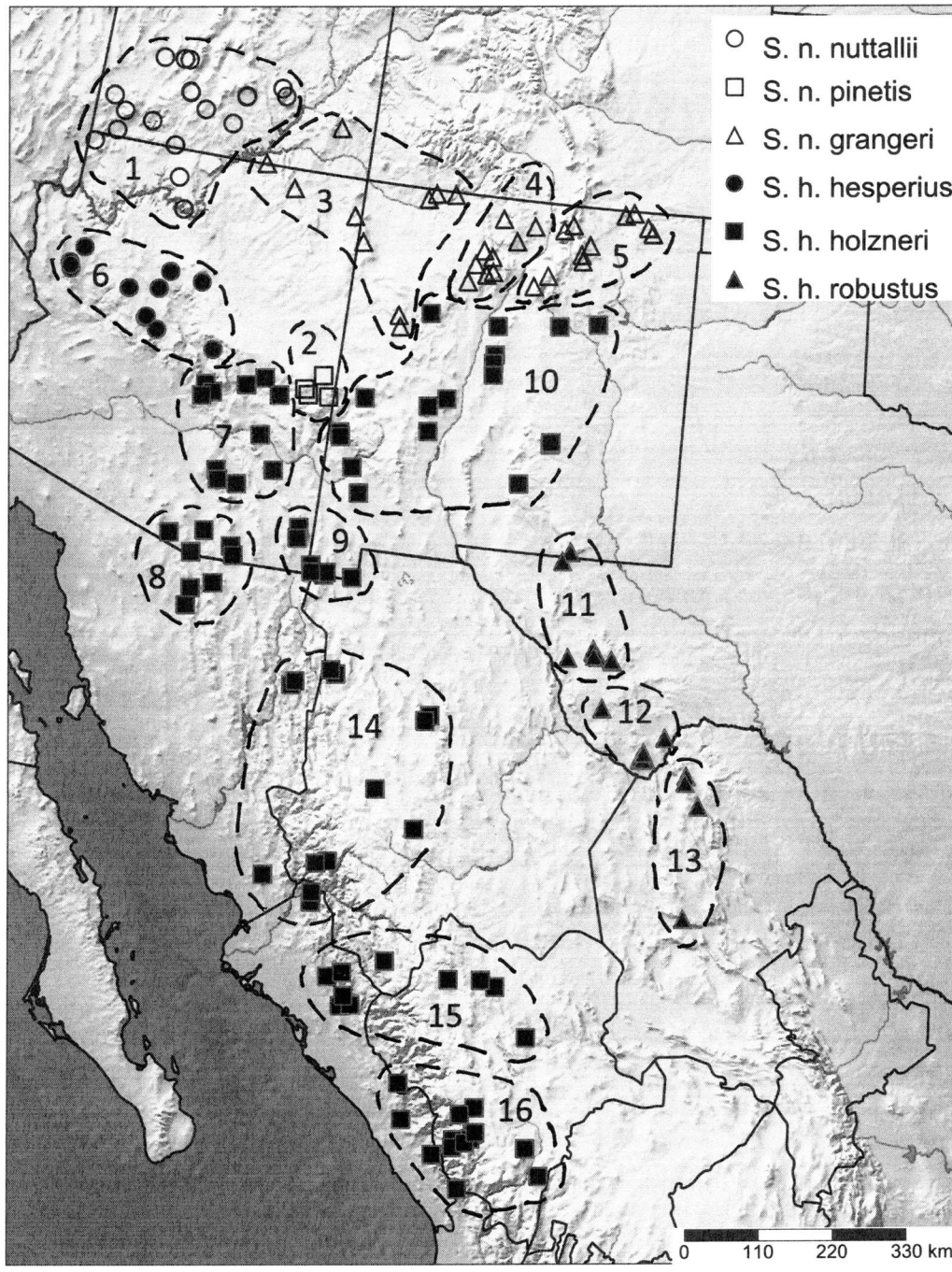

Fig. 7. Distribution map of the six taxa recognized in this study based on detailed analyses of skull morphology. The map also shows the 16 pooled samples currently referred to *S. nuttallii* (samples 1–5), *S. holzneri* (6–9, 14–16), *S. cognatus* (sample 10), and *S. robustus* (samples 11–13). The new taxonomy is given in the figure legend. See Table 1 for all pooled sample sizes, current taxonomy, and approximate geographic location. The exact geographic location of specimens examined is provided in Appendix I.

ture and interparietal size. The analysis of 140 skulls of the three recognized species, *S. nuttallii*, *S. holzneri*, and *S. cognatus*, shows there are two basic skull types that are separable beyond the 95% confidence limit. One skull type is highly arched front to back and has a small interparietal. This skull type is referable to *S. nuttallii*. The other skull type is relatively flat with a large interparietal and is referable to *S. holzneri*/*cognatus*. When not using these latter four characters, the 95% confidence limits for *S. nuttallii* and *S. holzneri*/*cognatus* overlap each other and identification often becomes based more on geography rather than morphology. The analysis of skull morphology in this DFA confirms that *S. nuttallii* is a distinct species and, strongly suggests that *S. holzneri* and *S. cognatus* are conspecific.

Comparison of S. holzneri *and* S. cognatus.—After removing all *S. nuttallii* from the data matrix and partitioning individuals of *S. holzneri* into several geographic pooled samples, the third DFA (Fig. 4) provides a more detailed analysis of the relationship of *S. holzneri* to *S. cognatus*. This analysis shows that specimens previously referred to *S. cognatus* from central New Mexico are indistinguishable from geographically adjacent cottontails from southwestern New Mexico, southeastern Arizona, and northern Mexico (samples 7–9), which includes topotypical specimens of *S. holzneri*. Ruedas (1998:1369) informally recommended that "*cognatus*" have species rank based on an analysis of morphological and dental characteristics. However, the PCA of the morphological data provided by the author (page 1362) showed the mean of the *cognatus* sample fell within the character space of the *S. holzneri* sample. He also concluded that dental characteristics of *S. cognatus* were unique from *S. holzneri*, but there was no statistical description of nongeographic versus geographic variation within and between *S. cognatus* and *S. holzneri*. Harris (2014), referring to characteristics of the third premolar, reported there is a fair amount of intraspecific variation and a degree of overlap between *S. nuttallii*, *S. audubonii*, and the mountain-inhabiting populations of *S. floridanus* [=*S. holzneri*, *S. cognatus*, and *S. robustus* of Ruedas] from New Mexico and western Texas. Therefore, until statistically defendable data are presented showing the unique, non-overlapping, dental morphology of *S. cognatus* from *S. holzneri*, the current morphological data supports the conclusion that *S. cognatus* is a synonym of *S. holzneri*.

We conducted several preliminary analyses that lead up to the final analysis that resulted in placing *S. cognatus* in synonymy under *S. holzneri*. Since there was never any detailed characterization of the skull of *S. cognatus* in the literature, it was impossible to define its range based on reported morphology. Reports of this taxon in the literature are as follows. Nelson (1907) described the species based on a single locality; i.e., the Manzano Mountains. Later, Nelson (1909) examined specimens from 4 localities (Manzano Mountains, Capitan Mountains, Datil Mountains, and Santa Rosa). From the latter two localities, Nelson referred specimens to *S. cognatus* using the caveats of "provisional" and "with hesitation". Ruedas (1998) examined specimens from the same localities, excluding the Datil Mountains. Frey (2004) referred specimens from the previous localities, in addition to Mount Taylor, Magdalena, San Mateo, Sandia, and Sacramento mountains but did not provide information on how this species was recognized. Frey (2004:23) did state "Findley et al. (1975) referred cottontails from the Mogollon Plateau in southern Catron Co. to *S. floridanus*; these animals are likely referable to *S. cognatus* or *S. nuttallii*." Based on our analysis, none of these specimens are *S. nuttallii*. And, we did find that Findley et al. (1975:87) recorded four specimens of *S. holzneri* [=*S. floridanus* of Findley et al.]

from 20 7/10 mi SW Datil on N. M. 12 (TU 2174), 21 1/10 mi SW Datil on N. M. 12 (TU 2172, 2173), and 15 mi N Glenwood on U. S. 180 (TU 2175). All of these specimens are *S. audubonii*. In our final preliminary analysis, we compared rabbits referred to *S. cognatus* from east of the Rio Grande (n = 13) to those referred to *S. holzneri* (then later to *S. cognatus*) from west of the Rio Grande north of Hidalgo County (n = 10). Those east of the river are slightly smaller, on average, reflected primarily in a slightly shorter rostrum, however, 24 of 26 cranial characters differed by less than 1 *SD*. When comparing these 2 "sub-samples" to other geographically adjacent pooled samples (such as 8, 9, and/or 11), these 2 sub-samples pooled together (broad overlap) in the character space when using PCA or DFA. Consequently, rabbits east and west of the Rio Grande were pooled together as sample 10. And, overall, rabbits in sample 10 could not be distinguished from topotypical *S. holzneri* from southern Arizona (sample 8).

Only three rabbits were available from the Capitan and Sacramento mountains (two from the Capitan and one from the Sacramento). From a biogeographic perspective, it might seem that the faunal affinities of these mountains might be closest to the Guadalupe and Davis mountains of southern New Mexico and Texas (sample 11) rather than the more northern Manzano and Sandia mountains. Accordingly, we treated the 3 rabbits from the Capitan and Sacramento mountains as unknowns in a DFA composed of 3 reference groups: 1) sample 11; 2) that part of sample 10 east of the Rio Grande (n = 13); and 3) that part of sample 10 west of the Rio Grande north of Hidalgo County (n = 10). In the analysis, the rabbit from the Sacramento Mountains was assigned to *S. h. robustus* (sample 11), and the two specimens from the Capitan Mountains were referred to *S. h. holzneri*, one to sub-sample 10 east of the Rio Grande and the other to sub-sample 10 west of the Rio Grande. Since two of the three unknowns in this region were assigned to Sample 10, the 3 specimens were grouped into sample 10. A larger sample is needed before one can state with confidence that rabbits from the Capitan and Sacramento mountains are best referred to *S. h. holzneri* rather than *S. h. robustus* or perhaps they should be treated as intergrades.

Comparison of S. holzneri *and* S. robustus.—The DFA in Fig. 5 shows that the skull morphology of cottontails from the mountains of south-central New Mexico (Guadalupe Mountains), trans-Pecos Texas, and northern Coahuila, Mexico differs from cottontails from the southeastern quadrant of Arizona and New Mexico in having a slightly larger skull and proportionately larger auditory bullae. It is important to note that the differences between the two taxa are average differences only. Some specimens of *S. h. holzneri* cannot be distinguished from some individuals of *S. h. robustus*. Lee et al. (2010) considered *robustus* a distinct species, but their comparison was with *S. f. chapmani*, which is a grassland-inhabiting taxon of *S. floridanus*. Comparisons of *robustus* to *cognatus* and *holzneri* were not done. Nalls et al. (2012), in their molecular comparison of *robustus* to *S. f. chapmani,* also included three specimens they referred to *S. floridanus* from the mountains of central New Mexico (two from the Sacramento Mountains, and one from the Capitan Mountains). Their results (Nalls et al. 2012:4) showed that two of the three individuals classified within the *robustus* group and one individual classified slightly outside the *robustus* and *S. f. chapmani* groups. This information further supports the conclusion that *S. holzneri* and *robustus* are conspecific. Ruedas (1998) gave *robustus* species rank based on an analysis of morphological and dental characteristics. His PCA of morphological data showed morphological overlap between

the two taxa. He also concluded that dental characteristics of *robustus* were unique from *S. holzneri*, however, there was no statistical description of nongeographic versus geographic variation within and between *robustus* and *S. holzneri*. Overall, current facts support the conclusion that *S. robustus* is a subspecies of *S. holzneri*.

Geographic variation within S. nuttallii.—Even though *S. nuttallii* varies geographically in size and proportions, the curvature of the skull remains consistently steep and diagnostic for the species. In general, the DFA (Fig. 3) of five pooled samples shows that geographically adjacent samples are morphologically most similar and those samples most distant are morphologically the most different. Cottontails north and west of the Colorado River in Arizona and southwestern Utah are smaller than all other populations and Hoffmeister (1986:135) referred specimens from the Kaibab Plateau, north of the Colorado River in Arizona to *S. n. grangeri*. Likewise, Durrant (1952:83) assigned specimens in Utah from north and west of the Colorado River to *S. n. grangeri* and those from east of the Colorado River in southeastern Utah to *S. n. pinetis*. At that time only 19 specimens of the species were available from the state. We examined 16 topotypical specimens of *S. n. nuttallii* from Malheur, Harney, and Grant counties, southeastern Oregon and 14 individuals of topotypical *S. n. grangeri* from Pennington and Custer counties, South Dakota. Sample means for four skull measurements are (sample mean for *S. n. nuttallii* listed first): greatest skull length 64.7 mm and 67.9 mm; zygomatic breadth 32.6 mm and 34.8 mm; maxillary toothrow length 12.6 mm and 13.2 mm; and bulla length 11.2 mm and 11.2 mm. The topotypical series of *S. n. nuttallii* compared closely to pooled sample 1 (see Appendix III) from southwestern Utah and northwestern Arizona whereas the topotypical series of *S. n. grangeri* averaged much larger. Accordingly, the small cottontails found north and west of the Colorado River in Arizona and southwestern Utah are referable to *S. n. nuttallii*.

A second DFA was conducted on the remaining samples of *S. nuttallii* (2–5) after sample 1 of *S. n. nuttalli* was removed (Fig. 8). The purpose of the analysis was to determine if populations from southeastern Utah, northeastern Arizona, and New Mexico are best referred to *S. n. pinetis*, which has a type locality in the White Mountains of east-central Arizona or to *S. n. grangeri*, which has a type locality in southwestern South Dakota. A topotypical sample of *S. n. grangeri* ($n = 14$) from Pennington and Custer counties, South Dakota was included in the analysis. Previously, both Findley et al. (1975) and Hoffmeister (1986) referred all *S. nuttallii* from New Mexico, and northeastern and east-central Arizona to *S. n. pinetis*. As shown in the DFA, samples 3–5 of *S. nuttallii* from northeastern Arizona and northern New Mexico broadly overlap the topotypical sample of *S. n. granger* from South Dakota. Topotypical sample 2 of *S. n. pinetis* from the White Mountains of Arizona is largely removed from the "*grangeri*" group on the 1st variate. Based on the character loadings (Appendix IIf) rabbits from the White Mountains have a skull that is similar in overall size, but exhibits unique shape differences such as much shorter maxillary and mandibular toothrows, smaller basioccipital (width and length), narrower rostrum (reflected in rostrum depth and breadth across nasals), slenderer mandibular ramus, and smaller auditory bullae. Of the 19 rabbits from the White Mountains, one classified in another group (sample 5) and 2 jackknifed out of the group (both into sample 5). Of the 65 specimens in samples 3–5, one jackknifed into sample 2. Accordingly, *S. n. pinetis* is restricted to the White Mountains. The unique morphology of this population indicates these

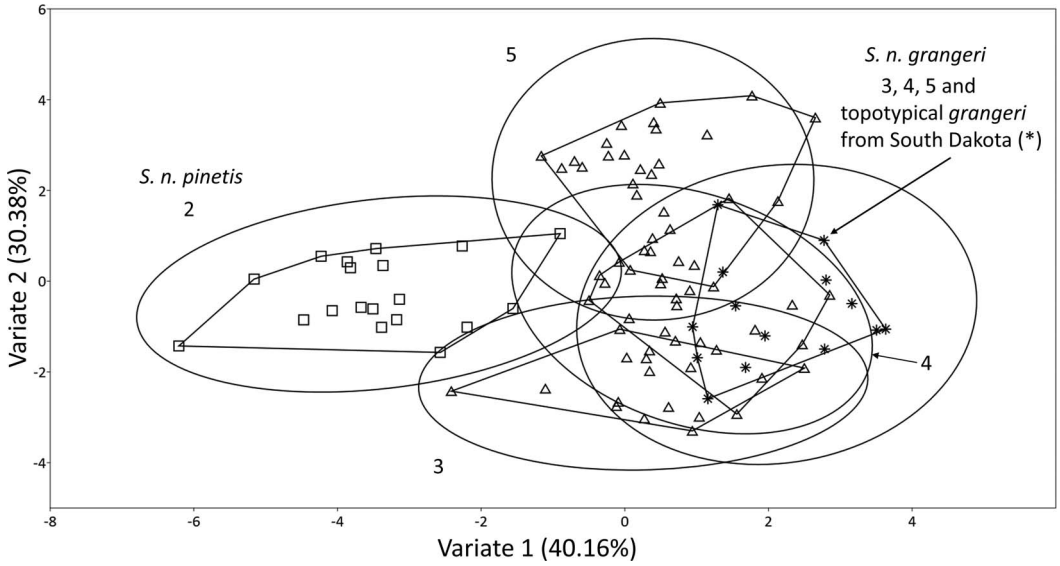

Fig. 8. A DFA comparing the skull morphology of samples 3–5 of *S. nuttallii* to the topotypical sample of *S. n. pinetis* (sample 2) from the White Mountains, Arizona and the topotypical sample of *S. n. grangeri* from South Dakota. The first variate separates sample 2 of *S. n. pinetis* from all other samples, which are referable to *S. n. grangeri*.

rabbits have been isolated from other more northern populations in Arizona and New Mexico. Current records show there is about a 150 km hiatus between the population from the White Mountains and the most southern extent of the northern population in the Zuni Mountains (Copperton USNM 137755, 137756 and 11 mi S, 14 mi W San Rafael MSB 54802), Cibola County, New Mexico. The name *S. n. grangeri* is assigned to all populations from New Mexico, and those south and east of the Colorado River in northeastern Arizona and southeastern Utah.

Geographic variation within S. holzneri.—Considering the numerous isolated plateaus and mountains occupied by *S. holzneri,* most populations are remarkably similar to each other over much of its range. The most distinctive population occurs along, and north of, the Mogollon Plateau of Arizona from the Hualapai Mountains southeast to the Sierra Ancha Mountains, a distance of about 175 miles. This population is referable to *S. h. hesperius*. This subspecies intergrades abruptly with *S. h. holzneri* in Gila County, Arizona. Another region where populations of *S. holzneri* have a unique morphology is from the Guadalupe Mountains of extreme south-central New Mexico, southward through trans-Pecos Texas, into the mountains of northern and central Coahuila, Mexico. These populations (samples 11–13), on average, have slightly larger skulls and proportionately larger auditory bullae and are referable to *S. h. robustus.*

Relationship of S. holzneri *to other cottontails from Mexico.*—The relationship of *S. holzneri* to cottontails from the central and southern mountains of Mexico currently referred to *S. floridanus* is yet to be determined. Diersing and Wilson (1980) reviewed the systematics of the cottontails from west-central Mexico. Their study included a morphological analyses of *S. holzneri* [=*S. floridanus holzneri* of these authors], *S. f. orizabae*, and the description of *S. f. macrocarpus*. It's likely these cottontails are conspecific with *S. holzneri*.

However, to be certain, any future study must include cottontails from the eastern lowlands of Mexico. Until then, this study shows that *S. nuttallii* is a distinct species occupying the central and northern Rocky Mountains and that the southern Rocky Mountains and plateaus of southwestern United States and northern Mexico are occupied by a single, polytypic species, *S. holzneri*, rather than a series of sister species, each isolated from the other by inhospitable habitat.

Systematics

Sylvilagus nuttallii Mountain Cottontail

Distribution.—In the study area, this rabbit occurs in the forested and brushy mountains and high plateaus of southern Utah, northern and east-central Arizona from north of the Colorado River, northeastern mountains, and White Mountains, and the northern third of New Mexico from the Zuni, Jemez, San Juan, Sangre de Cristo, and Capulin mountains.

Subspecies.—Based on the study results, three subspecies are recognized; *S. n. nuttallii*, *S. n. grangeri*, and *S. n. pinetis*. Previous to this study, only *S. n. grangeri* and *S. n. pinetis* were recognized as occurring in the study area.

Diagnosis.—A small to medium-sized cottontail with medium length ears. Body generally grayish with tail rufous-colored on the dorsum. Skull small to medium in size with relatively wide braincase and broad across the zygomatic arches, nasals narrow in breadth and short in length, medium-sized auditory bullae, slender mandibular ramus depth, interparietal small in breadth and length, skull high-arched front to back as measured by frontal curvature and parietal curvature.

Comparisons.—*Sylvilagus nuttallii* differs from *S. holzneri* in slightly shorter skull but relatively wider braincase and zygomatic arches, nasals shorter and narrower, basioccipital narrower, smaller interparietal, more strongly arched skull as measured in frontal curvature and parietal curvature, and slightly larger auditory bullae. A bivariate analysis (Fig. 9) plotting frontal curvature plus parietal curvature against interparietal width plus breadth separates 98% (137 of 140) of all skulls along their zone of parapatry in southwestern United States. Skull measurements are provided in Appendix III. Range-wide, *S. nuttallii* differs from *S. audubonii* in having: externally, shorter ears; cranially, smaller auditory bullae, narrower mandibular ramus, smaller interparietal, and broader mesopterygoid fossa; color, tail rufous colored on the dorsum rather than grayish.

Remarks.—Additional research (including morphology, molecular, chromosomal, and ecological) is needed to further explore the systematics and conservation of rabbits referred to this species, particularly from the more northern and western portions of its range.

Sylvilagus nuttallii nuttallii (Bachman, 1837)

1837. *Lepus nuttallii* Bachman, Journal of Academy of Natural Sciences of Philadelphia 7:345.

1904. *Sylvilagus nuttallii*, Lyon, Smithsonian Miscellaneous Collections 45:323. Name combination.

1839. *Lepus artemisia* Bachman, Journal of the Academy of Natural Sciences of Philadelphia 8:94. Type from the old Fort Walla Walla, Walla Walla County, Washington. Type not found, presumably lost.

1904. *Lepus l*[*aticinctus*] *perplicatus* Elliot, Field Columbian Museum, Publication 87, Zoological series 3:255. Type from Hannopec [=Hannaupah] Can-

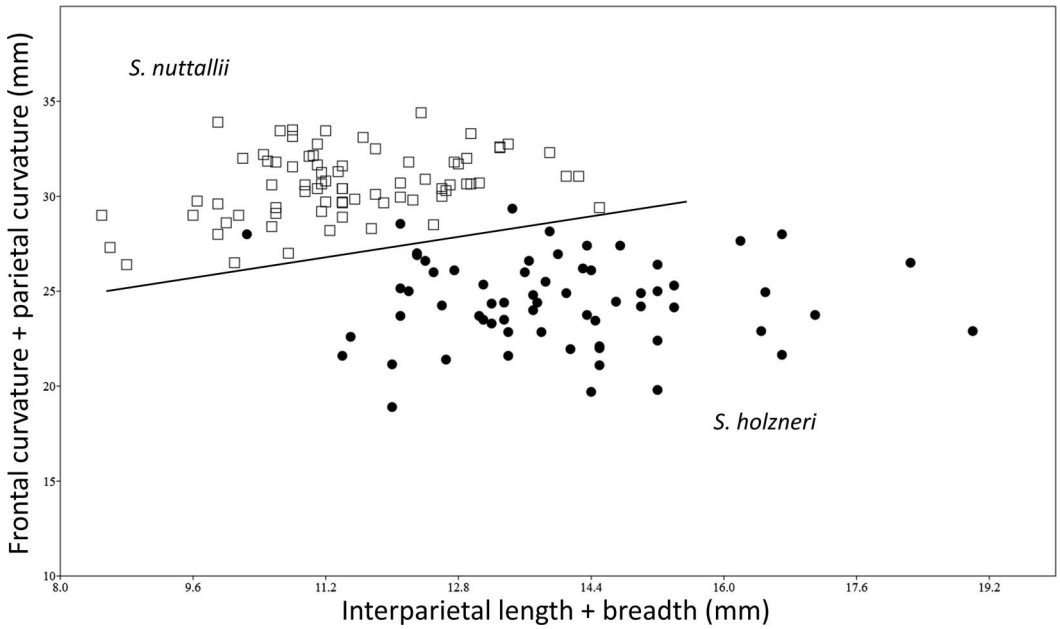

Fig. 9. A bivariate plot showing the primary differences in skull morphology between *S. nuttallii* and *S. holzneri* in Utah, Arizona, and New Mexico. In the figure, frontal curvature plus parietal curvature are plotted against interparietal length plus interparietal breadth. The diagonal line correctly separates 137 of 140 specimens of *S. nuttallii* and *S. holzneri*.

yon, Panamint Mountains, Inyo Co., California. Holotype examined.

Holotype.—Young (approximately 1 mo old), skin with skull inside, ANSP 382, collected west of the Rocky Mountains, perhaps near the mouth of the Mulheur River, Mulheur County, Oregon. Holotype examined.

Distribution.—In the study area, north and west of the Colorado River in southwestern Utah and northwestern Arizona.

Diagnosis.—Skull small in most measured features especially greatest skull length, zygomatic breadth, toothrow length (maxillary and mandibular), with short rostrum (reflected in breadth across infraorbital canals, rostrum depth, nasal length, and diastema length), and medium-sized auditory bullae.

Comparisons.—The skull of *S. n. nuttallii* differs from *S. n. pinetis* in generally smaller size especially reflected in greatest skull length, basal length, zygomatic breadth, braincase breadth, and rostrum length (as measured in nasal length, diastema length, and incisive foramen length) except with relatively large auditory bullae (as measured in bulla length, bullae breadth, and shield-bullae depth) and deep ramus height. A bivariate plot of greatest skull length and incisive foramen length (Fig. 10) separates 90% of individuals of *S. n. nuttallii* (sample 1) from 83% of individuals of *S. n. pinetis* (sample 2) and *S. n. grangeri* (samples 3–5).

Remarks.—Hoffmeister (1986) reported that *S. nuttallii* only occurred north of the Colorado River in northwestern Arizona on the Kaibab Plateau. In addition to their presence on the Kaibab Plateau, we examined a specimen (UMNH 2958) from Mohave County, Beaver Dam Wash, 2 miles south of the Utah state line in extreme northwestern Arizona. This locality is about 120 km west-northwest of the

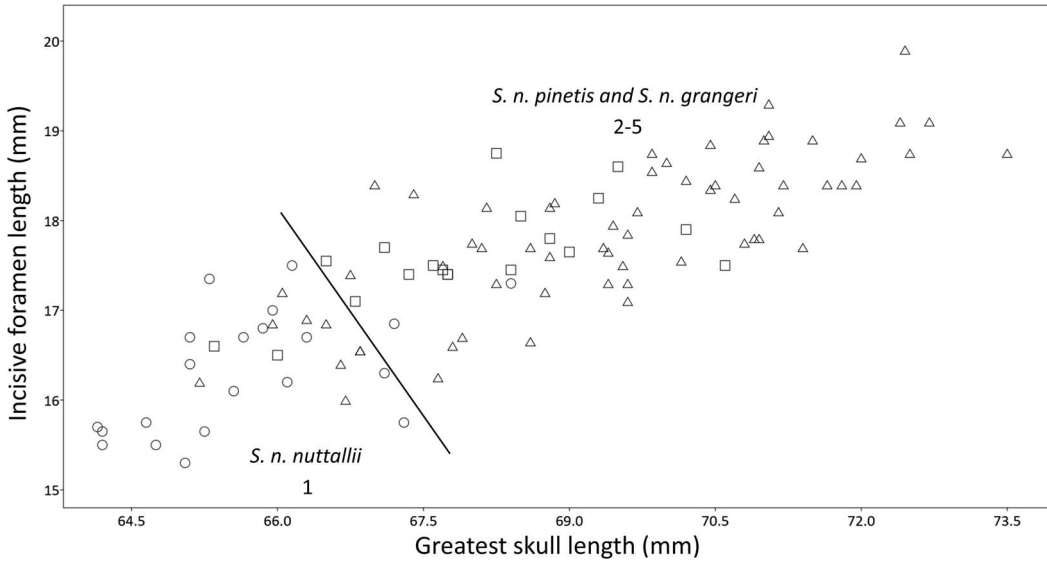

Fig. 10. A bivariate plot of incisive foramen length and greatest skull length. In the figure, 90% of the individuals of *S. n. nuttallii* from north and west of the Colorado River in Utah and Arizona (sample 1) are left of the diagonal line (open circles) and 83% of the individuals of *S. n. pinetis* (open squares) and *S. n. grangeri* (open triangles) from southeastern Utah, eastern Arizona, and New Mexico (samples 2–5) are right of the diagonal line.

Kaibab Plateau. It is referable to *S. n. nuttallii*.

Sylvilagus nuttallii pinetis (J. A. Allen, 1894)

1894. *Lepus sylvaticus pinetis* J. A. Allen, Bulletin of the American Museum of Natural History 19:348.

1909. *Sylvilagus nuttallii pinetis*, Nelson, North American Fauna 29:207. Name combination.

Holotype.—Juvenile, male, skin and skull, AMNH 9041/7336 from White Mountains, south of Mount Ord, Apache County, Arizona. Holotype examined.

Distribution.—Known only from the White Mountains of east-central Arizona.

Diagnosis.—Skull medium in most measured features except with small auditory bullae, small basioccipital (both in length and breadth), narrow rostrum, short maxillary and mandibular toothrows, and slender mandibular ramus depth.

Comparisons.—For a comparison of *S. n. nuttallii* with *S. n. pinetis* see "Comparisons" under that subspecies. The skull of *S. n. pinetis* can be distinguished from that of *S. n. grangeri* in having much shorter maxillary and mandibular toothrows. Maxillary toothrow length plus mandibular toothrow length in *S. n. pinetis* (sample 2) is 25.55 mm or less in 18 of 19 (94%) individuals and 25.80 mm or more in 14 of 15 (93%) *S. n. grangeri* (sample 3) from northwestern New Mexico, northeastern Arizona, and southeastern Utah.

Remarks.—Hoffmeister (1986) reported 2 locality records for *S. n. pinetis* in Greenlee County, east-central Arizona. We examined the specimen from Horse Cienega, 1 mi NNE Hannigan Meadows (MSB 163239) and found it too young to identify to species. We did not examine the specimen from Head Fish Creek, 9500 ft (MVZ 61327).

The unique morphology of this population in the White Mountains of Arizona indicates it has been isolated for some time

from other, more northern, populations of *S. nuttallii*. And, since the distribution of *S. holzneri* is known to encircle *S. n. pinetis* on the west, south, and east it's somewhat certain this taxon is restricted to suitable habitat in an area less than 2500 square kilometers in the White Mountains of Arizona in extreme southern Apache County and probably the adjacent northern part of Greenlee County. It is currently unknown from New Mexico.

Sylvilagus nuttallii grangeri (J. A. Allen, 1895)

1895. *Lepus sylvaticus grangeri* J. A. Allen, Bulletin of the American Museum of Natural History 7:264.

1909. *Sylvilagus nuttallii grangeri*, Nelson, North American Fauna 29:204. Name combination.

Holotype.—Older juvenile, female, skin and skull, AMNH 9094/7402 from "Hill City, Custer Co., S. Dak." Apache County. Holotype examined. Note: From the skin label the senior author recorded the type as a female, but the description states it is an adult male.

Distribution.—In the study area, east of the Colorado River in southeastern Utah, northeastern Arizona, and northern third of New Mexico.

Diagnosis.—Based on samples 4 and 5 from New Mexico, the skull is large in most measured features, particularly first upper incisor length, palate length, greatest skull length, breadth across maxillary toothrows, and mandibular ramus depth. Sample 3 of *S. n. grangeri*, which is an intergrading population with *S. n. nuttallii*, is, overall, slightly smaller than samples 4–5, except with slightly larger auditory bullae.

Comparisons.—For a comparison of *S. n. grangeri* with *S. n. pinetis* and *S. n. nuttallii* see "Comparisons" under those subspecies.

Remarks.—A specimen from 5 mi S El Rito, Rio Arriba County (KU 5943), catalogued as *S. nuttallii*, is *S. audubonii*. Two specimens of *S. n. grangeri* (USNM 247703 and 227616) were examined from the Tunicha Mountains, Apache County, Arizona. Both are juveniles and were not used in our analyses. The Tunicha Mountains are about 220 km north of the White Mountains. The specimen that Hoffmeister (1986) referred to *S. n. pinetis* from Ash Pit, SRP (Navajo) Generator Plant site, Page, Coconino Co., Arizona is only about 6 wk old and cannot be confirmed as *S. nuttallii* or *S. audubonii*.

Sylvilagus holzneri
Holzner's Cottontail

Distribution.—In the study area, occurs in the forested and brushy mountains and plateaus of Arizona, New Mexico, and western Texas southward into Mexico along the Sierra Madre Occidental in Sonora, Chihuahua, Sinaloa, and Durango, Mexico and Sierra Madre Oriental in the northern half of Coahuila, Mexico.

Subspecies.—The results of this study on cranial morphology document 3 subspecies; *S. h. hesperius*, *S. h. holzneri*, and *S. h. robustus*. Recognition of each subspecies is provided under the subspecies accounts.

Diagnosis.—A medium to large-sized cottontail with long ears. Body color is grayish with dorsum of tail rufous. Skull generally medium to large in size with long and broad nasals, broad basioccipital, medium-sized auditory bullae, medium-sized maxillary and mandibular toothrows, shallow ramus height, large interparietal, and flat skull as measured in frontal curvature and parietal curvature.

Comparisons.—For a comparison of *S. holzneri* with *S. nuttallii*, see "Comparisons" under that species. *Sylvilagus cunicularius* does not occur in the study area, but its range is parapatric with *S. holzneri* in coastal Sinaloa and Nayarit, Mexico. See Diersing and Wilson (1980:3) for recognition of this species. *Sylvilagus audubonii* differs from *S. holzneri* in having

larger auditory bullae, deeper ramus height, narrower basioccipital, and narrower mesopterygoid fossa. Although outside the study area, *S. holzneri* differs from the lowland-inhabiting *S. floridanus llanensis* (=*S. f. alacer* or *S. f. chapmani* of some authors) from the grasslands of the Great Plains of eastern New Mexico and panhandle of Texas in being grayish in color rather than reddish and having much longer ears (dry ear length ranges from 55.4 to 70.0 mm in 37 New Mexico *S. holzneri* and 44.6 to 54.6 mm in 27 New Mexico and Texas panhandle *S. floridanus llanensis*), larger auditory bullae (reflected in bulla length, bullae breadth, and shield-bullae depth), shorter maxillary and mandibular toothrows, smaller rostrum depth, and shallower ramus height. Farther south, in the lowland grasslands/shrublands of west-central and southwestern Texas and eastern Coahuila, Mexico, *S. floridanus chapmani* differs from *S. holzneri* in having much shorter ears, and smaller skull especially in greatest length of the skull, nasal length, shield-bullae depth, bulla length, and skull depth.

Remarks.—The taxonomy of this species is provisional until future studies are completed that document the affinities of *S. holzneri* to other mountain-inhabiting taxa from central and southern Mexico, and all mountain-inhabiting taxa from Mexico are compared to the adjacent lowland populations of *S. floridanus* from eastern Mexico (Coahuila, Nuevo Leon, Tamaulipas, San Luis Potosi, and Veracruz).

Sylvilagus holzneri hesperius Hoffmeister and Lee, 1963

1963. *Sylvilagus floridanus hesperius* Hoffmeister and Lee, The American Midland Naturalist 70:140.

Holotype.—Adult, male, skin and skull, MSB 163154 from 5 ¼ mi SE Kingman, Hualapai Mountains, Mohave Co., Arizona. Holotype examined.

Distribution.—Occurs in northwestern and central Arizona south of the Colorado River in the mountains and high plateaus from the Hualapai Mountains southeastward to the Sierra Ancha Mountains.

Diagnosis.—Skull small in all measured features especially in greatest skull length, basal length, rostrum depth, length of incisive foramen, except with a long palate and a relatively broad postero-ventral portion of the skull.

Comparisons.—*S. h. hesperius* differs from *S. h. holzneri* in being smaller, particularly in greatest skull length, basal length, zygomatic breadth, rostrum depth, and length of the incisive foramina. A bivariate plot (Fig. 11), using greatest skull length and zygomatic breadth, illustrates the difference in cranial size between the small *S. h. hesperius* (sample 6) and the large *S. h. holzneri* in central Arizona (samples 7 and 8). The diagonal line in the figure separates 79% (22 of 28) of the specimens of *S. h. hesperius* from 85% (50 of 59) of the individuals of *S. h. holzneri*.

Remarks.—Hoffmann and Smith (2005), without explanation, placed *S. h. hesperius* [=*S. floridanus hesperius*] in synonymy under *S. h. holzneri*. Our study documents the unique morphology of these cottontails referable to *S. h. hesperius*.

Sylvilagus holzneri holzneri (Mearns, 1896)

1896. *Lepus sylvaticus holzneri* Mearns, Proceedings of the U. S. National Museum 18:554.

1904. *Sylvilagus* (*Sylvilagus*) *floridanus holzneri*, Lyon, Smithsonian Miscellaneous Collections 45:336. Name combination.

1896. [*Lepus sylvaticus*] subspecies *rigidus* Mearns, Proceedings of the U. S. National Museum 18:555. Type from Carrizalillo, Luna Co., New Mexico. Holotype examined.

1903. *Lepus* (*Sylvilagus*) *durangae* J. A. Allen, Bulletin of the American Museum of Natural History 19:609. Type

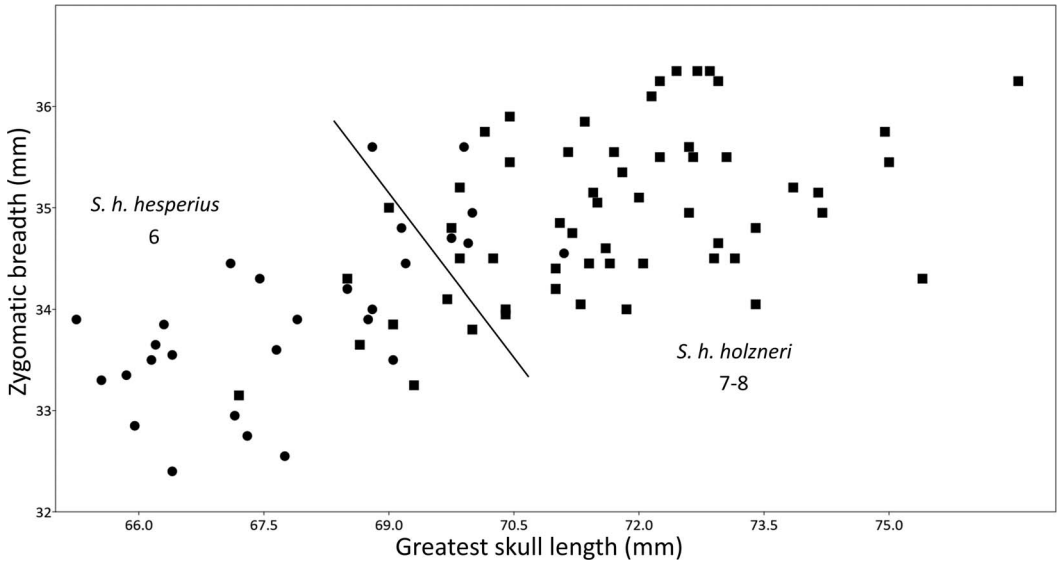

Fig. 11. A bivariate analysis plotting zygomatic breadth against greatest skull length. In the figure, 79% (22 of 28) of *S. h. hesperius* from central and northwestern Arizona (sample 6) fall to the left of the diagonal line and 85% (50 of 59) of *S. h. holzneri* from southeastern Arizona (samples 7–8) fall to the right of the diagonal line.

from Rancho Bailon, northwestern Durango, Mexico. Holotype examined.

1907. *Sylvilagus cognatus* Nelson, Proceedings of the Biological Society of Washington 20:82. Type from northeast side of Bosque Peak, 9450 ft, Torrance Co., New Mexico. Holotype examined. Specific locality fixed by Frey, Fisher, and Ruedas (1997).

Holotype.—Adult, female, skin and skull, USNM 58937 from the Douglas Spruce [=Douglas-fir] zone near the summit of the Huachuca Mountains, Cochise County, Arizona. Holotype examined.

Distribution.—Mountains and plateaus in the southeastern quadrant of Arizona, central and southern New Mexico from Mount Taylor, Manzano Mountains and Conchas River 35 mi N Santa Rosa southward through Sacramento Mountains, then southwest through southwestern New Mexico (except Guadalupe Mountains) and southeastern Arizona along the Sierra Madre Occidental of Chihuahua, Sonora, Durango, and Sinaloa.

Diagnosis.—Externally: medium to large size with long ears. Skull: medium to large in all features except small in rostrum depth, short and narrow maxillary toothrows, and shallow ramus height, but with medium-sized auditory bullae. Color: grayish dorsally.

Comparisons.—For comparison of *S. h. holzneri* with *S. h. hesperius* and *S. h. robustus* see "Comparisons" under those subspecies.

Remarks.—Previously, *S. holzneri* was recorded from only two localities in Sonora, Mexico (Hoffmeister and Lee, 1963). Both localities are in extreme southern Sonora at 7 mi WNW Alamos and 8 mi WNW Alamos. During the course of this study, eight additional specimens were examined from Sonora, all of which are catalogued as *S. audubonii*. Four were collected from north-central Sonora at 8 mi W Cananea (by road) on Mexican highway 2 (CSULB 5388); 2 mi W Magdalena, La Mision, 2650 ft (MVZ

83340); and 40 km S Nogales, Casita, 3300 ft (MVZ 106140, 106141). Four others were collected in east-central Sonora at 4 1/10 mi NW by road from Nacori Chico (MVZ 148861, 148862, 148866); and 6 mi N Nacori, east slope of Sierra de Mazatan, 2250 ft (MVZ 83343). All of these specimens are referable to *S. h. holzneri*. A skull only from Camp Grant, Arizona, catalogued as *S. floridanus holzneri* (USNM 7454) is *S. audubonii* based on narrow breadth across nasals (13.0 mm) which is typical for the species.

Northern Arizona University has an adult cottontail (NAU 886) collected from the White Mountains, 5 mi S Hawley Lake, Apache County, Arizona. This specimen represents the first record of *S. h. holzneri* from Apache County and this locality is about 15–20 km west of multiple locations where *S. n. pinetis* has been collected.

Sylvilagus holzneri robustus (V. Bailey, 1905)

1905. *Lepus pinetis robustus* V. Bailey, North American Fauna 25:159.

1951. *Sylvilagus floridanus robustus*, Hall and Kelson, University of Kansas Publications, Museum of Natural History 5:56.

1909. *Sylvilagus robustus*, Nelson, North American Fauna 29:194. Name combination.

1955. *Sylvilagus floridanus nelsoni* Baker, University of Kansas Publications, Museum of Natural History 7:611. Type from 22 mi S, 5 mi W Ocampo, 5925 ft, Coahuila, Mexico. Holotype examined.

Holotype.—Adult, female, skin and skull, USNM 18262/25165 from 6000 ft, Davis Mountains, Jeff Davis Co., Texas. Holotype examined.

Distribution.—Guadalupe Mountains of New Mexico and Texas, Davis, Chisos, and other mountains of western Texas, Sierra Madre Oriental of northern and central Coahuila, Mexico.

Diagnosis.—This is the largest subspecies of *S. holzneri* in southwestern United States. Skull long and broad, braincase broad, and auditory bullae large as reflected in bulla length, bullae breadth, shield-bullae depth, and skull depth.

Comparisons.—Fig. 12 shows a bivariate plot of 51 individuals of *S. h. holzneri* (samples 9 and 10) from New Mexico and adjacent southeastern Arizona and extreme northern Chihuahua, with 44 specimens of *S. h. robustus* (samples 11, 12 and 13) from extreme south-central New Mexico, trans-Pecos Texas, and mountains of northern and central Coahuila. In the figure, bulla length is plotted against shield-bullae depth. The diagonal line in the figure separates 80% of the individuals of *S. h. holzneri* from 80% of the specimens of *S. h. robustus*.

Remarks.—Baker (1955) described *S. h. nelsoni* [=*S. f. nelsoni* of Baker] from the central and northern mountains of Coahuila and considered it to be most like *S. h. robustus* of western Texas. This author considered *S. h. nelsoni* to differ from *S. h. robustus* primarily in having a broader rostrum, narrower braincase, smaller auditory bullae, and in being a paler gray color dorsally. Later, Raun (1965), after reviewing the morphology of *S. h. nelsoni* and *S. h. robustus*, maintained the two subspecies were virtually indistinguishable and that *S. h. nelsoni* should be a synonym of *S. h. robustus*. One specimen regarded as *S. h. robustus* by this author, KU 84388, from McKittrick Canyon, Guadalupe Mountains, Culberson County, Texas, based on our examination, is an individual of *S. audubonii*. This adult differs from all specimens of *S. h. robustus* in being smaller (greatest skull length 65.00 mm), shorter mandibular toothrow (12.30 mm), relatively larger auditory bullae (12.55 mm), and in having the dorsal surface of the tail grayish rather than rufous. This individual

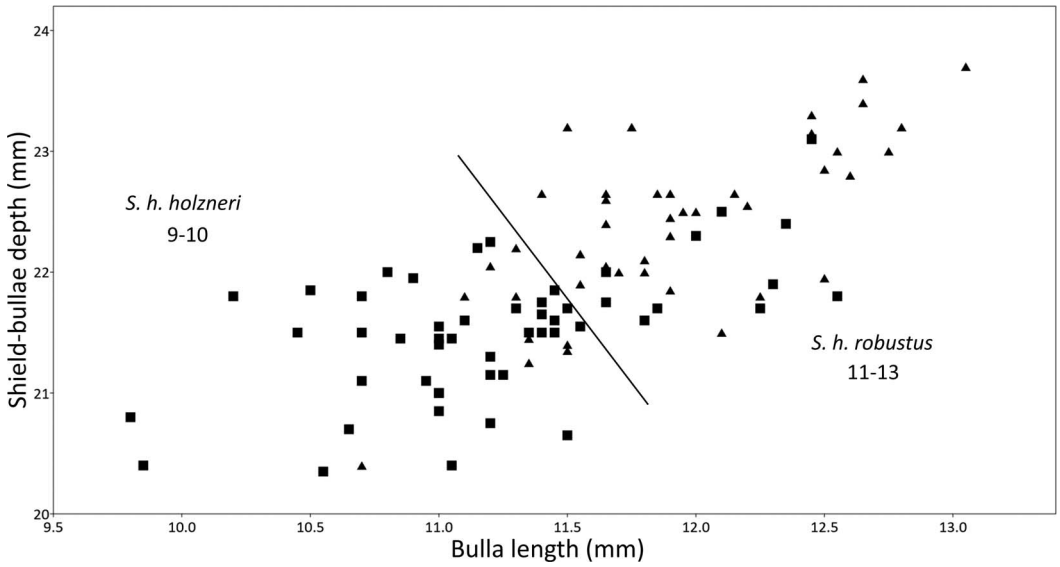

Fig. 12. A bivariate analysis plotting bulla length against shield-bullae depth. In the figure, 80% (41 of 51) of *S. h. holzneri* from southeastern Arizona, New Mexico, and adjacent northern Mexico (samples 9–10) are left of the diagonal line and 80% (35 of 44) of *S. h. robustus* from south-central New Mexico, trans-Pecos Texas, and Coahuila, Mexico (samples 11–13) are right of the diagonal line.

of *S. audubonii* is typical of the species from near the Guadalupe Mountains.

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Appendix I: Specimens Examined

Following is a list of specimens used in the data analyses with the museums where they are housed. Specimens are arranged by species and pooled sample number. In a few cases, additional specimens are listed at the end of a sample. These are specimens that were not used in the analyses because of a broken skull, being outside the study area, or being immature but the locality and fact that it was examined is important to note.

Sylvilagus nuttallii

Sylvilagus nuttallii nuttallii, pooled sample 1 (n = 21), north and west of the Colorado River in southwestern Utah and northwestern Arizona.—UTAH. GARFIELD COUNTY: Boulder, 6502 ft (UMNH 9064); 4 mi N Boulder, 7500 ft (UMNH 9063); ½ mi N Lonesome Beaver Campground, Sawmill Basin, 8000 ft, Mt. Ellen, Henry Mtns

(UMNH 19706); King's Ranch, Henry Mtns (BYU 12763); Mt. Ellen, Henry Mtns (USNM 157884, 157887); 3 mi N Panguitch, 6600 ft (AMNH 123737); 3 mi SE Panguitch, 6666 ft (AMNH 123739); 3 mi W Tropic (AMNH 123738). WASHINGTON COUNTY: Enterprise Reservoir, 11 mi SW Enterprise (UMNH 20174); Pine Valley Forest Camp, 7100 ft (UMNH 20173); Zion National Park (BYU 2614); Tonaquint Fields, St. George (UMNH 612). BEAVER COUNTY: 6 ½ mi S Milford, 5,020 ft (UMNH 24257); Beaver (USNM 22651); Baker Canyon, 4 mi E Beaver, 6500 ft (AMNH 124743). KANE COUNTY: Upper Kanab (USNM 189192); Rainbow Bridge Expedition, Kaiparowits Plateau, 7000 ft (AMNH 132540). ARIZONA. MOHAVE COUNTY: Beaver Dam Wash, 2 mi S Utah line, 2100 ft (UMNH 2958). COCONINO COUNTY: Kaibab, Big Springs, Grand Canyon (USNM 248802); Shiva Temple, Grand Canyon (AMNH 128097).

Additional specimens examined but not used in the data analyses.—Holotype for *S. nuttallii*; young (approximately 1 mo old), skin with skull inside, ANSP 382, collected west of the Rocky Mountains, perhaps near the mouth of the Mulheur River, Mulheur County, Oregon. Type (FMNH 12612) of *Lepus l*[*aticinctus*] *perplicatus* from Hannopec [=Hannaupah] Canyon, Panamint Mountains, Inyo Co., California, a synonym of *S. nuttallii*.

Sylvilagus nuttallii pinetis, pooled sample 2 (n = 19), east-central Arizona.—ARIZONA. APACHE COUNTY: T4N, R21E, Sec. 12 (ASU 3779); Baldy Peak, T6N, R26E, Sec. 23, 11,300 ft (ASU 3778); White Mtns (AMNH 9040/7335); Mount Thomas, White Mtns, east slope, 9500 ft (USNM 209244, 209243); Alpine, 8000 ft (USNM 205355); White Mtns, 9000 ft (USNM 157784); Springerville (USNM 14900/23099); 2 mi S Reservation Ranch, Apache Indian Reservation (MSB 163230); 6 ½ mi SW Greer, Phelps Bot. Area (MSB 163238, 163237); Greer (MSB 163235, 163234, 163236); ½ mi W Greer (MSB 163232, 163231, 163233); head San Francisco River, 8530 ft (MVZ 61326); White Mtns, 20 mi S Springerville, Big Lake Knoll, 9000 ft (TCWC 100).

Additional specimens examined but not used in the data analyses.—ARIZONA. APACHE COUNTY. Type specimen – juvenile, male, skin and skull, AMNH 9041/7336 from White Mountains, south of Mount Ord; 10 mi S Springerville (USNM 209242), partial skull. GREENLEE COUNTY. Horse Cienega, 1 mi NNE Hannigan Meadows, (MSB 163239), too young to identify to species.

Sylvilagus nuttallii grangeri, pooled sample 3 (n = 15), east of the Colorado River in southeastern Utah, northeastern Arizona, and northwestern New Mexico.—UTAH. SAN JUAN COUNTY [labelled as Navajo County, Arizona but locality estimated to be in Utah by about 1 mile]: Navajo Mtn, War God Spring, 8500 ft (AMNH 125929); 19 mi WNW Blanding, Babylon Meadows, 3 ½ mi N Kigalia Ranger Station (MSB 100157). ARIZONA. NAVAJO COUNTY. Bat Women Canyon, 16 mi W Kayenta, 6900 ft (MVZ 63002). APACHE COUNTY. Chuska Mtns, Tsaile Lake Rd to Roof Butte, 7800 ft (MNA Z9.823). NEW MEXICO. SAN JUAN COUNTY: Chusca [=Chuska] Mtns, 8000 ft (USNM 157819, 157820, 158546); Sambrito Creek, SE ¼ of SW ¼, sec 15, T32N, R6W (MSB 7277); W side sec 3, Pine River Rd, T31N, R7W (MSB 7275); San Juan River, river mi 166, 5090 ft (UMNH 16375); San Juan River, river mi 168, 6000 ft (UMNH 16376); Vells Canyon, river mi 165, 6150 ft (UMNH 16374). CIBOLA COUNTY [historically part of Valencia County]: Copperton (USNM 137755, 137756); 11 mi S, 14 mi W San Rafael (MSB 54802).

Sylvilagus nuttallii grangeri, pooled sample 4 (n = 22), north-central New Mexico west of the Rio Grande.—NEW MEXICO. RIO ARRIBA COUNTY: Tierra Amarillo (USNM 133690); Gallinas, 9500 ft (USNM 134900); 4 mi N El Rito, 7000 ft (KU 5945, 5944, 6280); 8 mi N El Rito, 8000 ft (KU 5942); 4 ½ mi N El Rito (KU 7509); 6 mi NW El Rito (MSB 163251, 163252); 8 mi SW Coyote (MSB 163255, 163254, 163253). SANDOVAL COUNTY: San Antonio Mtn, 8700 ft (USNM 133691); Bluebird Mesa, 5 mi E, 3 mi S Cuba, 8500 ft (MSB 4322, 4323, 6734); Fenton Lake, 10 mi N Jemez Springs (MSB 3270); 4 mi SE jct NM 44 and NM 444 on Fenton Lake Rd (MSB 25854); Jemez Mtns, near Battleship Rock (MSB 64370); 3 ½ mi S, 10 ½ mi W La Cueva (MSB 265725); 0.3 mi NNE of junction of FS Rd 534 on Smokey Bear Hill Rd (MSB 40078). TAOS COUNTY. Tres Piedras (USNM 133510).

Sylvilagus nuttallii grangeri, pooled sample 5 (n = 28), northeastern New Mexico east of the Rio Grande.—NEW MEXICO. SANTA FE COUNTY. vicinity Aspen Ranch, 2 mi N, 5 mi E Tesuque (MSB 75699). COLFAX COUNTY: Martinez (USNM 69963); Raton Range, Bear Canyon (USNM 130052); 5 mi NE Raton (MSB 163240, 163241, 163242, 163246, 163247, 163248, 163249, 163250,); 8 mi W Cimarron, Philmont Ranch (AMNH 131887); Cimarroncito Philmont Ranch, 4 ½ mi W Ranch Hdqtrs (AMNH 131888). MORA COUNTY: Hall's Peak (USNM 70913, 70914, 70915, 70916, 70917, 70918). UNION COUNTY: Sierra Grande, 8000 ft (USNM 128555); Capulin Mountain (MWSU 6375); SW base Capulin Mtn, 7300 ft (KU 95248, 95247). TAOS COUNTY: Costilla Pass (USNM 130054); 23

mi S, 6 mi E Taos, 8750 ft (KU 41630); 4 mi NE Tres Ritos (MSB 1424); 7 mi S, 1 mi W Red River, Goose Lake, 12,000 ft (MSB 1445); west slope Truchas Peaks, 35.96, 105.64 (MSB 64371).

Sylvilagus holzneri

Sylvilagus holzneri hesperius, pooled sample 6 (n = 28), Arizona, south of the Colorado River in Mohave, Yavapai, Coconino, and northwestern Gila counties.—ARIZONA. MOHAVE COUNTY. Hackberry (USNM 227834); Hualapai Mtns (USNM 117462, 117488, 117490, 117495); 10 mi E, 9 ½ mi S Kingman (MSB 163163); 10 mi E, 10 mi S Kingman (MSB 163164); 13 mi ESE Kingman (MSB 163147); 8 ½ mi SE Kingman (MSB 163160); 5 ½ mi SE Kingman, Hualapai Mtns (MSB 163157); 6 mi SE Kingman (MSB 163158); 5 mi SE Kingman (MSB 163150, 163151, 163152); 5 ¼ mi SE Kingman (MSB 163153, 163154, 163155, 163156); 4 mi E, 2 mi S Kingman (MSB 163161); 6 ½ mi SE Kingman, Hualapai Mtns (MSB 163148). YAVAPAI COUNTY. M. C. Canyon, 5 ¾ mi E, ¾ mi S Drake (MSB 163178); Prescott Nat. Forest, Walnut Creek (UA 21420); Prescott (USNM 46752); Mayer (USNM 247495); 3 mi N Fort Whipple, 5000 ft (USNM 214157). COCONINO COUNTY. Flagstaff (MNA Z93733); Williams (KU 2084). GILA COUNTY. 2 mi E Star Valley, near Payson (ASU 1363).

Additional Specimens examined but not used in the data analyses.—ARIZONA. COCONINO COUNTY. Flagstaff, Buffalo Park (NAU 2122), adult skin and broken skull; Pine Spring(s), 15 mi S Colorado Canyon (AMNH 2425), adult skin and partial skull.

Sylvilagus holzneri holzneri, pooled sample 7 (n = 24), central and east-central Arizona.—ARIZONA. NAVAJO COUNTY. 8 mi S Whiteriver (MVZ 113413). GILA COUNTY. Sierra Ancha Mtns, Reynolds Creek Range Station (USNM 247734); Sierra Ancha, near Carr's Ranch (MVZ 25501); Sierra Ancha, 27 mi NE Globe, 5600 ft (MVZ 114454); 8 mi NW Roosevelt (UWBM 6111); 1 mi S Parker Creek Flat, Sierra Ancha, 4900 ft (MSB 163137); 2 mi S Parker Creek Flat, Sierra Ancha, 4800 ft (MSB 163138); Tonto National Monument, 2800 ft (MSB 163140); T6N, R17E, sec 16, Cibeque Creek (ASU 2986); T4 ½N , R21E, sec 28 (ASU 2998); Mesquite Flat Rd, T6N, R17E, sec 16 (ASU 2997); T6N, R17E, sec 9, Salt River Canyon, 1 mi SSW confluence Cibeque and Salt River (ASU 2981); T7N, R16E, sec 8–17 (ASU 3784); R13N, T9E, SW ¼, sec 29 (ASU 6115); 4 ¾ mi S White Springs Ranger Station [exact location not found and not plotted] (ASU 2984). MARICOPA COUNTY. Fish Creek, Tonto National Forest, 2,000 ft (USNM 212833). GRAHAM COUNTY. 3 mi E Redington, south side Redfield Canyon (UA 3062); Marijilda Canyon, 4000 ft (ASU 2999); Graham Mtns, Ask Creek, 6200 ft (USNM 204364); north base Mount Tumbull, 4500 ft (USNM 214339); 1 ½ mi S, 2 mi W Maverick Mtn, Graham Mtns (MSB 163144); ¼ mi E Marijilda Campground, Graham Mtns (MSB 163142). PINAL COUNTY. 3 mi SW Oracle, ½ mi south Oracle Ranger Station (UA 3091). PIMA COUNTY. Santa Catalina Mtns (UMMZ 107659).

Additional Specimens examined but not used in the data analyses.—ARIZONA. APACHE COUNTY. 5 mi S Hawley Lake, White Mountains (NAU 886), adult skin with broken skull. GREENLEE COUNTY. Prieto Plateau [32 mi N, 2 mi W Clifton], S end Blue Range, 8000 ft (USNM 205564), partial skull.

Sylvilagus holzneri holzneri, pooled sample 8 (n = 35), south-central Arizona and north-central Sonora, Mexico.—ARIZONA. PIMA COUNTY. Santa Rita Mtns, Sawmill Canyon, 4000 ft (UA 5524); 40 mi S Tucson, Santa Rita Mtns, 4700 ft (TCWC 54); 4 mi W, 2 mi N Arivaca (MSB 163166); 1 mi W Arivaca (MSB 163165). COCHISE COUNTY. 15 mi S Fort Huachuca, Miller Canyon (MSB 163131, 163132, 163134); Huachuca Mtns, 8500 ft (USNM 58932, 58935); foothills of Huachuca Mtns, (FMNH 15026, 17678); Huachuca Mtns (USNM 58937, 58938, 58939, 58941, UMMZ 8345, 8346); Huachuca Mtns, Ramsey Canyon, 7200 ft (UMMZ 8343); Fort Huachuca (USNM 46321). SANTA CRUZ COUNTY. ½ mi S junction Gardner Canyon (UA 5815); Santa Rita Mtns, ¼ mi NE Onyx Cave, Gardner Canyon, 5450 ft (UA 13439); 7 mi N Patagonia, 4500 ft (CAS 5899); 3 mi SW Patagonia, 4000 ft (CAS 5900); 4 mi N, 2 mi W Patagonia (LSUMZ 10465); 2 ½ mi W, 2 mi N Nogales (MSB 163171, 163172, 163173, 163174, 163175); 1 mi W, 8 ½ mi N Nogales (MSB 163167); 5 ½ mi N Nogales (MSB 163168). MEXICO. SONORA. 40 km S Nogales, Casita, 3300 ft (MVZ 106140, 106141); 2 mi W Magdalena, La Mision, 2650 ft (MVZ 83340); 8 mi W Cananea (by road) on Mexico highway 2 (CSULB 5388).

Sylvilagus holzneri holzneri, pooled sample 9 (n = 28), Chiricahua Mountains, Arizona, southwestern New Mexico and northern Chihuahua, Mexico.—ARIZONA. COCHISE COUNTY. Chiricahua Mtns, Pinery Canyon, 7500 ft (USNM 247953); Pinery Canyon, 6000 ft (ANSP 13040, 13042); mouth of Bonito Canyon (USNM 66136); Rustler Park (UMMZ 77326); 1 mi N Rustler Park (UMMZ 77238); Portal, Southwestern Research Station (UA 2094); 7 mi NE Chiricahua Peak, Southwestern Research Station, 5000 ft (UA 6217); 1 mi SE Southwestern Research Station, 5000 ft (UA 6220); 8

mi NW Portal (UA 12571). NEW MEXICO. HIDALGO COUNTY. San Luis Mtns (USNM 35726, 35899); 8 mi NW Cloverdale (MSB 163179, 163180); Pasco Rd, R21W, T34S, sec 22 (MSB 5948); Clanton Canyon, Peloncillo Mtns, 22 mi S, 2 mi E Rodeo, 5700 ft (MSB 2620); Guadalupe Canyon, near monument 73 (USNM 36301); 3 mi NNW Dog Springs (MSB 163181, 163182, 163183, 163184, 163185, 163186, 163187). MEXICO. CHIHUAHUA. San Luis Mtns (USNM 157126); 2 mi S, 5 mi W San Francisco, 5500 ft (KU 73616, 73617); 6 mi N, 3 mi W San Francisco, 5,100 ft (KU 69662).

Additional specimens examined but not used in the data analyses.—NEW MEXICO. LUNA COUNTY. Carrizalillo Mountains (USNM 20336/35537), type of *S. h. rigidus*, skin with partial skull.

Sylvilagus holzneri holzneri, pooled sample 10 (n = 23), central New Mexico.—NEW MEXICO. BERNALILLO COUNTY. Sandia Mtn crest, 100 m E Stone Cabin (MSB 145827). SAN MIGUEL COUNTY. 2 mi SE Villanueva (MSB 163191, JDC 2738); 35 mi N Santa Rosa, on Conchas River (USNM 127446). CIBOLA COUNTY. Mirabal Spring, T12N, R8W, sec 26, Mount Taylor (MSB 10394). TORRANCE COUNTY. Tajique, Manzano Mtns, 10,000 ft (USNM 135755, 136567, 136568, 136569 [holotype *S. cognatus*]); Mount Manzano, Manzano Mtns (UMMZ 56073); east slope, extreme south end Manzano Mtns (USNM 130958). CATRON COUNTY. Gila Nat. Forest, 5 6/10 mi E Alma by Mineral Creek Rd (CSULB 8000); White Water Canyon, 5 mi E Glenwood (TU 2237); Tularosa Mtns, 33.90 lat. 108.52 long. (MSB 82061). SOCORRO COUNTY. Beartrap Canyon, San Mateo Mtns, 19 mi W, 20 mi S Magdalena (MSB 3093); Beartrap Canyon, San Mateo Mtns, 19 mi W, 23.3 mi S Magdalena (MSB 5128); San Mateo Mtns, US FS Rd 330, 5 1/10 mi N, 2 8/10 mi E Mt. Withington (MSB 140739); 5 mi E Monticello, Wier Tank, 7500 ft (MSB 61626). LINCOLN COUNTY. 5 mi NE Lincoln (MSB 163188); NE slope Capitan Mtns (USNM 128651). OTERO COUNTY. 1 mi N Cloudcroft, Sacramento Mtns (MSB 7189). GRANT COUNTY. Burro Mtns (USNM 157807); Gila River Valley, 17 km S Gila (MSB 157877).

Sylvilagus holzneri holzneri, pooled sample 14 (n = 23), Chihuahua, Sinaloa, and Sonora, Mexico.—CHIHUAHUA. 6 mi N Cerocahui, 6200 ft (KU 82378); near Colonia Garcia, 6400 ft (USNM 157126); 30 mi SW Gallego, Arroyo del Nido, 7000 ft (MVZ 121726); 2 mi W Minaca, 6900 ft (KU 81078); 7 mi SW Pacheco, Rio Gavilan, 5700 ft (MVZ 109679); 4 mi NW San Francisco de Borja, 5700 ft (KU 82377); 15 ½ mi NE Santa Clara, W side Sierra del Nido, 8,150 ft (MVZ 128261); Sierra del Nido, Arroyo Mesteno, 7600–8000 ft (MVZ 124792, 128260); Sierra del Nido, Canon del Alamo, 7,300 ft (MVZ 124793, 124795, 124796); 3 mi NE Temoris, 5,600 ft (KU 81080). SINALOA. 1 mi S El Cajon, 1800 ft (KU 100409, 100410); 16 km NNE Choix, 1700 ft (KU 89248, 89249). SONORA. 7 mi WNW Alamos (BYU 31742); 8 mi WNW Alamos (BYU 31743); 4 1/10 mi NW by road from Nacori Chico (MVZ 148861, 148862, 148866); 6 mi N Nacori, east slope Sierra de Mazatan, 2250 ft (MVZ 83343).

Sylvilagus holzneri holzneri, pooled sample 15 (n = 18), Chihuahua, Durango and Sinaloa, Mexico.—CHIHUAHUA. Sierra Madre near Guadalupe y Calvo, 7000 ft (USNM 95560). DURANGO. Guanacevi (AMNH 23842, 23843); mtns near Guanacevi, 7800 ft (USNM 95574, 95575); Inde, 6000 ft (USNM 95559); Rancho Bailon (AMNH 21377, 21384); 6 mi NW Rodeo, Rio Nazaz, 4200 ft (KU 62399); Sierra Madre, Cerro Prieto, 9000 ft (USNM 95576). SINALOA. 1 ½ mi N Badiraguato, 750 ft (KU 96546, 96548); 13 mi ESE Badiraguato, 800 ft (KU 96549); 20 km N, 5 km E Badiraguato, 1800 ft (KU 96544, 96545); 10 km S, 38 km E Sinaloa, 800 ft (KU 90011, 90777); 15 km N, 65 km E Sinaloa, 4700 ft (KU 90010).

Sylvilagus holzneri holzneri, pooled sample 16 (n = 22), Durango and Sinaloa, Mexico.—DURANGO. 12 km E Cosala, Santa Ana, 1300 ft (KU 90784, 90785); Coyotes (FMNH 14047); 24 mi SSE Durango, 7200 ft (MSU 3319); El Salto, 7600–8400 ft (USNM 94589, 94590, 94591); 28 mi S, 17 mi W Vicente Guerrero, 8300 ft (MSU 946, 947); 1 ½ mi S Laguna del Progreso (AMNH 146942); 5 mi W Las Adjuntas, 10,000 ft (KU 67565); 7 mi SW Las Adjuntas, 8900 ft (KU 54491); 6 mi SW El Salto, 8300–8350 ft (MSU 5714); 5 mi NE El Salto, Hacienda Coyotes (CAS 11074). SINALOA. 5 km SW Palmito, 6100 ft (KU 95021, 95022, 96776, 96777, 96778); Plomosas, 22 km E Matatan, 2500 ft (KU 92960); San Ignacio, 700 ft (KU 90781, 90782).

Sylvilagus holzneri robustus, sample 11 (n = 25), New Mexico and Texas, Guadalupe and Davis mountains area.—NEW MEXICO. EDDY COUNTY. Guadalupe Mtns, Dark Canyon, 1892 m, 32 degrees, 5.9 minutes N, 104 degrees, 45.7 minutes W (MSB 89015). TEXAS. CULBERSON COUNTY. Guadalupe Mtns, Frijole "The Bowl", 8000 ft (LSUMZ 658). JEFF DAVIS COUNTY. Fort Davis (USNM 25165); Fort Davis, 6000 ft (USNM 25164, 109095); 2 mi SW Rock Pile Park, 6100–6200 ft (ASNHC 549, 552, 553, 554); 1 mi S Rock Pile Park, scenic route 166, 6200 ft (ASNHC 544, 545); 3 mi N Rock Pile Park, scenic route 166, 5700 ft, (ASNHC 546); 1 mi W Rock Pile Park, Texas Highway Loop 166 (ASNHC 868); 5 mi E Mt. Livermore, upper Limpia Canyon, 5000 ft (UMMZ

79379); 2 mi NW Fort Davis (UMMZ 79380); 1 mi NW Fort Davis, 4800 ft (UMMZ 79381, 79382, 79383); 1 mi N Fort Davis, 4800 ft (TCWC 2515, 2516); 1 mi N Mt. Livermore (UMMZ 7986); 2 mi NW Ft. Davis, Limpia Canyon (TTU 3876); 1 mi N Fort Davis, Sawtooth area (ASNHC 1138). PRESIDIO COUNTY. 11 mi W Valentine (ASNHC 1995, 1996).

Sylvilagus holzneri robustus, pooled sample 12 (n = 12), Texas, Chisos Mountains area.—TEXAS. PRESIDIO COUNTY. 35 mi S Marfa, Lloyd's Ranch (USNM 25116). BREWSTER COUNTY. Chisos Mtns, The Basin, 5500 ft (TCWC 3655, 3656); Chisos Mtns, Emory Peak, 7500 ft (TCWC 3657); Chisos Mtns, Boot Springs, 6800 ft (TCWC 6042); Chisos Mtns, Green Gulch, 5000 ft (TCWC 6207, 6209); Chisos Mtns, 6000 ft (USNM 108695); Chisos Mtns, Pine Canyon, 4800 ft (UMMZ 90112); Big Bend, Oak Creek, 5000 ft (MVZ 80518); Dell Tank, 4 mi NE Black Gap Hq (DMNH no cat no. found); 3 mi S Government Spring (AMNH 136822).

Sylvilagus holzneri robustus, pooled sample 13 (n = 7), Mexico, mountains in northern half of Coahuila, Mexico.—MEXICO. COAHUILA. 85 mi NW Muzquiz, Hillcoat-Mesa, Santa Rosa Mtns (TMM 6026); 20 mi S, 4 mi W Ocampo, 5300 ft (KU 57768); 22 mi S, 5 mi W Ocampo, 5925 ft (KU 57771); 5 mi W Piedra Blanca, Sierra del Carmen, 5000 ft (MVZ 116978); 8 mi SW Piedra Blanca, Sierra del Carmen, 7000 ft (MVZ 116979, 116980, 116981).

Appendix II

Appendix IIa.—Character loadings for each skull character on the first 2 variates of the DFA shown in Fig. 2. Variate 1 accounted for 86.88% of the total variation and variate 2 accounted for an additional 9.79% on 4 combined pooled samples currently referred to *Sylvilagus nuttallii*, *S. holzneri*, and *S. cognatus*.

Skull character	Variate 1	Variate 2
First upper incisor length	−0.0605	0.0812
Palate length	−0.0430	−0.0903
Greatest skull length	−0.2020	1.0604
Basal length	−0.2135	0.6493
Zygomatic breadth	0.1137	0.3079
Braincase breadth	0.0388	0.1206
Nasal length	−0.1471	0.4364
Breadth across nasals	−0.1139	0.1713
Maxillary toothrow length (alveolar)	−0.0173	0.1603
Breadth across maxillary toothrows (alveolar)	−0.0482	0.1521
Postdental breadth	−0.0424	0.1412
Incisive foramen length	−0.0138	0.4025
Basioccipital length	−0.0465	0.1315
Basioccipital breadth	−0.1151	0.0994
Diastema length	−0.0684	0.3772
Rostrum depth	−0.0602	0.2984
Bulla length	0.0259	0.0601
Bullae breadth	0.0480	0.2392
Shield-bullae depth	−0.0081	0.2008
Skull depth	0.0158	0.3647
Carotid foramina breadth	−0.0250	0.1636
Infraorbital canals breadth	−0.1137	0.2672
Mandible height	−0.0043	0.5367
Mandible length	−0.1349	0.5010
Ramus height	−0.0388	0.2070
Mandibular toothrow length (alveolar)	−0.0350	0.1891
Interparietal length	−0.1415	0.0344
Interparietal breadth	−0.2585	0.0522
Frontal curvature	0.4239	0.1868
Parietal curvature	0.5935	−0.2024
Eigenvalues	9.7208	1.0959
Total variance explained (%)	86.88	9.795

Appendix IIb.—Character loadings for each skull character on the first 2 variates of the DFA shown in Fig. 3. Variate 1 accounted for 43.59% of the total variation and variate 2 accounted for an additional 29.17% on pooled samples 1–5 currently referred to *Sylvilagus nuttallii*.

Skull character	Variate 1	Variate 2
First upper incisor length	0.0832	0.0008
Palate length	0.0823	0.0324
Greatest skull length	0.7768	0.1146
Basal length	0.5609	0.1303
Zygomatic breadth	0.4675	0.0022
Braincase breadth	0.2565	0.0003
Nasal length	0.5028	0.0854
Breadth across nasals	0.1647	0.0778
Maxillary toothrow length (alveolar)	0.1486	0.1761
Breadth across maxillary toothrows (alveolar)	0.2513	0.1205
Postdental breadth	0.1224	0.0995
Incisive foramen length	0.2986	-0.0394
Basioccipital length	0.0308	0.1411
Basioccipital breadth	0.0817	0.1286
Diastema length	0.3349	−0.0697
Rostrum depth	0.1389	0.0721
Bulla length	−0.0908	0.0569
Bullae breadth	0.0106	0.1026
Shield-bullae depth	0.0276	0.0135
Skull depth	0.2857	0.0573
Carotid foramina breadth	0.1708	0.0024
Infraorbital canals breadth	0.1876	−0.0075
Mandible height	0.3550	0.1710
Mandible length	0.3269	0.2242
Ramus height	0.0933	0.1254
Mandibular toothrow length (alveolar)	0.1323	0.1580
Eigenvalues	4.0293	2.6962
Total variance explained (%)	43.59	29.17

Appendix IIc.—Character loadings for each skull character on the first 2 variates of the DFA shown in Fig. 4. Variate 1 accounted for 58.91% of the total variation and variate 2 accounted for an additional 22.48% on pooled samples 6–9 currently referred to *Sylvilagus holzneri* and sample 10 to *S. cognatus*.

Skull character	Variate 1	Variate 2
First upper incisor length	0.1113	−0.1188
Palate length	−0.0450	0.0193
Greatest skull length	1.0805	0.0327
Basal length	0.8382	−0.3639
Zygomatic breadth	0.3321	0.1616
Braincase breadth	0.1235	0.1692
Nasal length	0.4075	−0.0136
Breadth across nasals	0.1647	0.0581
Maxillary toothrow length (alveolar)	0.1830	−0.0857
Breadth across maxillary toothrows (alveolar)	0.1691	0.0115
Postdental breadth	0.1053	0.1183
Incisive foramen length	0.4028	−0.0555
Basioccipital length	0.1075	−0.0139
Basioccipital breadth	0.0459	0.1054
Diastema length	0.3983	0.0718
Rostrum depth	0.2746	0.0337
Bulla length	0.1316	−0.1968
Bullae breadth	0.2006	−0.0329
Shield-bullae depth	0.1866	−0.0019
Skull depth	0.3398	0.0605
Carotid foramina breadth	0.1193	0.1175
Infraorbital canals breadth	0.2451	−0.0198
Mandible height	0.6777	−0.1056
Mandible length	0.5349	−0.0317
Ramus height	0.2539	−0.0130
Mandibular toothrow length (alveolar)	0.1832	−0.0234
Eigenvalues	2.1091	0.8047
Total variance explained (%)	58.91	22.48

Appendix IId.—Character loadings for each skull character on the first 2 variates of the DFA shown in Fig. 5. Variate 1 accounted for 46.73% of the total variation and variate 2 accounted for an additional 25.55% on pooled samples 8–13 currently referred to *Sylvilagus holzneri* (samples 8–9), *S. cognatus* (sample 10), and *S. robustus* (samples 11–13).

Skull character	Variate 1	Variate 2
First upper incisor length	−0.0546	−0.1224
Palate length	−0.0400	0.0264
Greatest skull length	0.4376	−0.0552
Basal length	0.2092	−0.3769
Zygomatic breadth	0.1255	0.1082
Braincase breadth	0.1457	0.1364
Nasal length	−0.0141	−0.0262
Breadth across nasals	0.0100	0.0494
Maxillary toothrow length (alveolar)	0.0743	−0.1086
Breadth across maxillary toothrows (alveolar)	0.1068	−0.0208
Postdental breadth	0.1080	0.0719
Incisive foramen length	−0.0568	−0.0616
Basioccipital length	0.1163	−0.0231
Basioccipital breadth	−0.0272	0.0983
Diastema length	0.0423	0.0518
Rostrum depth	0.0657	0.0157
Bulla length	0.1787	−0.2173
Bullae breadth	0.3598	−0.1005
Shield-bullae depth	0.3109	−0.0473
Skull depth	0.2571	−0.0103
Carotid foramina breadth	0.0366	0.1032
Infraorbital canals breadth	−0.0389	−0.0269
Mandible height	0.1640	−0.1652
Mandible length	0.0111	−0.0694
Ramus height	−0.0189	−0.0286
Mandibular toothrow length (alveolar)	0.0806	−0.0535
Eigenvalues	1.7219	0.9414
Total variance explained (%)	46.73	25.55

Appendix IIe.—Character loadings for each skull character on the first 2 variates of the DFA shown in Fig. 6. Variate 1 accounted for 74.62% of the total variation and variate 2 accounted for an additional 12.84% on pooled samples 8–9 and 14–16 currently referred to *Sylvilagus holzneri* from southern Arizona (8), southern New Mexico (9), and Sierra Madre Occidental of Mexico (14–16).

Skull character	Variate 1	Variate 2
First upper incisor length	−0.0654	−0.1820
Palate length	0.0145	0.0368
Greatest skull length	0.3456	0.2218
Basal length	0.3223	0.0895
Zygomatic breadth	0.0763	0.1353
Braincase breadth	−0.0767	0.1071
Nasal length	−0.0074	−0.3052
Breadth across nasals	0.1357	0.0918
Maxillary toothrow length (alveolar)	0.1122	−0.1009
Breadth across maxillary toothrows (alveolar)	0.1735	−0.0522
Postdental breadth	0.1460	−0.0023
Incisive foramen length	0.0120	−0.0555
Basioccipital length	0.0419	0.0916
Basioccipital breadth	0.0313	0.0737
Diastema length	0.0518	0.1033
Rostrum depth	0.1260	0.1579
Bulla length	−0.0709	−0.1605
Bullae breadth	0.0828	−0.1230
Shield-bullae depth	0.0769	−0.0179
Skull depth	0.1146	0.1501
Carotid foramina breadth	0.0505	0.1762
Infraorbital canals breadth	−0.0286	0.0298
Mandible height	0.1445	−0.0118
Mandible length	0.1794	0.0664
Ramus height	0.0010	0.0526
Mandibular toothrow length (alveolar)	0.0592	−0.0790
Eigenvalues	2.7917	0.4804
Total variance explained (%)	74.62	12.84

Appendix IIf.—Character loadings for each skull character on the first 2 variates of the DFA shown in Fig. 8. Variate 1 accounted for 40.44% of the total variation and variate 2 accounted for an additional 30.34% on pooled samples 2–5 currently referred to *Sylvilagus nuttallii* and the topotypical sample of *S. n. grangeri* from South Dakota.

Skull character	Variate 1	Variate 2
First upper incisor length	−0.0212	0.0676
Palate length	−0.0586	0.0476
Greatest skull length	−0.1704	0.3137
Basal length	−0.1768	0.3782
Zygomatic breadth	−0.0611	0.2165
Braincase breadth	−0.0330	0.0008
Nasal length	−0.0563	0.1406
Breadth across nasals	−0.0228	−0.0155
Maxillary toothrow length (alveolar)	−0.1902	0.0292
Breadth across maxillary toothrows (alveolar)	−0.1593	0.1112
Postdental breadth	−0.0695	0.0628
Incisive foramen length	0.0159	0.0801
Basioccipital length	−0.0972	0.0383
Basioccipital breadth	−0.1171	0.1358
Diastema length	0.0559	0.2652
Rostrum depth	−0.1034	−0.0540
Bulla length	−0.0196	−0.1555
Bullae breadth	−0.1088	−0.0735
Shield-bullae depth	−0.0088	−0.0817
Skull depth	−0.0245	0.0771
Carotid foramina breadth	−0.0181	0.1291
Infraorbital canals breadth	0.0041	0.0628
Mandible height	−0.1123	0.1757
Mandible length	−0.2499	0.1835
Ramus height	−0.1347	0.0102
Mandibular toothrow length (alveolar)	−0.1637	0.0146
Eigenvalues	3.3900	2.5433
Total variance explained (%)	40.44	30.34

Appendix III.—Table of Measurements (cont.)

Skull features measured (mm) on cottontails in16 pooled samples. The 4 additional skull features were later incorporated in some samples. Statistics are mean, standard deviation and range. Sample size (n) for interparietal length is given first, followed by interparietal breadth, frontal curvature, and parietal curvature.

	S. nuttalli nuttallii		*S. nuttallii pinetis*	
	Sample 1 ($n = 21$)		Sample 2 ($n = 19$)	
Skull features	Mean ± *SD*	Range	Mean ± *SD*	Range
First upper incisor length	6.54 ± 0.56	5.75–8.05	6.81 ± 0.41	6.25–7.70
Palate length	5.36 ± 0.37	4.50–6.00	5.50 ± 0.29	5.15–6.10
Greatest skull length	65.68 ± 1.12	64.15–68.40	68.02 ± 1.37	65.35–70.60
Basal length	52.75 ± 1.12	51.20–55.75	54.16 ± 1.26	51.30–56.05
Zygomatic breadth	33.38 ± 0.83	31.65–35.10	35.04 ± 0.68	33.60–36.10
Braincase breadth	25.53 ± 0.77	24.25–27.15	26.54 ± 0.54	25.50–27.35
Nasal length	28.48 ± 1.40	25.85–30.90	30.03 ± 1.07	27.25–31.50
Breadth across nasals	13.31 ± 0.71	11.85–14.45	13.68 ± 0.48	12.70–14.50
Maxillary toothrow length	12.53 ± 0.31	12.00–13.30	12.35 ± 0.32	11.45–12.75
Maxillary toothrows breadth	17.84 ± 0.53	16.75–19.10	18.23 ± 0.43	17.60–19.00
Postdental breadth	7.52 ± 0.37	6.80–8.20	7.55 ± 0.30	7.00–8.00
Incisive foramen length	16.31 ± 0.67	15.30–17.50	17.60 ± 0.56	16.50–18.75
Basioccipital length	8.34 ± 0.39	7.70–9.20	7.85 ± 0.32	7.30–8.35
Basioccipital breadth	8.14 ± 0.44	7.35–9.10	7.83 ± 0.43	7.10–8.65
Diastema length	17.82 ± 0.61	16.75–18.85	19.25 ± 0.77	17.60–20.65
Rostrum depth	12.17 ± 0.50	11.10–13.10	12.44 ± 0.48	11.60–13.50
Bulla length	11.58 ± 0.79	10.75–13.40	11.11 ± 0.33	10.45–11.75
Bullae breadth	25.28 ± 0.72	23.90–26.60	24.95 ± 0.65	23.75–26.25
Shield-bullae depth	21.06 ± 0.70	20.05–22.60	21.17 ± 0.39	20.55–21.85
Skull depth	29.65 ± 0.59	28.70–30.80	30.51 ± 0.48	29.40–31.25
Carotid foramina breadth	8.97 ± 0.48	8.40–10.55	9.53 ± 0.42	8.75–10.25
Infraorbital canals breadth	16.21 ± 0.55	15.55–17.55	16.94 ± 0.65	15.50–18.25
Mandible height	31.61 ± 1.13	29.50–33.20	32.19 ± 0.92	30.40–34.20
Mandible length	32.33 ± 0.91	30.60–34.20	32.52 ± 0.66	31.20–33.80
Ramus height	9.65 ± 0.52	9.00–10.90	9.48 ± 0.35	8.75–10.05
Mandibular toothrow length	12.90 ± 0.29	12.50–13.75	12.74 ± 0.34	12.10–13.50
Additional skull features	$n = 14, 14, 11, 11$		$n = 15, 15, 15, 15$	
Interparietal length	2.86 ± 0.50	2.00–4.00	3.50 ± 0.58	2.70–4.60
Interparietal breadth	7.37 ± 0.54	6.60–8.30	8.27 ± 0.83	7.05–10.25
Frontal curvature	7.04 ± 1.06	5.75–9.75	8.15 ± 0.66	7.20–9.30
Parietal curvature	21.69 ± 1.20	20.10–23.75	23.50 ± 0.87	22.00–25.10

Appendix III.—Extended.

S. nuttallii grangeri					
Sample 3 ($n = 15$)		Sample 4 ($n = 22$)		Sample 5 ($n = 28$)	
Mean ± *SD*	Range	Mean ± *SD*	Range	Mean ± *SD*	Range
6.64 ± 0.46	5.90–7.50	6.96 ± 0.33	6.50–7.80	6.96 ± 0.47	5.95–8.15
5.45 ± 0.49	4.40–6.10	5.81 ± 0.30	5.40–6.40	5.75 ± 0.32	5.20–6.40
68.53 ± 1.72	66.30–72.00	69.57 ± 1.36	66.85–71.80	69.85 ± 2.30	65.20–73.50
54.38 ± 1.86	51.10–57.45	55.33 ± 1.94	51.60–58.80	55.91 ± 2.51	50.45–59.65
34.90 ± 0.73	33.90–36.50	35.56 ± 0.84	34.05–37.75	35.99 ± 0.92	34.40–37.80
26.84 ± 0.66	25.95–28.50	26.96 ± 0.62	26.15–28.40	26.87 ± 0.67	25.80–28.75
30.83 ± 0.80	29.75–32.75	31.10 ± 0.87	29.50–32.65	31.19 ± 1.69	27.70–33.50
14.37 ± 1.14	12.40–16.80	14.43 ± 0.61	13.05–15.60	14.06 ± 0.91	11.85–15.50
13.04 ± 0.41	12.10–13.60	13.40 ± 0.38	12.60–14.00	13.26 ± 0.45	12.20–14.10
18.41 ± 0.40	17.35–19.05	19.17 ± 0.43	18.45–19.85	19.12 ± 0.62	18.10–20.20
7.87 ± 0.45	7.05–8.40	8.17 ± 0.50	7.40–9.20	8.15 ± 0.42	7.40–9.00
17.78 ± 0.80	16.40–19.30	17.81 ± 0.73	16.55–18.85	17.96 ± 0.98	16.00–19.90
8.34 ± 0.33	7.70–8.95	8.52 ± 0.43	7.80–9.30	8.48 ± 0.50	7.35–9.25
8.20 ± 0.37	7.55–8.90	8.23 ± 0.57	6.90–9.20	8.77 ± 0.41	7.95–9.75
18.80 ± 0.67	17.85–20.05	19.15 ± 0.86	17.50–20.65	19.82 ± 1.04	17.55–21.55
12.96 ± 0.48	12.30–14.10	13.07 ± 0.43	12.30–13.65	12.82 ± 0.72	11.30–13.80
11.66 ± 0.43	11.10–12.55	11.45 ± 0.41	10.55–12.35	10.94 ± 0.44	10.00–11.90
25.52 ± 0.90	23.85–26.90	25.50 ± 0.83	23.60–27.10	25.26 ± 0.91	23.80–26.65
21.45 ± 0.67	20.55–22.65	21.39 ± 0.45	20.50–22.10	21.12 ± 0.60	19.60–22.10
31.12 ± 0.70	29.95–31.95	31.09 ± 0.60	29.90–32.25	31.24 ± 0.88	29.35–33.00
9.29 ± 0.32	8.45–9.70	9.71 ± 0.59	8.10–10.95	9.93 ± 0.46	8.90–10.75
16.70 ± 0.66	15.85–18.55	17.32 ± 0.56	16.35–18.60	17.10 ± 0.72	15.00–18.45
32.89 ± 0.92	31.35–34.50	33.40 ± 0.90	31.40–36.05	33.52 ± 1.46	30.60–36.70
33.09 ± 1.07	31.65–35.65	33.87 ± 0.99	32.15–35.60	34.12 ± 1.36	30.75–36.20
9.91 ± 0.32	9.55–10.50	10.29 ± 0.32	9.75–11.00	10.03 ± 0.46	9.30–11.20
13.26 ± 0.26	12.90–13.80	13.78 ± 0.43	12.90–14.60	13.45 ± 0.42	12.70–14.50
$n = 10, 10, 10, 10$		$n = 16, 16, 17, 17$		$n = 24, 24, 24, 24$	
4.35 ± 0.36	3.70–4.80	3.71 ± 0.74	1.70–5.30	3.46 ± 0.52	2.80–4.50
8.30 ± 0.95	6.50–10.00	7.58 ± 0.85	6.20–9.80	8.02 ± 0.94	6.70–10.40
7.39 ± 0.80	6.30–8.70	7.33 ± 0.77	5.45–8.60	7.39 ± 0.78	5.50–8.80
23.15 ± 0.76	22.20–24.60	23.27 ± 1.10	21.25–25.45	23.54 ± 0.90	22.20–25.50

Appendix III.—Table of Measurements (cont.)

Skull features measured (mm) on cottontails in 16 pooled samples. The 4 additional skull features were later incorporated in some samples. Statistics are Mean, *SD*, and Range.

	S. holzneri hesperius		*S. holzneri holzneri*	
	Sample 6 ($n = 28$)		Sample 7 ($n = 24$)	
Skull features	Mean ± *SD*	Range	Mean ± *SD*	Range
First upper incisor length	7.05 ± 0.33	6.30–7.65	7.22 ± 0.49	6.40–8.35
Palate length	6.02 ± 0.44	4.90–6.80	5.88 ± 0.51	4.65–6.80
Greatest skull length	67.83 ± 1.59	65.25–71.10	71.58 ± 1.73	69.00–75.40
Basal length	54.72 ± 1.41	52.50–57.45	57.71 ± 1.31	56.25–60.35
Zygomatic breadth	33.91 ± 0.83	32.40–35.60	34.87 ± 0.62	33.95–36.35
Braincase breadth	26.20 ± 0.82	25.00–27.80	26.55 ± 0.70	25.30–27.95
Nasal length	30.75 ± 1.35	27.30–32.90	32.30 ± 1.46	29.45–34.80
Breadth across nasals	14.52 ± 0.61	13.20–16.10	15.01 ± 0.65	14.05–16.55
Maxillary toothrow length	12.77 ± 0.45	11.80–13.70	13.30 ± 0.37	12.75–14.45
Maxillary toothrows breadth	18.69 ± 0.66	17.40–20.20	19.15 ± 0.52	18.25–20.00
Postdental breadth	7.96 ± 0.45	7.00–8.85	8.01 ± 0.41	7.15–8.75
Incisive foramen length	16.97 ± 0.64	16.00–18.25	18.33 ± 0.86	16.55–20.15
Basioccipital length	8.46 ± 0.38	7.75–9.30	8.92 ± 0.42	7.75–9.85
Basioccipital breadth	8.90 ± 0.61	8.25–11.10	8.90 ± 0.44	8.05–9.60
Diastema length	18.84 ± 0.73	17.50–20.55	20.17 ± 0.80	18.75–21.65
Rostrum depth	12.66 ± 0.62	11.45–14.05	13.55 ± 0.62	12.45–15.00
Bulla length	10.93 ± 0.43	10.10–11.70	11.38 ± 0.43	10.45–12.40
Bullae breadth	24.70 ± 1.06	22.90–26.80	25.18 ± 0.67	24.05–26.65
Shield-bullae depth	20.85 ± 0.43	19.70–21.60	21.64 ± 0.54	20.30–22.50
Skull depth	30.18 ± 0.78	28.65–32.00	31.04 ± 0.68	29.30–32.45
Carotid foramina breadth	9.56 ± 0.50	8.45–10.50	9.81 ± 0.58	8.75–11.35
Infraorbital canals breadth	17.25 ± 0.67	16.05–18.70	18.01 ± 0.54	16.85–19.55
Mandible height	31.81 ± 1.20	29.50–34.00	33.78 ± 1.28	31.35–36.10
Mandible length	33.25 ± 1.08	30.80–34.90	34.69 ± 1.02	32.30–36.45
Ramus height	9.79 ± 0.36	9.10–10.70	10.39 ± 0.52	9.50–11.40
Mandibular toothrow length	13.17 ± 0.53	11.95–14.15	13.60 ± 0.36	12.80–14.40
Additional skull features	$n = 23, 23, 24, 24$		$n = 9, 9, 9, 9$	
Interparietal length	4.46 ± 0.76	3.00–6.00	4.36 ± 0.63	3.10–5.10
Interparietal breadth	9.78 ± 1.28	7.30–13.00	9.66 ± 0.98	8.00–11.30
Frontal curvature	4.34 ± 0.83	2.15–5.50	5.45 ± 0.85	3.80–6.80
Parietal curvature	18.87 ± 0.92	16.70–20.30	20.11 ± 1.28	17.30–21.95

Appendix III.—Extended.

S. holzneri holzneri					
Sample 8 ($n = 35$)		Sample 9 ($n = 28$)		Sample 10 ($n = 23$)	
Mean ± *SD*	Range	Mean ± *SD*	Range	Mean ± *SD*	Range
7.62 ± 0.53	6.20–8.80	7.38 ± 0.49	6.25–8.85	7.26 ± 0.43	6.30–8.45
5.80 ± 0.52	4.95–7.55	5.91 ± 0.42	5.10–6.70	5.85 ± 0.43	4.90–6.80
71.59 ± 1.98	67.20–76.55	71.93 ± 1.94	68.45–75.55	71.66 ± 1.59	67.30–74.20
57.86 ± 1.58	54.25–61.45	57.98 ± 1.77	55.00–61.40	56.80 ± 1.69	53.55–59.70
34.91 ± 0.95	33.15–36.35	35.20 ± 0.87	33.30–36.85	35.33 ± 0.59	34.10–36.40
26.45 ± 0.82	25.15–28.35	26.68 ± 0.75	25.40–28.10	26.93 ± 0.70	25.10–28.10
32.12 ± 1.59	29.00–36.60	32.45 ± 1.09	30.40–35.05	32.04 ± 1.72	28.40–35.70
14.94 ± 0.62	13.45–16.30	15.30 ± 0.72	14.00–17.15	15.07 ± 0.77	13.40–16.70
13.56 ± 0.62	12.70–16.00	13.39 ± 0.53	12.35–14.40	13.30 ± 0.41	12.50–14.05
19.32 ± 0.55	17.85–20.80	19.29 ± 0.70	18.25–20.50	19.33 ± 0.46	18.55–20.15
8.31 ± 0.51	7.20–9.65	8.25 ± 0.33	7.60–8.95	8.60 ± 0.52	7.85–9.80
18.59 ± 0.87	16.40–20.40	18.31 ± 0.84	16.65–19.90	18.42 ± 0.80	16.85–19.60
8.82 ± 0.46	7.85–9.85	8.93 ± 0.60	7.40–10.25	8.78 ± 0.43	7.55–9.45
8.91 ± 0.54	7.90–10.15	9.16 ± 0.54	7.45–10.10	9.18 ± 0.47	8.20–10.00
20.23 ± 0.75	18.25–21.50	20.31 ± 0.90	18.70–21.65	20.39 ± 0.88	18.70–22.35
13.59 ± 0.65	12.55–15.30	13.77 ± 0.56	12.80–15.00	13.63 ± 0.82	11.90–14.95
11.63 ± 0.57	10.65–12.55	11.33 ± 0.49	10.55–12.45	11.09 ± 0.70	9.80–12.55
25.48 ± 0.78	24.20–27.00	25.40 ± 0.97	23.40–27.15	25.37 ± 1.15	22.65–27.25
21.54 ± 0.60	19.95–22.85	21.49 ± 0.65	20.35–23.10	21.56 ± 0.44	20.40–22.40
31.34 ± 0.95	29.40–34.75	31.48 ± 0.78	29.65–33.40	31.43 ± 0.86	29.20–32.90
9.78 ± 0.42	8.70–10.40	10.17 ± 0.54	8.70–11.70	10.05 ± 0.48	9.15–10.70
18.16 ± 0.63	16.70–20.00	18.14 ± 0.80	16.40–19.95	18.08 ± 0.72	16.45–19.15
34.26 ± 1.16	32.25–36.70	34.46 ± 1.01	31.80–36.55	33.86 ± 0.97	31.60–36.30
35.14 ± 1.03	33.45–38.35	35.33 ± 1.19	33.25–38.30	34.96 ± 0.81	33.40–36.25
10.67 ± 0.45	9.50–11.60	10.85 ± 0.43	9.95–11.80	10.54 ± 0.52	9.80–11.50
13.89 ± 0.55	12.55–14.90	13.81 ± 0.55	12.80–14.85	13.80 ± 0.38	13.10–14.60
$n = 6, 6, 18, 18$		$n = 7, 7, 16, 16$		$n = 18, 18, 19, 19$	
4.28 ± 0.58	3.30–4.90	4.55 ± 0.61	3.50–5.00	4.46 ± 0.62	3.55–5.60
8.90 ± 0.50	8.00–9.55	9.17 ± 0.65	8.50–10.10	9.41 ± 1.45	6.30–12.65
5.31 ± 0.95	3.80–7.10	5.00 ± 1.10	3.10–6.90	5.38 ± 0.81	3.40–6.40
19.90 ± 1.24	17.85–22.25	19.95 ± 1.83	15.80–22.90	20.29 ± 1.46	17.80–22.35

Appendix III.—Table of Measurements (cont.)
Skull features measured (mm) on cottontails in16 pooled samples. Statistics are Mean, *SD*, and Range.

	S. holzneri robustus			
	Sample 11 ($n = 25$)		Sample 12 ($n = 12$)	
Skull features	Mean ± *SD*	Range	Mean ± *SD*	Range
First upper incisor length	7.22 ± 0.55	6.25–8.30	7.56 ± 0.43	6.70–8.20
Palate length	5.70 ± 0.52	5.00–7.40	5.98 ± 0.39	5.15–6.45
Greatest skull length	72.44 ± 1.71	69.25–75.90	74.26 ± 2.49	69.80–78.75
Basal length	57.71 ± 1.85	52.50–60.50	59.48 ± 2.29	54.55–63.35
Zygomatic breadth	35.44 ± 0.75	34.10–36.90	35.94 ± 0.80	34.50–37.50
Braincase breadth	26.84 ± 0.53	25.75–27.70	27.47 ± 0.66	26.60–28.50
Nasal length	32.28 ± 1.27	28.45–34.40	32.68 ± 1.67	30.35–35.95
Breadth across nasals	15.14 ± 0.79	13.45–16.45	15.25 ± 0.73	14.20–16.45
Maxillary toothrow length	13.66 ± 0.41	12.85–14.60	13.78 ± 0.48	13.10–14.70
Maxillary toothrows breadth	19.59 ± 0.53	18.40–20.50	19.82 ± 0.66	19.05–21.40
Postdental breadth	8.62 ± 0.47	7.60–9.70	8.79 ± 0.43	7.85–9.35
Incisive foramen length	18.08 ± 0.78	16.10–19.15	18.67 ± 0.97	17.35–20.40
Basioccipital length	9.12 ± 0.49	8.00–10.05	9.21 ± 0.59	8.45–10.40
Basioccipital breadth	8.97 ± 0.54	7.50–9.70	9.02 ± 0.37	8.40–9.80
Diastema length	20.11 ± 0.98	17.60–22.00	21.02 ± 1.04	19.85–22.90
Rostrum depth	13.72 ± 0.54	12.85–14.90	14.15 ± 0.61	13.20–14.85
Bulla length	11.75 ± 0.37	11.10–12.65	12.28 ± 0.50	11.30–13.05
Bullae breadth	26.27 ± 1.16	23.75–28.50	26.91 ± 0.75	25.85–28.35
Shield-bullae depth	22.28 ± 0.49	21.40–23.40	22.72 ± 0.63	21.50–23.70
Skull depth	32.21 ± 0.68	31.20–33.90	32.20 ± 0.58	31.25–33.30
Carotid foramina breadth	10.11 ± 0.52	8.95–11.00	10.00 ± 0.45	9.15–10.65
Infraorbital canals breadth	17.96 ± 0.82	16.45–20.20	18.26 ± 0.62	17.15–19.10
Mandible height	34.69 ± 1.23	32.25–37.10	35.22 ± 1.47	32.55–37.65
Mandible length	35.17 ± 1.14	33.10–38.00	35.62 ± 1.33	33.30–38.60
Ramus height	10.67 ± 0.40	9.80–11.45	10.74 ± 0.59	10.05–11.65
Mandibular toothrow length	14.07 ± 0.61	13.00–16.30	14.19 ± 0.35	13.65–14.80

Appendix III.—Extended.

S. holzneri robustus		*S. holzneri holzneri*			
Sample 13 ($n = 7$)		Sample 14 ($n = 23$)		Sample 15 ($n = 18$)	
Mean ± *SD*	Range	Mean ± *SD*	Range	Mean ± *SD*	Range
7.18 ± 0.71	6.10–8.05	7.16 ± 0.50	6.20–8.05	7.26 ± 0.47	6.65–8.60
5.45 ± 0.38	4.95–6.15	5.83 ± 0.50	4.80–7.05	5.94 ± 0.52	5.10–6.95
72.42 ± 3.44	68.10–77.55	72.02 ± 3.22	66.10–76.90	71.97 ± 2.41	66.90–77.15
58.29 ± 2.65	55.00–62.35	58.02 ± 2.80	52.20–63.10	58.25 ± 2.36	53.30–63.10
34.53 ± 1.41	32.10–35.95	35.10 ± 1.41	32.45–38.00	34.97 ± 1.28	33.10–37.15
26.86 ± 0.89	25.60–28.20	26.59 ± 1.02	25.10–28.40	26.28 ± 1.08	24.80–28.30
30.95 ± 2.22	26.65–33.45	32.34 ± 1.66	29.55–35.35	31.34 ± 1.73	27.60–34.90
14.94 ± 0.80	13.75–15.95	14.86 ± 0.90	13.60–16.90	15.11 ± 0.68	14.10–16.40
13.38 ± 0.49	12.80–14.30	13.39 ± 0.46	12.45–14.35	13.70 ± 0.38	13.00–14.30
19.22 ± 0.64	18.40–20.10	19.28 ± 0.86	17.50–20.65	19.70 ± 0.61	18.50–20.90
8.34 ± 0.60	7.65–9.25	8.33 ± 0.38	7.70–9.10	8.53 ± 0.38	7.80–9.15
18.36 ± 1.03	17.35–20.25	18.53 ± 1.18	16.25–21.30	18.34 ± 0.86	16.55–20.10
9.34 ± 0.47	8.80–9.85	9.00 ± 0.58	7.75–10.10	8.87 ± 0.42	8.30–10.00
8.97 ± 0.65	7.80–9.75	8.90 ± 0.58	7.75–9.80	8.94 ± 0.45	8.30–9.65
20.27 ± 1.01	19.35–21.70	20.31 ± 1.39	17.30–22.70	20.03 ± 1.00	17.80–21.75
13.71 ± 0.63	12.85–14.55	13.92 ± 0.71	12.80–15.40	13.85 ± 0.71	12.55–15.50
11.81 ± 0.74	10.70–12.65	11.30 ± 0.54	10.30–12.60	11.21 ± 0.53	10.05–12.35
26.04 ± 1.61	23.00–27.70	25.42 ± 1.19	22.80–26.90	25.95 ± 1.02	24.35–27.30
22.08 ± 1.17	20.40–23.60	21.59 ± 0.72	20.20–22.75	21.70 ± 0.66	20.80–22.80
31.60 ± 0.98	30.45–33.30	31.55 ± 1.42	29.20–34.30	31.31 ± 0.96	29.45–33.20
10.19 ± 0.28	9.65–10.50	10.03 ± 0.78	8.60–11.50	10.05 ± 0.46	9.20–10.90
17.87 ± 0.62	17.35–19.05	18.17 ± 0.86	16.65–19.80	17.96 ± 0.89	15.95–19.10
34.01 ± 1.65	31.80–35.70	34.17 ± 1.54	31.75–37.15	34.41 ± 1.60	31.45–36.75
34.74 ± 1.69	31.95–36.50	35.13 ± 1.47	33.10–38.10	35.14 ± 1.59	31.80–37.40
10.52 ± 0.47	9.90–11.10	10.73 ± 0.59	9.85–12.00	10.82 ± 0.59	9.85–12.30
13.82 ± 0.64	13.10–14.55	13.69 ± 0.65	12.80–14.85	13.90 ± 0.50	13.10–14.60

Appendix III.—Skull features measured (mm) on cottontails in16 pooled samples. Statistics are Mean, *SD*, and Range.

	S. holzneri holzneri	
	Sample 16 ($n = 22$)	
Skull features	Mean ± *SD*	Range
First upper incisor length	7.22 ± 0.55	6.10–8.55
Palate length	5.92 ± 0.49	4.95–6.80
Greatest skull length	73.64 ± 1.85	70.55–78.20
Basal length	59.56 ± 1.77	56.85–64.20
Zygomatic breadth	35.53 ± 0.96	33.35–37.00
Braincase breadth	26.32 ± 1.01	23.90–27.75
Nasal length	32.64 ± 1.39	30.30–35.65
Breadth across nasals	15.79 ± 0.94	14.60–18.00
Maxillary toothrow length	13.98 ± 0.38	13.40–14.80
Maxillary toothrows breadth	20.05 ± 0.59	19.15–21.00
Postdental breadth	8.99 ± 0.49	7.75–10.05
Incisive foramen length	18.64 ± 1.01	17.05–21.20
Basioccipital length	9.09 ± 0.54	8.10–10.35
Basioccipital breadth	9.23 ± 0.52	8.30–10.35
Diastema length	20.68 ± 0.94	19.15–23.30
Rostrum depth	14.30 ± 0.45	13.60–15.40
Bulla length	11.20 ± 0.50	10.55–12.30
Bullae breadth	25.67 ± 0.75	23.80–27.20
Shield-bullae depth	21.89 ± 0.64	20.30–22.60
Skull depth	32.13 ± 0.81	30.65–33.85
Carotid foramina breadth	10.19 ± 0.62	9.25–11.80
Infraorbital canals breadth	18.11 ± 0.61	16.95–19.20
Mandible height	35.07 ± 1.02	33.10–37.05
Mandible length	36.22 ± 1.12	34.40–38.00
Ramus height	10.73 ± 0.43	9.95–11.60
Mandibular toothrow length	14.14 ± 0.44	13.50–15.00