

A propaedeutic to the taxonomy of the Eastern cottontail rabbit (Lagomorpha: Leporidae: *Sylvilagus floridanus*) from Central America

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To ascertain the taxonomic identity of cottontail rabbits from Costa Rica, we examined the holotypes of all the taxa of *Sylvilagus* currently subsumed within the *Sylvilagus floridanus* species complex as defined by Philip Hershkovitz. The almost 40 named taxa contained in *S. floridanus* are widespread from northeastern to north-central North America in the north (including southern Canada), through Central America to northwestern South America. Here, we examine Mesoamerican taxa in the complex, on the basis of holotypes, and test the hypothesis of conspecificity among them. Our examination of the holotypes, along with uni- and multivariate assessments of mensural variation as well as character variation in existing and newly acquired specimens from Costa Rica, indicate that *S. floridanus* (J. A. Allen, 1890) *sensu stricto* is restricted to North America, with its southern limit at the Isthmus of Tehuantepec. *Sylvilagus yucatanicus* (Miller, 1899) is limited to the Yucatan Peninsula. *Sylvilagus hondurensis* Goldman, 1932 is retained as a species, with *S. h. costaricensis* Harris, 1933 as a junior synonym. Costa Rica is revealed to have three described species: *S. gabbi* (J. A. Allen, 1877), *S. hondurensis costaricensis*, and *S. dicei* Harris, 1932. However, there are indications that this taxonomic scheme may in fact underrepresent the existing number of biological species of *Sylvilagus* present in that country.

Para cerciorarnos de la identidad taxonómica de las especies de conejos silvestres en Costa Rica, examinamos los holotipos de todos los taxones de *Sylvilagus* descritos en el grupo *Sylvilagus floridanus* tal como fuera delimitado por Philip Hershkovitz. El grupo comprende cerca de 40 taxones nombrados, ampliamente distribuidos a partir del norte entre el noreste y noroeste de Norteamérica (incluyendo el sur del Canadá), a través de Centroamérica, hasta el noroeste de Sudamérica. En la presente obra, examinamos los taxones Centroamericanos, a partir de holotipos, del complejo *S. floridanus* para así poner a prueba la hipótesis que están todos comprendido en una sola especie. Nuestro examen de estos holotipos, así como análisis de caracteres, y análisis univariado y multivariado de medidas tanto de especímenes en museos como especímenes resultado a partir de nuevos muestreos en Costa Rica, sugieren que *S. floridanus* (J. A. Allen, 1890) *sensu stricto* debe restringirse al norte del Istmo de Tehuantepec. Restringimos *Sylvilagus yucatanicus* (Miller, 1899) a la Península de Yucatán. *Sylvilagus hondurensis* Goldman, 1932 es una especie válida, con *S. h. costaricensis* Harris, 1933 como subespecie incluida. En Costa Rica, distinguimos tres especies descritas: *S. gabbi* (J. A. Allen, 1877), *S. hondurensis costaricensis* y *S. dicei* Harris, 1932. Sin embargo, existen indicios que esta hipótesis taxonómica pueda de hecho infravalorar el actual número de especies biológicas de *Sylvilagus* presentes en ese país.

Keywords: Biogeography; evolution; morphological homogeneity; species limits, taxonomy.

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Introduction

Because of their conservative morphology, lagomorphs are notoriously difficult, to dissemble into biologically realistic evolutionary entities. [Bachman \(1837:282\)](#) notably stated that, “many of the species so greatly resemble each other in many particulars that the student in natural history has sometimes been greatly perplexed in deciding on the exact species referred to by authors.” Forty years later, [Allen \(1877\)](#), in listing examined specimens of *Sylvilagus palustris*—currently understood to be circumscribed to the southeastern United States (western limit to Mobile Bay)—listed specimens from Veracruz and Yucatán, México, as belonging in that species. It was not until the skull had been removed for examination that Allen instead admitted that the specimen from Veracruz should belong

to its own discrete species, *S. truei* [= *S. gabbi truei*] (Allen, 1890b:192), noting that “the single record from so remote a point [i. e., from Florida] as Mirador, México, has of late seemed open to serious [taxonomic] question” thereby first remarking on congruence between geographic features and taxonomy of *Sylvilagus*. Taxonomic decisions at the time were routinely undertaken—with few but notable exceptions—based on external appearance. Since that time, increasingly detailed analyses have been undertaken, and an expanding tool chest of morphological characters have successively been employed to more accurately distinguish among lagomorph taxa ([Baird 1857](#); [Gray 1867](#); [Lyon 1904](#); [Nelson 1909](#); [Thomas 1913](#); [Hummelinck 1940](#); [Hershkovitz 1950](#); [Hall 1951](#); [Palacios et al. 1980](#); [Ruedas 1998, 2017](#); [Ruedas et al. 2017](#)).

Philip Hershkovitz's 1950 treatise in particular, nominally focused on Colombia but in fact covering most, if not all, of South America, stands apart as the first attempt at a comprehensive treatment of the lagomorphs of any continent, albeit closely followed by E. R. Hall's 1951 synopsis of North American lagomorphs. The vast scope, both geographic and taxonomic, of Hershkovitz's work meant that, years later, the taxonomy he proposed for Central and South American cottontails remained in force. For example, for Central American *S. brasiliensis*, [Hall \(1951, 1981\)](#) showed no changes relative to the scheme of [Hershkovitz \(1950\)](#). [Cabrera \(1961\)](#) similarly had few taxonomic changes in either *S. "brasiliensis"* or *S. "floridanus"* (both *sensu lato*) of South America, although *S. nigrorufus* Hartert, 1894, the oldest available name for South American taxa considered to be subsumed within *S. floridanus*, was inexplicably omitted from Cabrera's treatment.

However, and notwithstanding its eminent worth, the passage of time has revealed that some errors made their way into Hershkovitz's 1950 treatise. As [Musser et al. \(1998:10\)](#) pointed out with particular respect to oryzomysine rodents, parts of some of Hershkovitz's revisions could represent an "unfortunate example of taxonomic revision undocumented by specimens or other data and one that misleadingly simplified a complex reality". In the case of the treatment of South American cottontails, for example, Hershkovitz did not examine all the pertinent holotypes, and when he did, it is unclear how carefully he scrutinized key morphological characters that could have led to a more accurate reflection of the underlying biological reality ([Ruedas 2017](#)). In fact, Hershkovitz's conclusion (1950:327) that his "review shows [*S. brasiliensis* and *S. floridanus*] to be the only recognizably valid species of leporids indigenous to South America" could not, in retrospect, have been further from the mark, given the recognized presence of a much larger number of species of *Sylvilagus*: at least 12 in the "*brasiliensis*" group alone ([Ruedas et al. 2019](#)).

In the present work, we began by questioning the taxonomy of individuals in the genus *Sylvilagus* from Costa Rica. Costa Rica, at 51,100 km², covers only 0.034 % of the land surface of the Earth, but with over 230 species present of terrestrial mammals, contains approximately 4 % of the World's known mammal species: 121 times more than expected by strict proportionality between area and biodiversity. Insofar as cottontails (*Sylvilagus*) are concerned, that is reflected in the presence of three recognized taxa ([Hall 1951, 1981; Mora 2000; Ruedas and Salazar-Bravo 2007; Rodríguez-Herrera et al. 2014](#)): *S. g. gabbi* (J. A. Allen, 1877), *S. dicei* Harris, 1932, and *S. floridanus costaricensis* Harris, 1933. In describing *S. f. costaricensis*, [Harris \(1933\)](#) undertook comparisons of that taxon with *S. f. aztecus* (J. A. Allen, 1890) and *S. f. hondurensis* Goldman, 1932. Goldman in turn, in his description of *S. f. hondurensis*, undertook comparisons between that taxon and *S. f. chiapensis* (Nelson, 1904).

We accordingly undertook comparisons of taxa in the *Sylvilagus floridanus* group present in Costa Rica and the

region in order to better ascertain their taxonomic identity. The Costa Rican—and indeed, Central American—taxa of *Sylvilagus* remain inadequately described, let alone diagnosed. We therefore undertook a detailed analysis of cranial and dental anatomy of Costa Rican taxa of *S. floridanus* within the broader context of their current nominal identification to species, by undertaking comparisons using all the pertinent holotypes: of *S. floridanus* (J. A. Allen, 1890): those of the species and subspecies listed above, and that of the geographically proximal *S. f. yucatanicus* (Miller, 1899), thereby enabling us to robustly define the species of *S. floridanus* complex in Costa Rica and adjacent areas. Identification of species is, we believe, critical to generating phylogenetic trees that bear any semblance to the reality of life, because accurate trees can only result from the combination of adequate taxon sampling with sufficient data. Otherwise, one is left with what [Coddington and Scharff \(1996:139\)](#) so trenchantly remarked: "A fully resolved tree that makes no sense is still nonsensical."

Materials and methods

Specimens. Specimens examined are listed in Appendix 1, with their original taxonomic designation as well as current taxonomy, localities (georeferenced insofar as possible), repository, and collection number. For geographic and taxonomic reasons, as described above, we chose to focus on the following taxa: *Sylvilagus f. floridanus*, *S. f. costaricensis*, *S. f. hondurensis*, *S. f. aztecus*, *S. f. chiapensis*, *S. f. yucatanicus*, *S. gabbi*, *S. dicei*, and *S. brasiliensis surdaster* (Thomas, 1901). *Sylvilagus b. surdaster* was included because, although the type locality is in Ecuador (Esmeraldas Prov.; Río Bogotá, Carondelet; ca. 1° 07' 27" N, 78° 45' 45" W, ca. 20 m), and there would be scant probability of conspecificity, it is the most proximal lowland taxon affine to *S. brasiliensis* broadly writ and the name *brasiliensis* has previously been used for Costa Rican lowland rainforest rabbits following [Hall \(1981\)](#).

Morphological data: mensural characters. We measured 37 craniodental morphological variables. Terminology of cranial characters and features generally follows [Wible \(2007\)](#), and [Ruedas \(1998\)](#); measurements were defined by [White \(1987\)](#) and [Ruedas \(1998, 2017\)](#), and were extensively detailed and illustrated in [Ruedas et al. \(2017\)](#). Mensural characters included: GLS, greatest length of skull; POSTORB, width of postorbital constriction; BROSTR and DEPROSTR, breadth and depth (height) of rostrum; BBRAIN, breadth of braincase; ZYGO1, greatest width across the masseteric spine; ZYGO2, zygomatic breadth; LZGO, length of zygomatic arch; NASALL, greatest length of nasal bone; NASALW, greatest width across left and right nasal bones; I2P2, least alveolar length of I2–P2 diastema; P2M3, greatest alveolar length of P2–M3 toothrow; HBRAIN, height of braincase; HBULLA, height of bulla; CONDL, condylopreamaxillary length of cranium; LPALFOR, WPALFOR, length and width of incisive foramina; PALONG, palatal length; PALBRIDGE, greatest anteroposterior dimension of palatal bridge; BASIOC, anteroposterior length of basioccipital; WIDBULL,

width of auditory bulla; ANTNULL, anteroposterior length of auditory bulla, from the most anterior projection of the ectotympanic to the most posterior point between the occipital and the paracondylar processes of the exoccipital; INTBD, least breadth across the basioccipital between the ectotympanic bones; OCCOND, width across the occipital condyles; INTBOC, length between the posteriormost edge of the palatal bridge and the suture between the basioccipital and basisphenoid bones; CHOANA1, breadth of nasopharynx; CHOANA2, breadth of alisphenoid constriction; MASTOID, greatest breadth across the mastoid exposure of the petrosal; DEPZYGO, least anteroposterior length across the maxillary bone at the base of the masseteric spine on the maxillary portion of the zygomatic arch; IP3, least alveolar length of i–p3; MANDEP, depth of mandibular body; P3M3, greatest alveolar length of p3–m3; HMAND, height of the mandible; HPTT, distance from ventral aspect of angular process (labial to pterygoid shelf) to most dorsal aspect of pterygoid tuberosity; BCON, length of condyloid process; WCON, breadth of articular facet of condyloid process; LMAND, length of mandibular body.

Statistical analyses were carried out using the Statistical Analysis System (SAS) software, version 9.4 (2002–2012; [SAS Institute 1988a, 1988b](#)), generally following [Ruedas \(1995, 1998\)](#); significance in all analyses was set at $\alpha = 0.05$. Due to the paucity of specimens available, little could be made to determine presence or extent of sexual dimorphism in the taxa examined, although sexual dimorphism has been reported in measurements of *Sylvilagus* ([Orr 1940](#)) and could affect results of multivariate analyses ([Reyment et al. 1984; Marcus 1990](#)) given the small intraspecific sample sizes of the present study (Appendix 1). Univariate statistics (mean, standard deviation) were calculated using the UNIVARIATE procedure of SAS. Analysis of variance was carried out using the GLM procedure, enabling the MEANS routine with option REGWQ, which uses the Ryan–Eynot–Gabriel–Welsch multiple range test, and controls for Type I error ([Day and Quinn 1989](#)). A principal component analysis (procedure PRINCOMP) was carried out on the covariance matrix of log-transformed normalized measurement values data. Such a posteriori grouping methods are preferred by us over a priori grouping methods (multiple range tests, discriminant analyses) because there is no prior hypothesis as to the putative identity of specimens examined. These data further are useful to examine ontogenetic growth patterns, which in the sample covariance matrix can be construed as the dispersion of points along the major long axis of each sample, with the first eigenvector representing Huxley's allometric equation ([Voss et al. 1990](#)). We used the broken stick method of [Frontier \(1976\)](#) as implemented by [Jackson \(1993\)](#) to assess the significance of each principal component's eigenvalue; broken-stick distributions for principal component eigenvalues were generated using the "broken.stick" function of R (v. 3.3.1; [R Core Team 2016](#)).

Dental characters. Drawings of p3 were made by tracing from photographs taken using a Canon EOS 30D digital

camera mated to a Canon MP-E 65 mm f/2.8 1–5X Macro Photo lens, or a Canon EOS 6D mated to the same lens or an AmScope CA–CAN–SLR–III camera adapter for microscopes, shooting either through a camera tube on a binocular dissecting microscope or an ocular tube with the ocular removed, also on a binocular dissecting microscope, as made available by the collections housing the specimens under consideration. Among leporids, p3 generally constitutes the most informative dental element for taxonomic and systematic purposes ([Dalquest 1979; Dalquest et al. 1989; Hibbard 1963; Palacios and López Martínez 1980; Ruedas 1998; Ruedas et al. 2017; White 1987, 1991; White and Morgan 1995; Winkler and Tomida 2011](#)). Discrete characters were deemed the most important in this particular research; accordingly, resulting figures were oriented and scaled to the same size in linear dimensions to carry out size-independent comparisons of interspecific characters. Characters considered follow the standard terminology of [Palacios and López Martínez \(1980\)](#), were described in Appendix I of [Ruedas \(1998\)](#) and illustrated here (Figure 1) with some modifications from [Ruedas et al. \(2017\)](#) in that all cusps are identified by incorporating features from [López Martínez \(1974, 1977, 1980, 1989\)](#), [López-Martínez et al. \(2007\)](#), and [Angelone and Sesé \(2009\)](#). Additional characters useful in distinguishing among lagomorph species were extracted from [Palacios \(1996\)](#) and [Palacios et al. \(2008\)](#). The LSID for this publication is: urn:lsid:zoobank.org:pub:601C073B-6DFA-421E-8B4B-F7F44BF62D3F.

Results

Statistical analyses of morphology. Univariate statistics (means \pm standard deviation, minimum–maximum) for the variables measured in each individual taxon (represented in certain taxa only by the holotypes or, in the case of *S. gabbi*, by the lectotype) are shown in Table 1. Also shown in Table 1 are the results of the Ryan–Einot–Gabriel–Welsch multiple range test. Thirty of the 37 characters examined showed some level of significance in discriminating among groups of individuals or taxa. This proportion (81.1 %) is markedly higher than the two characters that would be expected to differ significantly by chance alone with significance set at $\alpha = 0.05$. However, some of the variables that are significantly different among taxa do not discriminate into distinct groups (e.g., depth of rostrum, mastoid breadth, length of mandibular toothrow, length of mandible). Similarly, most of the significantly different groups displayed a great deal of overlap. The one consistent result obtained from the analysis is that *S. f. yucatanicus* is immoderately larger than remaining taxa in almost all characters. That taxon differs significantly from all taxa but *S. dicei* in breadth of braincase, and from all other taxa in breadth of incisive foramina; it also has the longest skull of any *Sylvilagus* species examined for the present study, and beyond statistical significance ([Moyé 2006; Wasserstein and Lazar 2016; Wasserstein et al. 2019](#)), does not overlap with the GLS of any of the remaining *Sylvilagus* taxa.

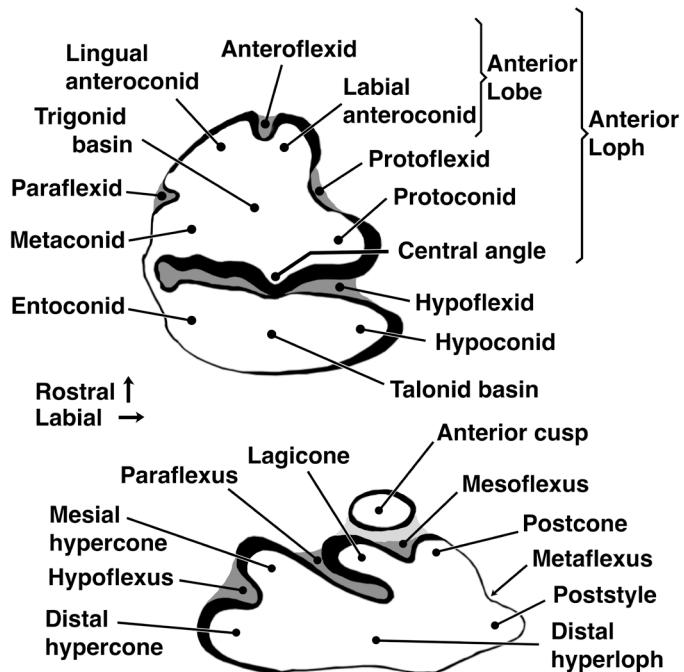


Figure 1. Standard nomenclature for dental features of Recent leporid lagomorphs' third lower premolar (p3, top) and second upper premolar (P2, bottom), adapted from Figure 1 of Palacios and López Martínez (1980:62), and expanded from Ruedas *et al.* (2017) in identifying all cusps by incorporating features from López Martínez (1974, 1977, 1980, 1989) and Angelone and Sesé (2009). The term "anterior loph," preferred herein, was used interchangeably with "trigonid" by Hibbard (1963). López-Martínez *et al.* (2007) considered only the caudal portion of the anterior loph of pm3 to constitute the trigonid, with the rostral portion (anterior lobe) instead collectively constituting the anteroconids.

The results of the principal component analysis, carried out on the covariance matrix of a reduced set of natural log-transformed variables ($n = 22$; reduced as a compromise to embrace as many specimens as possible while maintaining as many measurements as possible), are shown in Figure 2 and Tables 2 and 3. The principal component analysis accounts for 15.4 % of the overall variance. Principal component 1 accounts for 36.2 % of that variation, with PC 2 accounting for 14.9 %; PCs 1–7 jointly account for >80 %, and 1–10 for >90 %. Just over half (50.5 %) of the variation in PC 1 is accounted for by only five of the 22 characters: width of bulla (13.5 %), width of incisive foramina (11.6 %), width of nasal bones (11.3 %), length of nasal bones (8.5 %), and breadth of rostrum (5.6 %). Remaining characters each contribute less than 5 % to the variation in his principal component.

Figure 2 shows the great deal of overlap among most taxa in the *floridanus* species group. Within the limits imposed by a reduced number of samples, the major axis of dispersion for points in these taxa is primarily along principal component 1, which in this instance is a size component. The major axis of dispersion has been shown to be associated with age-correlated growth (Voss *et al.* 1990). In the particular instance of our analysis, this is borne out by the relative homogeneity of the magnitude of the eigenvector scores for PC 1 (Table 3): while some variables have eigenvector scores that are somewhat low (maxillary toothrow, interbullar distance, breadth of braincase) or somewhat high (width of bulla, width of nasal bones, width

of incisive foramina), the remaining characters are fairly homogeneous, and eigenvectors average 0.200 ± 0.08 . The homogeneity of the eigenvectors exhibited in PC1 is not evident in PC 2 through 6 or subsequent principal components (Table 3). For PC2, these average 0.041, but the standard deviation jumps to 0.209, with eigenvectors ranging from -0.456 (width of bulla) to 0.625 (breadth of nasopharynx). Subsequent principal components show similar trends with respect to standard deviation, maxima, and minima, of the characters' eigenvector scores. Such lack of homogeneity in eigenvector scores usually is associated with shape-based, rather than size-based variation.

In Figure 2, principal component 2 (14.9 % of the total variation) distinguishes primarily between the *floridanus* group *Sylvilagus* species and remaining species, including *S. gabbi* and *S. dicei*. Only two characters contribute well over half (59.9 %) of the variation to this principal component: breadth of nasopharynx (39.1 %) and width of bulla (20.8 %).

The results of the principal component analysis reinforce the suggestion derived from the multiple range test that *S. f. yucatanicus* is exceptionally distinct from remaining taxa examined. That taxon is markedly separated in principal component 1 from remaining individuals examined (Figure 2), this despite the fact that we undertook natural log-transformation of the variables in order to minimize the effects of size. Width of incisive foramina is the second most important character in PC1, contributing to 11.6 % of the variation in that PC. Breadth of braincase in contrast only contributes to 1.1 % of the variation in PC 1.

Notwithstanding the informative nature of the exploratory principal components analysis, we acknowledge that said analysis is not without issues. Application of the broken stick method to assess the significance of eigenvalues suggested that only the first two principal components contained meaningful information. These two components cumulatively accounted for 51.1 % of the variation. Because the overall PCA accounted for 15.4 % of the variance, the result is that only 7.9 % of the morphological variation is accounted for in the PCA as implemented in the present study. It is possible that more judicious selection of variables may have influenced the analysis one way or another (e. g., selecting only those variables found to be significant in the multiple range test). We chose however to maintain the variables employed rather than cherry-pick the data. Our PCA results underscore that the morphological conservatism manifested in craniodental mensural variables throughout the genus *Sylvilagus*—and indeed, in other lagomorph genera—is not readily tractable to these morphometric analyses, although the analyses do have certain illuminative properties.

*Taxonomic identity of *Sylvilagus floridanus costaricensis* Harris, 1933.*

Analysis of morphological data. To ascertain the taxonomic identity of *S. f. costaricensis*, we undertook comparisons between this taxon and all other pertinent regional

Table 1. Craniodental measurements of holotypes (marked by a superscripted star; *S. gabbi* has a lectotype) and taxa (means including holotype $\pm SD$, minimum–maximum) considered in this paper, in mm. Variable abbreviations defined in Ruedas et al. (2017). Our sample sizes made impossible the evaluation of sexual dimorphism within species. *Sylvilagus boylei* was synonymized with *S. floridanus superciliaris* by Hershkovitz (1950); *S. f. chiapensis* was considered a junior synonym of *S. f. aztecus* by Hoffmann and Smith (2005); *S. daulensis* was synonymized with *S. brasiliensis surdaster* by Cabrera (1961); *S. russatus* was synonymized with *S. floridanus* by Nelson (1909); “*Lepus*” [= *Sylvilagus*] *margaritae* was synonymized with *S. floridanus* by Hershkovitz (1950); *S. salentus* was synonymized with *S. brasiliensis* by Hershkovitz (1950); “*Lepus*” [= *Sylvilagus*] *superciliaris* was synonymized with *S. floridanus* by Hershkovitz (1950). Superscripts by variable name indicate significance of variable in the Ryan–Einot–Gabriel–Welsch multiple range test, as follows: †: not significant; 0.05 \geq^* > 0.01 ; 0.01 \geq^{**} > 0.001 ; 0.001 \geq^{***} > 0.0001 ; 0.0001 \geq^{****} . Means or values indicated by the same superscript letters by the variable indicate groups that are not significantly different (not shown for holotypes representing sample sizes greater than 1).

Taxon	<i>S. f. aztecus*</i> ♂	<i>S. f. aztecus</i>	<i>S. boylei*</i> ♀	<i>S. f. chiapensis*</i> ♀	<i>S. f. chiapensis</i>	<i>S. f. connectens*</i> ♂	<i>S. f. connectens*</i> ♀	<i>S. f. costaricensis*</i> ♂	<i>S. f. costaricensis*</i> ♀	<i>S. daultensis*</i> ♀	<i>S. daultensis*</i> ♂	<i>S. dicei*</i> ♀	<i>S. dicei*</i> ♂	<i>S. f. floridanus*</i> ♂	<i>S. f. floridanus*</i> ♀
Variable (); museum number (→)	AMNH 31162438	(n = 12)	AMNH 37794	USNM 75953	(n = 4)	USNM 63660	USNM 65232	AMNH 34671	AMNH 64043	TTU 114374	AMNH 31162438				
Greatest length of skull*	72.9	72.6 \pm 3.9, 65.0–73.3 ^{ab}	76.2 ^{ab}	78.9	77.0 \pm 2.1, 74.2–78.9 ^{ab}	74.4 ^{ab}	76.3 ^{ab}	69.2 ^b	77.3 ^{ab}	70.5 ^{ab}	72.9				
Postorbital constriction	11.2	11.7 \pm 1.0, 10.0–13.3	12.3	11.6	11.9 \pm 0.7, 11.4–12.9	12.2	12	10.9	10.1	12	11.2				
Breadth of rostrum†	20.6	18.6 \pm 1.5, 15.2–20.6	20.7	21.2	19.9 \pm 1.5, 18.4–21.2	18.6	20.9	18	22.6	17.2	17.1				
Depth of rostrum***	18.2	15.8 \pm 1.3, 14.0–18.2 ^b	17.2 ^b	15.6	15.8 \pm 0.8, 14.9–16.8 ^a	17.3 ^a	15.2 ^a	15.3 ^a	16.1 ^a	14.0 ^a	15.5				
Breadth of braincase***	26.1	25.4 \pm 0.7, 23.9–26.1 ^{bc}	26.1 ^{bc}	25.7	26.1 \pm 0.9, 25.1–27.1 ^{bc}	26.1 ^{bc}	25.5 ^{bc}	23.2 ^f	27.9 ^{bc}	27.1 ^{bc}	26.3				
Zygomatic breadth***	33.6	33.7 \pm 1.3, 32.0–36.0 ^{bcd}	35.1 ^{abcd}	35.6	35.1 \pm 1.2, 33.6–36.4 ^{abc}	34.4 ^{abcd}	35.1 ^{abcd}	30.3 ^d	39.0 ^{ab}	36.0 ^{ab}	33.4				
Zygomatic breadth**	35	34.4 \pm 1.0, 32.3–36.4 ^{abcd}	35.3 ^{abcd}	36.5	35.6 \pm 1.2, 34.0–36.5 ^{abc}	35.4 ^{abc}	34.2 ^{bc}	31.4 ^f	38.4 ^{ab}	36.6 ^{ab}	-				
Length of zygomatic arch**	31.1	30.7 \pm 1.8, 26.4–33.1 ^{ab}	33.7 ^{ab}	33.8	32.5 \pm 0.9, 31.8–33.8 ^{ab}	33.4 ^{ab}	32.2 ^{ab}	29.0 ^b	33.5 ^{ab}	31.6 ^{ab}	31.5				
Nasal bone length***	33.9	31.9 \pm 1.9, 27.9–34.2 ^{abcd}	31.8 ^{abcd}	36.9	34.5 \pm 1.6, 33.4–36.9 ^{abcde}	34.6 ^{abcd}	35.3 ^{abc}	27.3 ^f	33.6 ^{abcde}	30.3 ^{abcde}	30.4				
Width of nasal bones***	17.2	15.7 \pm 1.2, 13.9–17.4 ^{abde}	17.7 ^{ab}	17.6	15.4 \pm 1.6, 14.1–17.6 ^{abcde}	15.4 ^{abcde}	17.4 ^{abc}	13.7 ^{abcde}	14.8 ^{abcde}	12.7 ^{abcde}	14.9				
Length of upper diastema***	19.8	19.7 \pm 1.1, 17.1–21.4 ^{ab}	20.4 ^{ab}	22.3	21.2 \pm 0.7, 20.8–22.3 ^{ab}	20.2 ^{ab}	20.3 ^{ab}	18.5 ^b	21.2 ^{ab}	19.9 ^{ab}	19.6				
Length of maxillary toothrow†	13.5	13.2 \pm 0.7, 11.8–14.2	14.1	14.4	13.6 \pm 0.9, 12.4–14.4	14	13.7	13.1	15	13.5	14.6				
Height of braincase***	22.7	23.2 \pm 1.4, 21.3–25.4 ^{ab}	23.3 ^{ab}	24.1	24.4 \pm 0.3, 24.1–24.7 ^{ab}	24.2 ^{ab}	23.1 ^{ab}	20.7 ^{abcd}	22.8 ^{abcd}	21.7 ^{abcd}	23.9				
Height of bulla***	12.6	12.7 \pm 0.6, 11.7–13.9 ^{bcd}	12.6 ^{bcd}	14.1	13.6 \pm 1.3, 13.3–14.1 ^{abc}	14.1 ^{ab}	14.0 ^{ab}	10.3 ^d	11.6 ^{cd}	11.1	13.1				
Condylopennaxillary length*	62.8	63.7 \pm 3.2, 57.6–67.6 ^{ab}	67.7 ^{ab}	70.5	67.3 \pm 2.8, 64.8–70.5 ^{ab}	67.3 ^{ab}	69.0 ^{ab}	62.2 ^b	69.4 ^{ab}	63.0 ^{ab}	65.7				
Length of incisive foramina***	16.9	16.1 \pm 0.7, 13.7–17.4 ^b	18.9 ^{ab}	20.4	17.9 \pm 1.6, 16.7–20.4 ^{ab}	18.5 ^{ab}	16.8 ^{ab}	15.9 ^b	17.5 ^{ab}	17.0 ^{ab}	17.2				
Width of incisive foramina***	6.5	5.9 \pm 0.7, 4.6–7.0 ^b	4.9 ^b	7.4	6.8 \pm 0.6, 6.2–7.4 ^b	6.4 ^b	6.4 ^b	5.4 ^b	7.2 ^b	5.7 ^b	6.9				
Length of palate***	27.8	27.2 \pm 1.4, 23.5–28.6 ^{ab}	28.2 ^{ab}	30.4	28.9 \pm 1.2, 27.6–30.4 ^{ab}	29.1 ^{ab}	28.7 ^{ab}	25.6 ^b	28.4 ^{ab}	26.8 ^{ab}	27.8				
Length of palatal bridge**	7	6.8 \pm 0.5, 6.0–7.5 ^{ab}	6.4 ^{ab}	7.1	7.0 \pm 0.2, 6.7–7.1 ^{ab}	7.3 ^{ab}	7.7 ^{ab}	6.0 ^{ab}	6.8 ^{ab}	6.0 ^{ab}	7.1				
Length of basioccipital***	9.4	9.2 \pm 0.6, 8.1–10.2 ^{ab}	9.3 ^{ab}	9.2	9.0 \pm 0.4, 8.4–9.4 ^{ab}	9.8 ^a	9.6 ^a	8.8 ^{ab}	9.2 ^{ab}	8.4 ^{ab}	9				
Width of bulla†	6.4	6.4 \pm 1.2, 5.4–9.8	7.2	6.5	6.4 \pm 0.3, 6.0–6.5	7.1	6.5	5.2	6.5	4.6	4.4				
Anteriorposterior length of bulla***	9.6	9.7 \pm 0.5, 8.9–10.6 ^{ab}	11.2 ^{ab}	9.6	10.0 \pm 0.5, 9.6–10.6 ^{ab}	10.6 ^{abc}	9.0 ^{abcde}	8.2 ^{abc}	8.4	9.6	10.9				
Interbulbar breadth†	8	7.5 \pm 0.4, 6.3–8.0 ^{ab}	7.9 ^{ab}	7.1	6.8 \pm 0.6, 5.9–7.4 ^{ab}	6.9 ^b	8.5 ^a	7.4 ^{ab}	8.5 ^{ab}	7.5 ^{ab}	8.3				
Breadth of occipital condyle†	14.1	13.8 \pm 0.3, 13.4–14.2	14.5	14.3	13.4 \pm 0.7, 12.8–14.3	13.1	14.5	13.7	14.6	12.7	12.4				
Length palaate to basioccipital-basisphenoid suture†	20.2	19.8 \pm 1.3, 17.8–21.8	20.5	23	21.3 \pm 1.4, 19.7–23.0	21.1	21.2	18.9	22	19.1	21.1				
Breadth of nasopharynx***	6.2	5.4 \pm 0.5, 4.4–6.2 ^{abcd}	5.7 ^{abcd}	6.2	5.9 \pm 0.2, 5.7–6.2 ^{abcd}	5.1 ^d	6.2 ^{abc}	4.2 ^{cd}	7.9 ^a	7.1 ^a	6.4				
Length of mandibular diastema*	-	8.9 \pm 0.3, 8.5–9.6 ^{ab}	-	10	9.2 \pm 0.5, 8.8–10.0 ^{ab}	9.2 ^{ab}	9.5 ^{ab}	8.5 ^b	11.3 ^a	10.3 ^a	-				
Mastoid breadth**	24	23.9 \pm 1.0, 22.6–25.3 ^a	24.5 ^a	24.2	24.1 \pm 0.6, 23.2–24.8 ^a	23.7 ^a	25.6 ^a	23.1 ^a	26.7 ^a	23.5 ^a	22.4				
Depth of zygomatic arch**	5.3	5.06 \pm 0.3, 4.4–5.5 ^b	5.6 ^{ab}	5	5.1 \pm 0.4, 4.6–5.7 ^{ab}	5.8 ^{ab}	5.3 ^{ab}	4.4 ^{bc}	4.2 ^{cd}	4.8 ^{ab}	6				
Length of mandibular diastema*	15.8	15.6 \pm 1.0, 13.2–16.8 ^{ab}	16.0 ^{ab}	17	16.3 \pm 0.5, 15.8–17.0 ^{ab}	15.6 ^{ab}	15.2 ^{ab}	15.2 ^{ab}	16.4 ^{ab}	15.0 ^{ab}	16.1				
Depth of mandibular ramus***	11.9	11.4 \pm 0.5, 10.7–12.1 ^{bcd}	11.2 ^{bcd}	12.1	11.6 \pm 0.6, 10.8–12.1 ^{bcd}	12.2 ^b	12.6 ^b	9.8 ^{cd}	11.0 ^{bcd}	10.6 ^{bcd}	11.5				
Length of mandibular toothrow***	14.6	13.4 \pm 0.6, 12.6–14.6 ^a	14.4 ^a	15.1	14.2 \pm 0.7, 13.5–15.1 ^a	13.9 ^a	14.4 ^a	13.4 ^a	15.5 ^a	14.2 ^a	14.8				
Height of mandible***	35.8	34.9 \pm 1.5, 32.1–37.1 ^{bcd}	38.1 ^{abcd}	38	37.1 \pm 0.7, 36.4–38.0 ^{abc}	37.5 ^{abc}	37.5 ^{abc}	30.9 ^d	37.2 ^{bcd}	34.0 ^{bcd}	37.2				
Length from angular process to pterygoid tuberosity***	25	24.8 \pm 1.3, 22.7–26.2 ^{abc}	27.8 ^{ab}	27.8	26.6 \pm 0.5, 25.6–27.8 ^{ab}	27.0 ^{ab}	26.0 ^{abc}	21.4 ^f	26.1 ^{abc}	24.8 ^{abc}	26.3				
Length of condyloid process**	8.4	8.2 \pm 0.4, 7.5–8.7 ^a	8.6 ^a	8.8	8.4 \pm 0.5, 7.6–8.8 ^a	8.8 ^a	8.9 ^a	8.7 ^a	10.2 ^a	9.5 ^a	8.9				
Width of articular facet**	3.4	3.4 \pm 0.1, 3.3–3.7 ^{ab}	3.1 ^b	4.1	3.6 \pm 0.3, 3.4–4.1 ^{ab}	3.5 ^{ab}	55.3 ^a	54.0 ^a	50.5 ^a	56.6 ^a	54.6 ^a	55			
Length of mandible*	53	52.4 \pm 2.6, 48.0–56.2 ^{ab}	55.2 ^{ab}	57.5	55.7 \pm 1.4, 54.2–57.5 ^a										

Table 1. Continuation...

Taxon	Variable (); museum number (→)	(n = 11)	AMNH 17203	USNM 1371/37794	MCZ Bangs 8441	USNM 179569	USNM 257062	(n = 13)	USNM 63217	AMNH 33050	AMNH 15428	USNM 37772
<i>S. f. floridanus</i>	<i>S. f. russatus*</i> ♂	72.0 ± 1.4, 69.4–73.8 ^{ab}	78.6 ^{ab}	70.9 ^b	73.9 ^b	72.5 ^{ab}	74.7	76.1 ± 1.4, 73.2–77.6 ^{ab}	78.8 ^b	–	78.4 ^{ab}	81.1 ^a
Postorbital constriction†		11.2 ± 0.8, 10.0–12.7	11.2	10.5	13.2	12.4	12.4	12.2 ± 1.3, 10.4–15.1	14.5	–	12.9	13.2
Breadth of rostrum†		19.2 ± 1.0, 17.1–20.8	20.2	17.1	20.8	18.8	19.2	19.3 ± 1.0, 17.6–20.7	22.3	–	20.5	21.7
Depth of rostrum***		15.3 ± 0.4, 14.7–15.9 ^a	16.8 ^a	14.4 ^a	14.9 ^a	15.4 ^a	17.3	17.1 ± 0.7, 15.6–18.0 ^a	17.6 ^a	–	17.5 ^a	17.5 ^a
Breadth of braincase***		25.9 ± 0.6, 25.2–27.4 ^{bc}	25.6 ^{bc}	25.0 ^{bc}	24.0 ^c	24.0 ^c	25.5	25.8 ± 0.7, 23.9–26.5 ^{bc}	25.6 ^{bc}	–	25.3 ^{bc}	29.0 ^a
Zygomatic breadth at spine***		33.9 ± 0.6, 33.0–35.0 ^{abcd}	35.0 ^{ab}	32.6 ^{cd}	35.2 ^{bc}	35.3 ^{abc}	34.9	35.0 ± 1.1, 32.8–36.1 ^{abc}	36.1 ^{abc}	–	34.6 ^{abcd}	38.5 ^a
Zygomatic breadth***		35.2 ± 0.6, 34.5–36.0 ^{abc}	35.2 ^{abc}	33.4 ^{bc}	35.0 ^{abc}	35.0 ^{abc}	34.4	35.0 ± 1.1, 33.1–36.9 ^{abc}	36.1 ^{abc}	–	35.4 ^{abc}	38.6 ^a
Length of zygomatic arch**		31.0 ± 0.8, 29.4–32.2 ^{ab}	33.5 ^{ab}	30.8 ^{ab}	32.0 ^b	30.6 ^{ab}	31	32.6 ± 1.1, 31.0–34.3 ^{ab}	32.5 ^{ab}	–	33.1 ^{ab}	34.7 ^a
Nasal bone length***		30.5 ± 1.0, 28.4–31.9 ^{abcd}	36.9 ^a	27.9 ^{ef}	30.5 ^{abcd}	28.8 ^{def}	34.2	34.5 ± 1.3, 32.0–36.3 ^{abcde}	36.3 ^{ab}	28.2 ^{def}	33.5 ^{abcd}	37.2 ^a
Width of nasal bones****		14.3 ± 1.1, 12.8–16.5 ^{abcde}	17.3 ^{abcd}	12.1 ^e	13.0 ^{abcde}	12.6 ^e	15.8	16.2 ± 0.7, 15.1–17.6 ^{abcde}	18.2 ^a	12.7 ^{def}	16.2 ^{abcde}	17.1 ^{abcd}
Length of upper diastema***		19.1 ± 0.6, 18.3–20.4 ^{ab}	21.1 ^{ab}	20.4 ^{ab}	20.4 ^{ab}	20.0 ^{ab}	20.7	20.5 ± 0.7, 19.8–21.6 ^{ab}	22.9 ^a	–	20.4 ^{ab}	23.2 ^a
Length of maxillary toothrow†		13.9 ± 0.8, 13.0–15.5	14.4	13.8	14.4	13.5	13.6	13.8 ± 0.4, 13.0–14.6	14.5	12.7	14.6	14
Height of braincase****		22.6 ± 0.7, 21.6–23.9 ^{bc}	23.2 ^{ab}	21.1 ^{cd}	18.6 ^d	19.0 ^{cd}	23.1	23.7 ± 0.9, 22.1–25.0 ^{ab}	22.4 ^{abcd}	–	24.8 ^{ab}	25.3 ^a
Height of bulla***		13.4 ± 0.7, 12.4–14.5 ^{bc}	14.8 ^{ab}	10.3 ^d	–	10.3 ^d	12.9	13.3 ± 0.7, 12.5–14.7 ^{bc}	12.4 ^{cd}	–	12.0 ^{cd}	15.5 ^a
Condylopalmaxillary length*		64.4 ± 1.7, 61.6–66.5 ^{ab}	67.4 ^{ab}	64.4 ^{ab}	66.3 ^{ab}	64.2 ^{ab}	66.2	66.8 ± 1.4, 64.5–68.5 ^{ab}	70.2 ^{ab}	–	69.3 ^{ab}	72.7 ^a
Length of incisive foramina***		15.9 ± 1.0, 14.7–17.2 ^{ab}	18.8 ^{ab}	16.2 ^b	16.2 ^b	16.2 ^b	16.6	16.8 ± 0.7, 15.5–18.3 ^{ab}	19.5 ^{ab}	–	18.7 ^{ab}	20.5 ^a
Width of incisive foramina***		6.3 ± 0.5, 5.2–6.9 ^b	5.3 ^b	4.6 ^b	5.7 ^b	5.9 ^b	5.9	6.1 ± 0.4, 5.1–6.9 ^b	6.4 ^b	–	5.0 ^b	9.1 ^a
Length of palate***		26.5 ± 1.0, 25.3–28.3 ^b	29.5 ^{ab}	27.1 ^{ab}	28.0 ^b	27.4 ^{ab}	28.7	28.2 ± 0.7, 27.2–29.4 ^{ab}	31.3 ^a	–	28.6 ^{ab}	31.4 ^a
Length of palatal bridge**		6.6 ± 0.5, 5.8–7.5 ^{ab}	7.4 ^{ab}	7.5 ^{ab}	8.4 ^a	7.3 ^{ab}	7.7	7.2 ± 0.5, 6.4–8.0 ^{ab}	7.2 ^{ab}	7.5 ^{ab}	6.5 ^b	7.4 ^{ab}
Length of basioccipital***		8.5 ± 0.6, 7.7–9.4 ^{ab}	8.9 ^{ab}	8.2 ^{ab}	–	8.2 ^{ab}	10.5	9.5 ± 0.5, 8.7–10.5 ^{ab}	9.7 ^a	–	10.6 ^a	9.6 ^a
Width of bulla†		6.7 ± 0.9, 4.4–7.7	7.1	5	5.3	5.7	6.7	6.4 ± 0.5, 5.4–7.2	6.9	–	6.7	7.9
Anteroposterior length of bulla***		10.8 ± 0.6, 9.5–11.5 ^{bc}	9.8 ^{abcd}	7.2 ^e	9.1 ^{bcde}	8.7 ^{abc}	10.5	10.2 ± 0.5, 9.4–10.8 ^{abcd}	10.1 ^{abcd}	–	11.4 ^{abc}	12.0 ^a
Interbulbar breadth†		7.4 ± 0.4, 6.8–8.3 ^{ab}	6.2 ^b	7.0 ^{ab}	8.5 ^a	7.0 ^{ab}	7.4	7.5 ± 0.6, 6.8–8.7 ^{ab}	7.8 ^{ab}	–	7.6 ^{ab}	8.1 ^{ab}
Breadth of occipital condyle†		13.9 ± 0.8, 12.4–15.1	14.1	12.8	13.4	12.3 ^a	13.1	13.3 ± 0.4, 12.6–14.2 ^a	14.7 ^a	–	15.6	–
Length palate to basioccipital–basisphenoid suture†		21.4 ± 0.5, 20.8–22.2	20.5	20.7	21.1	21.34	20.5	21.3 ± 0.9, 19.9–22.8	21.9	–	21.6	22.2
Breadth of nasopharynx****		5.9 ± 0.4, 5.2–6.4 ^{abcd}	6.2 ^{abc}	6.3 ^{abc}	7.0 ^{abc}	7.1 ^{ab}	5.6	5.8 ± 0.4, 4.6–6.4 ^{abcd}	6.6 ^{abc}	–	6.2 ^{abc}	6.6 ^{bc}
Breadth of alisphenoid constriction****		8.8 ± 0.4, 7.9–9.3 ^b	9.2 ^{ab}	9.4 ^{ab}	10.3 ^{ab}	10.4 ^{ab}	9.4	9.0 ± 0.4, 8.0–9.4 ^{ab}	9.8 ^{ab}	–	–	–
Mastoid breadth**		22.6 ± 1.1, 21.3–25.0 ^a	23.0 ^a	24.3 ^a	23.9 ^a	23.9 ^a	24.4	24.5 ± 0.5, 23.1–25.4 ^a	25.6 ^a	–	24.3 ^a	–
Depth of zygomatic arch**		5.3 ± 0.6, 4.3–6.0 ^{ab}	5.8 ^{ab}	3.3 ^c	5.0 ^{ab}	5.0 ^{ab}	4.8	5.0 ± 0.2, 4.6–5.3 ^{ab}	4.8 ^{abc}	–	5.0 ^{abc}	6.1 ^a
Length of mandibular diastema*		14.9 ± 0.7, 13.5–16.1 ^{ab}	15.1 ^{ab}	16.2 ^{ab}	15.7 ^b	16.0 ^{ab}	16.8	16.4 ± 0.7, 15.3–17.8 ^{ab}	17.2 ^{ab}	14.3 ^b	16.2 ^{ab}	18.4 ^a
Depth of mandibular ramus***		11.5 ± 0.5, 10.6–12.1 ^{abcd}	11.8 ^{abcd}	9.7 ^{cd}	12.0 ^{ab}	9.6 ^d	12.8	12.0 ± 0.5, 11.3–12.9 ^{ab}	12.0 ^{ab}	10.9 ^{abcd}	12.1 ^{abc}	12.8 ^a
Length of mandibular toothrow**		14.5 ± 0.7, 13.5–15.7 ^a	14.6 ^a	14.8 ^a	14.4 ^a	14.4 ^a	14.4	13.9 ± 0.4, 13.3–14.5 ^a	15.0 ^a	14.4 ^a	14.6 ^a	14.2 ^a
Height of mandible****		35.4 ± 1.0, 33.9–37.2 ^{abcd}	39.6 ^{ab}	33.3 ^{cd}	37.4 ^{abc}	33.0 ^{cd}	37.3	36.7 ± 1.1, 34.6–38.0 ^{abc}	35.5 ^{abcd}	–	36.8 ^{abcd}	40.8 ^a
Length from angular process to pterygoid tuberosity***		25.1 ± 1.1, 23.2–27.4 ^{abc}	28.6 ^a	24.2 ^{abc}	25.0 ^{abc}	23.3 ^{bc}	26.6	26.2 ± 1.0, 24.6–27.8 ^{ab}	24.9 ^{bc}	–	24.9 ^{bc}	–
Length of condyloid process**		8.3 ± 0.6, 7.4–9.1 ^a	9.5 ^a	8.9 ^a	10.0 ^a	7.9	8.7 ± 0.5, 7.9–9.4 ^a	10.1 ^a	–	9.8 ^a	8.2 ^a	–
Width of articular facet**		3.8 ± 0.2, 3.5–4.1 ^{ab}	4.2 ^a	3.4 ^{ab}	4.1 ^a	3.6 ^{ab}	3.2	3.6 ± 0.3, 3.2–4.1 ^{ab}	3.2 ^{ab}	–	3.8 ^{ab}	4.2 ^a
Length of mandible		53.8 ± 1.5, 50.9–55.9 ^a	56.2	53.2 ^a	57.2 ^a	53.8 ^a	55	55.5 ± 1.4, 53.1–58.2 ^a	57.0 ^a	–	56.3 ^a	–

taxa, as noted in the introduction. Figures 3–5 show the dorsal, ventral, and lateral perspectives, respectively, of the focal taxa: as one might expect from the results of the principal component analysis described above, observed differences among the various taxa are subtle. Nevertheless, they are present and telling. Notwithstanding, one obvious difference between the taxa under consideration is in greatest length of skull. In this character, our sample of *S. f. floridanus* show sexual dimorphism: in males, the mean in $\text{mm} \pm \text{SD}$ (min–max) is 70.8 ± 1.1 (69.4 to 72.1), whilst in females, it is 72.7 ± 0.9 (71.3 to 73.8); $t_9 = 2.9125, P < 0.0172, \delta_{\text{means}} = 2.0 \text{ mm}, 95\% \text{ CI} = 0.4\text{--}3.5 \text{ mm}$. However, our sample of adults of *S. f. hondurensis* includes only one female (AMNH 126205); remaining individuals are either unknown (AMNH 123378) or males ($n = 7$). Our comparisons in measurements are therefore made grouping the sexes. Between *S. f. floridanus* and *S. f. hondurensis*, the respective data are 72.0 ± 1.4 (69.4 to 73.8), versus 76.4 ± 1.0 (74.6 to 77.6), $t_{18} = 7.6512, P < 0.0001, \delta_{\text{means}} = 4.4 \text{ mm}, 95\% \text{ CI} = 3.1\text{--}5.6 \text{ mm}$. The holotype of *S. f. costaricensis*, at 76.3 mm, is congruent with the mean of *S. f. hondurensis*. The same pattern obtains, albeit without sexual dimorphism in *S. f. floridanus* ($P = 0.1142$), in breadth of skull at the zygomatic spine: 33.9 ± 0.6 (33.0 to 35.0), versus 35.5 ± 0.4 (34.9 to 36.1), $t_{15} = 6.033, P < 0.0001, \delta_{\text{means}} = 1.7 \text{ mm}, 95\% \text{ CI} = 1.1\text{--}2.2 \text{ mm}$.

The region of the frontonasal suture, and the shape of the latter, is a character that has been used extensively in previous taxonomic studies of lagomorphs. For a selected subset of the specimens employed herein, that feature is shown in Figure 6. The specimens in the top row all are *S.*

Table 2. Results of the Principal Component analysis showing the eigenvalues for the first 10 principal components of the correlation matrix of the reduced set ($n = 22$) of natural log-transformed variables. The total variance accounted for using the morphometric variables we used was 15.9%.

Principal component	Eigenvalue	Proportion	Cumulative proportion
1	0.056	0.369	0.362
2	0.023	0.150	0.511
3	0.015	0.010	0.606
4	0.012	0.080	0.684
5	0.008	0.050	0.734
6	0.007	0.048	0.781
7	0.007	0.046	0.827
8	0.005	0.036	0.863
9	0.004	0.026	0.889
10	0.004	0.025	0.914

f. floridanus collected contemporaneously; these all show the posterodorsal process of the premaxilla extending caudad of the frontonasal suture (even with the terminus in USNM 76711), along with a short, marked intrusion of the frontal bone extending between the posterodorsal process of the premaxilla and the nasal bone. The caudally projecting posterodorsal process of the premaxilla is apparent in Central American taxa only in *S. g. gabbi*. The nasal bones themselves are significantly smaller in *S. f. floridanus* than in *S. f. hondurensis*: means in $\text{mm} \pm \text{SD}$ (min–max) are respectively 30.5 ± 1.0 (28.4 to 31.9), versus 34.8 ± 0.9 (33.2 to 36.3), $t_{17} = 9.2366, P < 0.0001, \delta_{\text{means}} = 4.3 \text{ mm}, 95\% \text{ CI} = 3.3\text{--}5.2 \text{ mm}$. The holotype of *S. f. costaricensis* is congruent with *S. f. hondurensis* in nasal bone length (35.3 mm), and in morphology in that the posterodorsal process of the max-

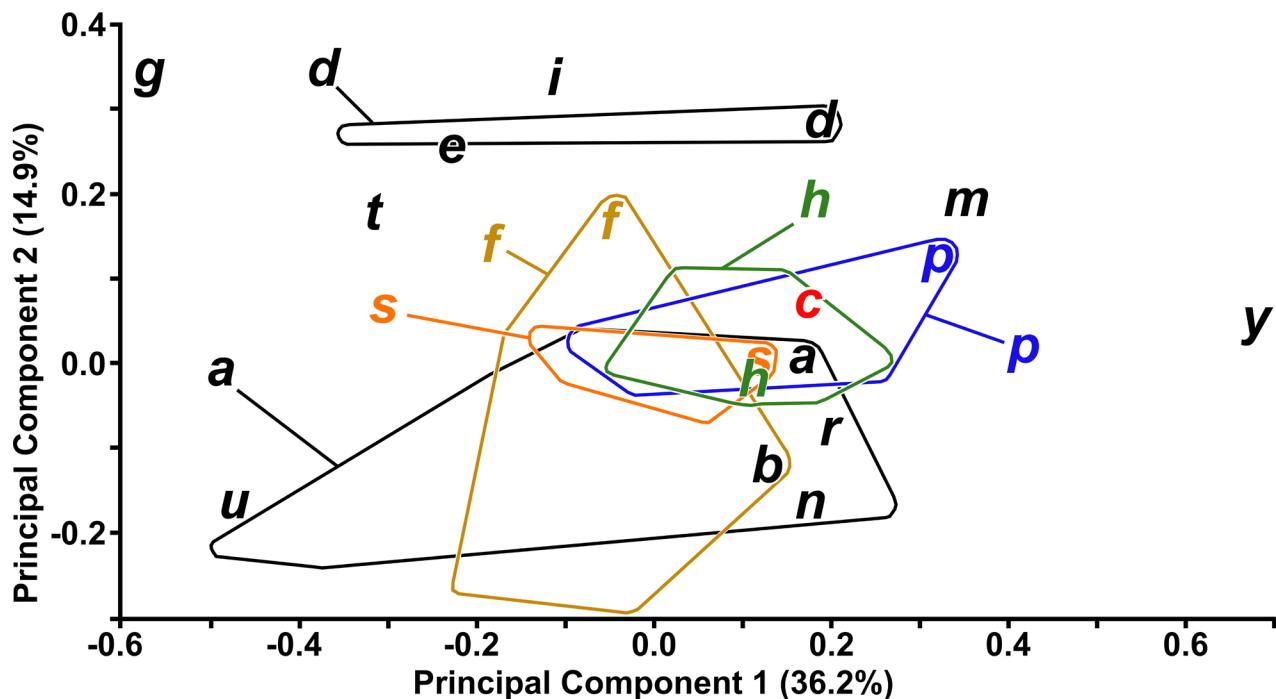


Figure 2. Graphical results of the Principal Component Analysis undertaken on the correlation matrix of the reduced set ($n = 22$) of natural log-transformed variables. Letter codes as follows, **a**: *S. f. aztecus*; **b**: *S. f. boylei*; **c**: *S. f. costaricensis*; **d**: *S. f. dicei*; **e**: *S. f. messorius*; **f**: *S. f. floridanus*; **g**: *S. f. gabbi*; **h**: *S. f. hondurensis*; **i**: *S. f. incitatus*; **m**: *S. f. margaritae*; **n**: *S. f. connectens*; **p**: *S. f. chiapensis*; **r**: *S. f. russatus*; **s**: *S. f. superciliaris*; **t**: *S. f. truei*; **u**: *S. f. daulensis*; **y**: *S. f. yucatanicus*. Where the labelled polygon encloses its same designation letter (e.g., **a**, *S. f. aztecus*, or **f**, *S. f. floridanus*), the enclosed letter shows the location of the holotype in the first two dimensions of multivariate space; otherwise, letters refer to holotype (e.g., **m**, *S. f. margaritae*, or **y**, *S. f. yucatanicus*).

Table 3. Results of the Principal Component Analysis showing the eigenvector scores of principal components 1 through 10 for the reduced set of natural log-transformed variables.

Character	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10
POSTORB	0.173	0.032	0.135	0.020	0.387	0.291	-0.791	-0.122	0.017	0.106
BROSTR	0.236	0.132	-0.045	-0.153	0.124	0.024	0.226	0.074	0.024	0.187
DEPROSTR	0.225	-0.023	0.198	-0.022	-0.012	0.121	0.002	0.013	-0.353	0.152
BBRAIN	0.104	-0.015	-0.052	0.053	-0.014	-0.040	0.070	-0.037	0.192	-0.067
ZYGO1	0.134	0.110	-0.039	-0.015	0.027	-0.040	0.008	-0.015	0.128	-0.070
NASALL	0.292	0.036	0.218	0.091	-0.154	-0.093	0.014	-0.046	0.052	-0.245
NASALW	0.336	-0.099	0.344	0.146	-0.027	0.300	0.231	-0.044	-0.266	-0.268
I2P2	0.167	0.178	0.121	-0.044	-0.119	-0.053	-0.011	-0.069	0.251	0.074
P2M3	0.094	0.143	0.003	-0.065	0.129	0.014	0.201	-0.009	0.042	0.093
HBRAIN	0.181	-0.168	0.123	0.052	-0.224	0.105	0.004	-0.104	-0.110	-0.222
HBULL	0.215	-0.237	-0.215	0.128	0.293	0.075	0.245	-0.207	-0.289	0.555
LPALFOR	0.206	0.161	0.132	-0.078	-0.187	0.132	0.105	-0.434	0.343	0.231
WPALFOR	0.341	0.079	-0.602	0.206	-0.525	0.059	-0.269	0.179	-0.108	0.089
PALLONG	0.175	0.133	0.152	0.017	-0.073	-0.086	0.013	-0.086	0.213	0.110
PALBRIDG	0.149	0.218	0.303	0.235	0.155	-0.582	-0.092	0.392	-0.119	0.175
WIDBULL	0.368	-0.456	-0.078	-0.697	0.075	-0.205	-0.079	0.184	0.149	-0.074
INTBD	0.103	0.141	-0.098	0.103	0.277	0.518	0.197	0.579	0.331	-0.082
INTBOC	0.154	0.080	-0.045	-0.046	-0.050	-0.116	0.113	0.165	-0.129	0.125
CHOANA1	0.136	0.625	-0.292	-0.291	0.265	-0.072	0.039	-0.245	-0.289	-0.344
DEPZYGO	0.222	-0.258	-0.282	0.465	0.366	-0.286	0.064	-0.250	0.291	-0.273
IP3	0.174	0.165	0.120	0.072	-0.112	-0.028	-0.071	0.047	0.211	0.185

illa is retracted rostrally relative to the caudal terminus of the nasal bone. One might expect that because of the longer GLS, the Central American taxon would naturally have a longer nasal bone. However, the Pearson product-moment correlation coefficients between GLS and NASAL suggest that this is not necessarily the case: for *S. f. hondurensis*, $R = 0.611$ ($R^2 = 0.373$, $P = 0.108$), whereas for *S. f. floridanus* $R = 0.753$ ($R^2 = 0.567$, $P = 0.007$); the holotype of *S. f. costaricensis* is almost identical in these two measurements to *S. f. hondurensis* AMNH 126203. We therefore predict that given larger sample sizes, *S. f. costaricensis* will be more closely allied to the pattern displayed by *S. f. hondurensis*.

A corollary of the shorter nasal bone in *S. f. floridanus* is that that bone does not extend as close to the orbit in *S. f. floridanus* as in *S. f. costaricensis* and *S. f. hondurensis* (Figure 3). Measured from the most posterolateral point of the nasal, the distance to the caudalmost point in the notch between the antorbital process and the frontal bone is 6.3 mm in *S. f. floridanus*, 3.5 mm in *S. f. hondurensis*, and 3.8 mm in *S. f. costaricensis*.

In the holotype of *S. f. costaricensis*, there is a small intrusion of frontal bone, the nasopremaxillary process of the frontal, separating the caudal tip of posterodorsal process of the premaxilla from the caudal tip of the nasal bone (measured from the tip of the posterodorsal process of the premaxilla, right: 3.3 mm, left: 4.5 mm). This intrusion is absent from the holotype of *S. f. hondurensis* and largely absent from examined specimens in this taxon, although some (e. g., AMNH 123378, Figure 6) have a minute manifestation of this feature. The frontonasal suture also may vary in shape, being either parallel with a transverse plane

starting laterally then angling rostrally to meet the opposite nasal bone at the medial plane, or on an approximate diagonal plane in a caudo-lateral to rostromedial direction. *Sylvilagus f. floridanus* displays the former, whereas *S. f. costaricensis* represents the latter condition; in this character, *S. f. hondurensis* is more similar to *S. f. floridanus*.

Other characters of the dorsal aspect are somewhat more shrouded. Pitting in the parietal and frontal bones has for example been employed as a character in distinguishing between taxa ([Wible 2007](#); [Ruedas et al. 2017](#); [Ruedas 2017](#)). However, there is a thin layer of tissue covering this portion of the skull of the holotype of *S. f. costaricensis* that, despite its slenderness, obscures this character. Similarly, the angle of the suture between the parietal and supraoccipital is somewhat descending ventrally from external to medial direction in *S. f. floridanus*, but is horizontal or ascending in *S. f. hondurensis*. However, it is not clearly visible in the holotype of *S. f. costaricensis*.

From a lateral perspective (Figure 5), the length of the zygomatic arches of *S. f. floridanus* differ significantly with little overlap in size from those of *S. f. hondurensis*: 31.0 ± 0.8 (29.3 to 32.2) v. 33.0 ± 1.1 (31.0 to 34.3), $t_{18} = 4.621$, $P = 0.0002$, $\delta_{\text{means}} = 2.0$ mm, 95 % CI = 1.1–2.9 mm. The zygomatic arch of *S. f. costaricensis*, at 32.2 mm, is at the upper limit of those of *S. f. floridanus*, but is firmly ensconced within those of *S. f. hondurensis*. The relative brevity of the zygomatic arch of *S. f. floridanus* gives it a more robust dorsoventral appearance than those of *S. f. costaricensis* and *S. f. hondurensis*; however, vertical depth of the zygomatic arch does not differ significantly among the taxa: 5.3 ± 0.5 (4.3 to 6.0) v. 5.0 ± 0.3 (4.6 to 5.3), $t_{17} = 1.3771$, $P = 0.1863$,

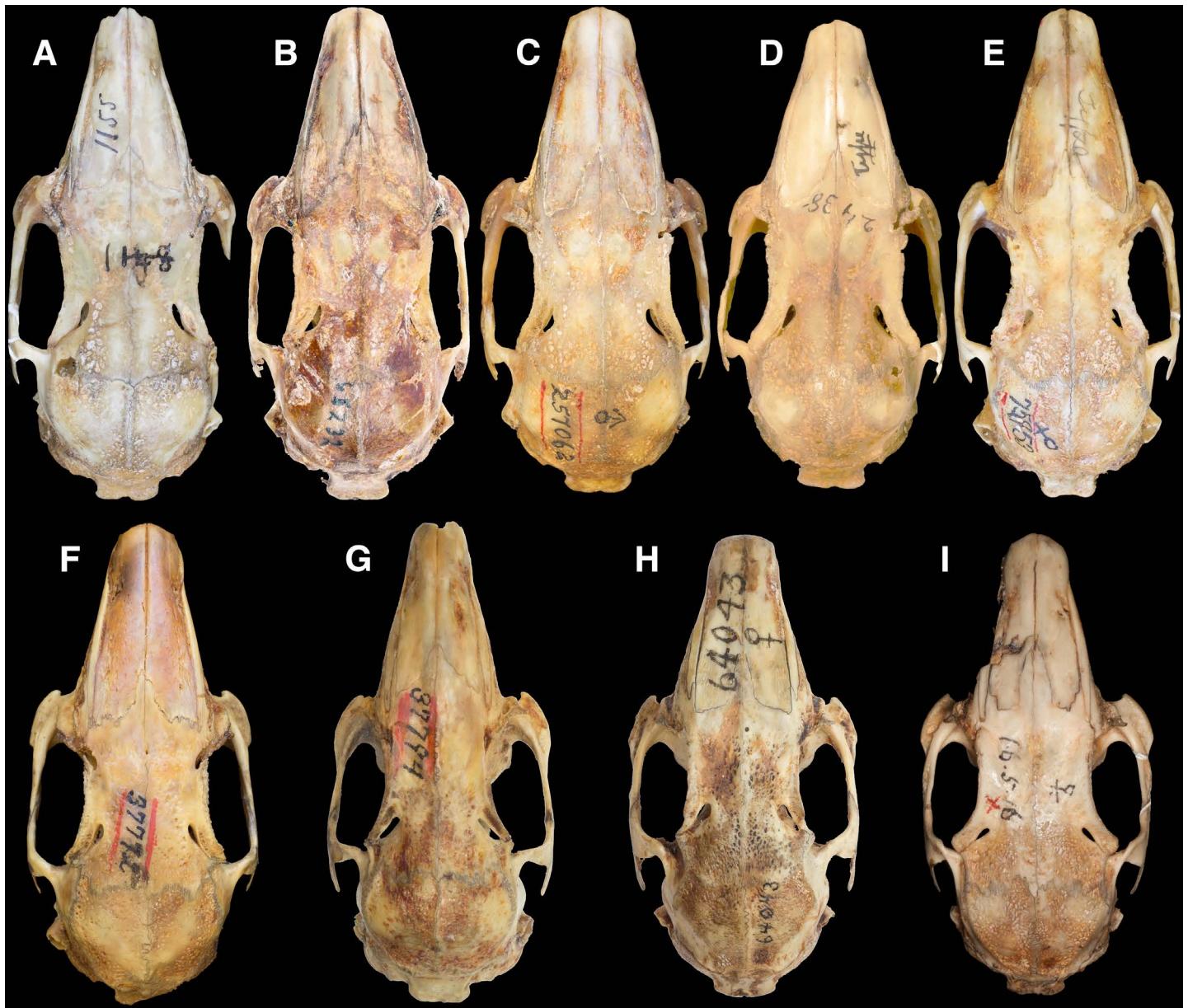


Figure 3. Dorsal views of the crania of the Central and South American taxa under consideration herein (current nomenclature), scaled to the same greatest length of skull. A: *Sylvilagus f. floridanus*, holotype, AMNH 1890/1155 (♀), greatest length of skull (GLS): 71.9 mm; B: *S. f. costaricensis*, holotype, UMMZ 65232 (♀), GLS: 76.3 mm; C: *S. f. hondurensis*, holotype, USNM 257062 (♂), GLS: 74.7 mm; D: *S. f. aztecus*, holotype, AMNH 3116/2438 (♂), GLS: 72.9 mm; E: *S. f. chiapensis*, holotype, USNM 75953 (♀), 78.9 mm; F: *S. f. yucatanicus*, holotype, USNM 37772 (♀), GLS: 81.1 mm; G: *S. g. gabbi*, lectotype, USNM 11371/37794 (♂), GLS: 70.9 mm; H: *S. dicei*, holotype, UMMZ 64043 (♀), 77.3 mm; I: *S. brasiliensis surdaster*, holotype, MNR 1901.6.5.16 (♀), GLS: 72.7 mm.

δ_{means} = 0.3 mm, 95 % CI = -0.21–0.7 mm; the holotype of *S. f. costaricensis* has a zygomatic depth of 5.3 mm, congruent with either taxon. As in length of nasal bones, this likely is a manifestation of the differences in GLS, given that *S. f. floridanus* and *S. f. hondurensis* have almost identical zygomatic length relative to GLS: 43.0 % and 43.2 %; 42.1 % in *S. f. costaricensis*. Also as in the nasal bones, however, the length of the zygomatic arch is significantly correlated with GLS in *S. f. floridanus* ($R = 0.761$, $R^2 = 0.579$, $P = 0.006$), but not in *S. f. hondurensis* ($R = 0.384$, $R^2 = 0.148$, $P = 0.307$).

Analysis of dental morphology. Substantial and substantive differences are exhibited in the dental morphology the taxa under consideration herein (Figure 7). In the tooth most commonly used to discriminate among species of lagomorphs, lower premolar 3, *S. f. costaricensis* differs

from *S. f. floridanus* in several key features: the anteroflexid is relatively deep and U-shaped, with a narrow constriction on the rostral surface, whereas in *S. f. floridanus*, the anteroflexid is broadly open and V-shaped; *S. f. hondurensis* displays a condition similar to *S. f. costaricensis*. Other Central and South American comparator taxa examined here display a more complex pattern on the rostral surface of pm3, with multiple anteroflexids or, if single, with a complex internal structure (e. g., *S. f. chiapensis*). In *S. dicei*, the rostral architecture of pm3 is of such complexity that a lingual anteroconid is identifiable as a region only, rather than as a distinct feature of the tooth.

The central angle, an almost universal feature of the lagomorph rostral hypoflexid, is present as a singular inflection in *S. floridanus*, but as an unusual double inflection in *S.*

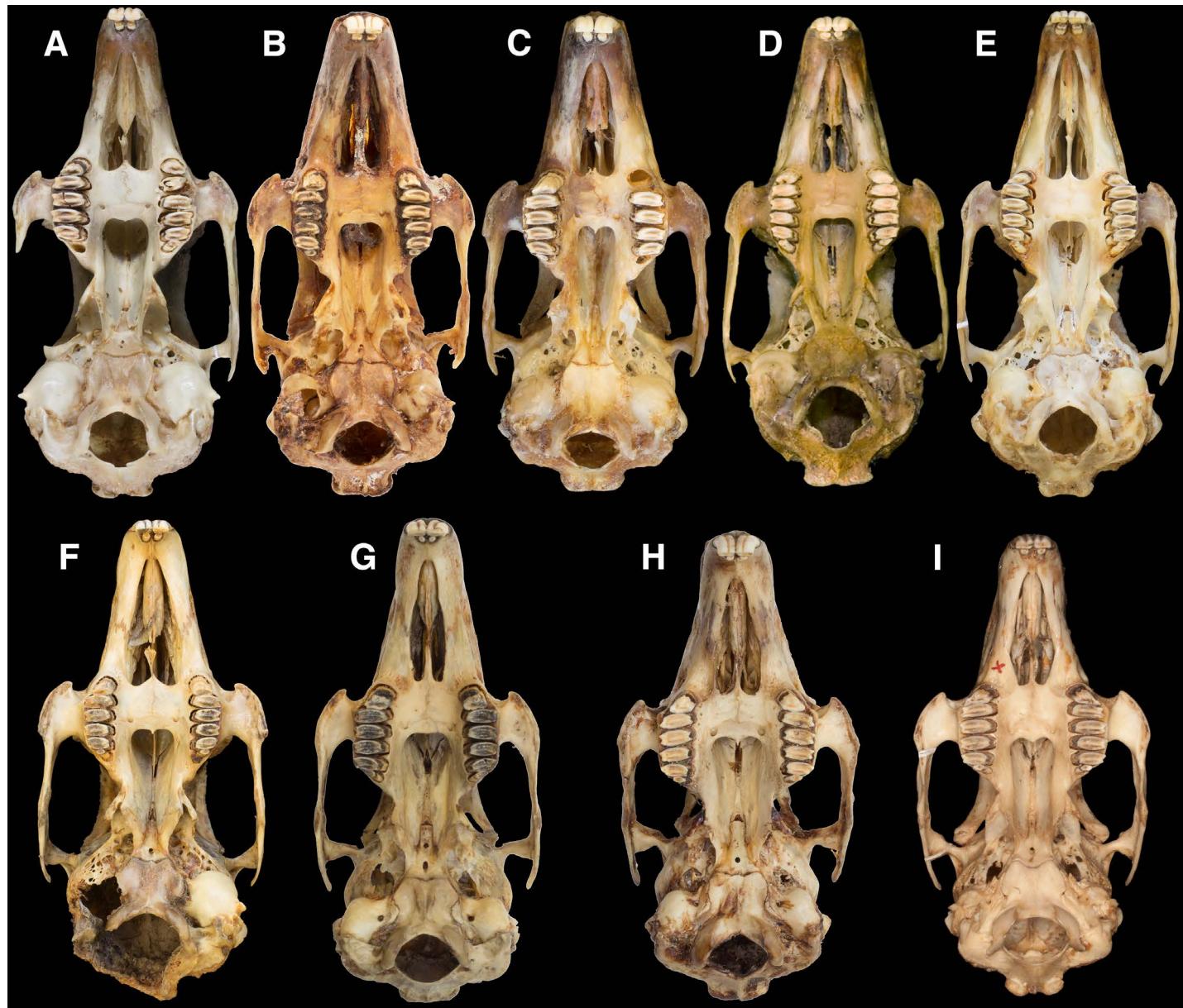


Figure 4. Ventral views of the crania of the Central American taxa under consideration herein, scaled to the same width. Specimens shown are the same as in Figure 3 and disposed in the same order.

f. costaricensis. The central angle is indistinct in *S. f. chiapensis* because of the complexity of the enamel pattern, and possibly double in the lectotype of *S. g. gabbi*. *Sylvilagus brasiliensis surdaster* displays a very weak central angle. The caudal surface of the hypoflexid is relatively smooth (labial portion) to somewhat crenulate (lingual portion) in *S. f. floridanus* versus highly complex and strongly crenulate in *S. f. costaricensis*. Other regional taxa display the range from similarly crenulate morphologies (*S. dicei*, *S. f. yucatanicus*) to somewhat less crenulate (*S. f. aztecus*, *S. f. chiapensis*), to completely smooth (*S. b. surdaster*).

While *S. f. floridanus* definitively does not exhibit a paraflexid (being instead convex), there is a slight inflection in that portion of pm3 of *S. f. costaricensis*. *Sylvilagus f. hondurensis* has a concavity at the base of the anteroconid that we likewise interpret as a paraflexid, as does *S. b. surdaster*. Otherwise, this surface of the tooth is relatively featureless

from slightly convex (*S. f. yucatanicus*) to slightly concave (*S. f. aztecus*, *S. f. chiapensis*).

In PM2 of *S. f. floridanus*, the hypoflexus is marked by a slight depression, barely demarcating mesial from distal hypercones. In *S. f. costaricensis*, there is a distinct, deep, U-shaped hypoflexus in PM2, resulting in distinct mesial and distal hypercones. The area of PM2 between postcone and poststyle PM2 in *S. f. floridanus* is convex, with no trace of a metaflexus. In contrast, *S. f. costaricensis* has a small but distinct inflection marking the metaflexus.

The first upper incisor, although generally neglected as featureless among lagomorphs, also is distinct between the two taxa: in *S. f. costaricensis*, lingual and labial cusps are subequal in height relative to the rostral groove demarcating them; *S. f. hondurensis* is almost identical in the morphology of its I1. In contrast, the lingual cusp of I1 in *S. f. floridanus* is distinctly expanded rostrally relative to the labial cusp.

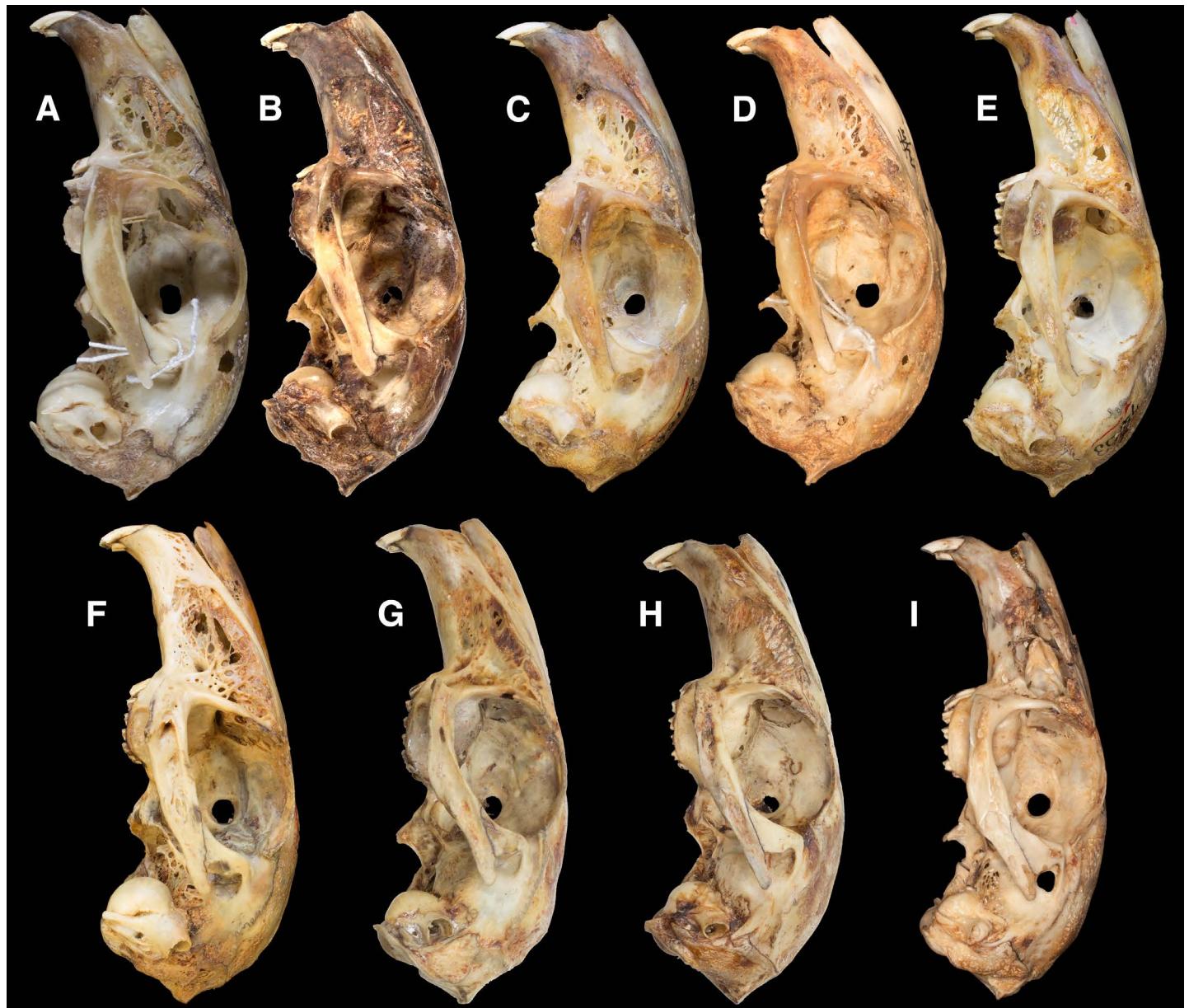


Figure 5. Lateral views of the crania of the Central American taxa under consideration herein, scaled to the same width. Specimens shown are the same as in Figure 3 and disposed in the same order. Inverted for consistency are: *S. f. costaricensis* and *S. f. aztecus*. The latter also was not taken on a completely lateral plane, making the profile appear more dorsoventrally bowed than it is in reality.

An additional, and unusual, feature is present in I2 of *S. f. costaricensis*. This tooth is invariably small, cylindrical, with a circular cross section in every species of *Sylvilagus* we have examined to date. However, in *S. f. costaricensis*, I2 is roughly triangular in cross section, with the base caudal and apex rostral, and has two distinct grooves on the caudal aspect of the tooth (Figure 8). The only other taxon of *Sylvilagus* that we have examined for this study to display these characters is *S. f. hondurensis*.

Taxonomic conclusion: identity of *Sylvilagus floridanus costaricensis*. In light of the foregoing analyses, particularly those based on cranial and dental characters, it is clear that the differences between *S. f. costaricensis* and *S. f. floridanus* are interspecific in nature insofar as taxa of *Sylvilagus* are concerned. As described above, the skulls differ significantly in magnitude in a number of measurements; they also dif-

fer significantly in a number of cranial and dental characters. However, *S. f. costaricensis* are not distinct from *S. f. hondurensis* in the same characters. Most significantly, both taxa share two unique synapomorphies: a triangular cross section to I2, which is marked by two grooves on its caudal facies. We therefore consider that *S. f. costaricensis* are not distinct from *S. f. hondurensis* at the species level. *Sylvilagus floridanus hondurensis* was described by Edward A. Goldman on 30 July 1932; *S. f. costaricensis* by William P. Harris on 28 June 1933. As a consequence, the name *hondurensis* has priority. Until a greater number of specimens are available for examination of population level and broader extent of geographic variation, there are sufficient differences between the two taxa—for example, the comparative extent and degree of crenelation of the caudal aspect of the pm3 hypoflexid—that we recommend the prudent cause of action to keep

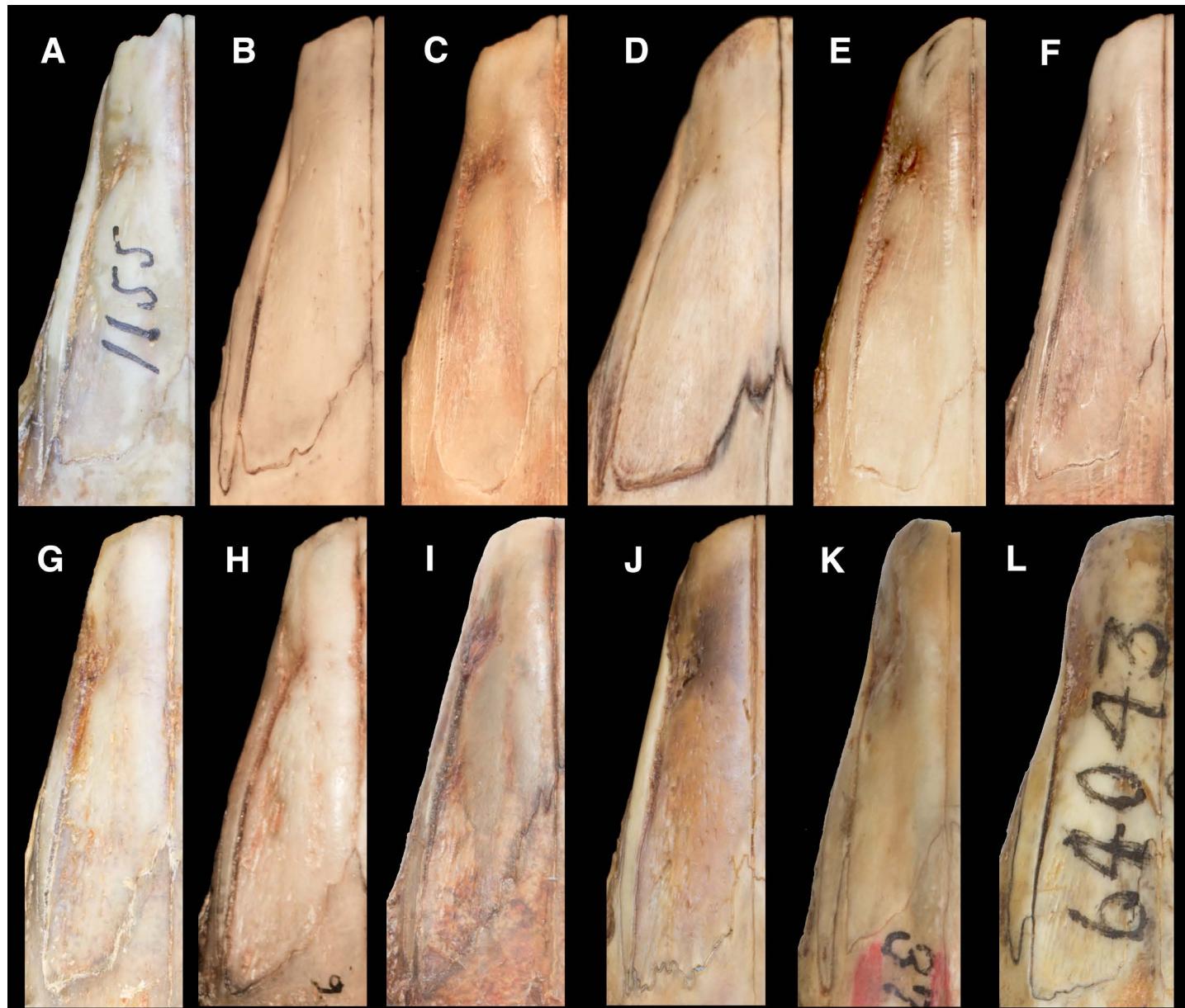


Figure 6. Detail of the left frontonasal suture and posterodorsal process of premaxillary bone in selected individuals, all scaled to the same anteroposterior length for consistency. A: *Sylvilagus f. floridanus*, AMNH 1890/1155 (♀, holotype; greatest length of nasal, in straight line from facialmost to caudalmost point: 30.4 mm); B: USNM 70870 (♀; 30.6 mm); C: USNM 76711 (♂; 29.4 mm); D: USNM 77113 (subadult ♂; 22.4 mm; note the difference in proportions of dimensions); E: USNM 77114 (♀; 31.1 mm); F: USNM 77115 (♂; 31.4 mm); G: *S. f. hondurensis*, USNM 257062 (♂, holotype; 34.2 mm); H: *S. f. hondurensis*, AMNH 126146 (♂; 35.0 mm); I: *S. f. costaricensis*, UMMZ 65232 (♀, holotype; 35.3 mm); J: *S. f. yucatanicus*, USNM 37772 (♀, holotype; 37.2 mm); K: *S. g. gabbi*, USNM 11371/37794 (♂, lectotype; 27.9 mm); L: *S. dicei*, UMMZ 64043 (♀, holotype; 33.6 mm). Key features include: caudal terminus of the posterodorsal process of premaxilla relative to the caudal terminus of the nasal bone, and absence, presence, and rostral extent of process on frontal bone extending between posterodorsal process of premaxilla and posterolateral margin of nasal bone (nasopremaxillary process of frontal bone).

both names, as *Sylvilagus hondurensis hondurensis* E. A. Goldman, 1932, and *S. hondurensis costaricensis* Harris, 1933.

Discussion

We consider our study foundational to any future regional or focused taxonomic study of biogeography, evolution, and phylogeny of cottontails. Revolutions in the practice of taxonomy and phylogenetics have led to a more nuanced understanding of species delimitation and, as a result, of species boundaries. [Ruedas et al. \(2017\)](#) noted that there is a lack of cohesion between philosophical and operational approaches to species; as in that work, we apply what [Sangster \(2014\)](#) called “methodological introgression” of species concepts applied in an operationally coherent manner to

“discover, describe, and order into our classification system” ([Mayden 1997](#):387) the individuals within, or constituting, the species category, independent of the properties of the species category. We used previously ([Ruedas et al. 2017](#)) an integrative approach to species delimitation (sensu [Padial et al. 2010](#); [Schlick-Steiner et al. 2010](#)) as implemented by [Naomi \(2011\)](#). This approach, using a morphological character set vastly expanded over that of [Hershkovitz \(1950\)](#), resulted in hypotheses of taxonomic species in *Sylvilagus* that reflected the underlying biological reality imposed by abiotic criteria such as elevation, temperature, and precipitation regimes, soils, etc., as well as the effects of those abiotic factors on vegetation, which ultimately is reflected by the species inhabiting the ecosystems under

consideration. While there have been controversies regarding the application of, for example, the phylogenetic species concept to particular instances (e.g., [Groves and Grubb 2011](#) vs. [Zachos et al. 2013](#); [Zachos 2015](#)), the integrative approach yields coherent and biologically relevant taxonomic hypotheses: a single widespread species of *Sylvilagus* (*S. "brasiliensis"* *sensu* Linnaeus 1758) distributed from the Atlantic to the Pacific coasts of South America, from 0

to >5,000 m in elevation, and from Veracruz, México, in the north, to Argentina in the south is neither coherent, nor biologically realistic. The taxonomic hypotheses we propose herein for *S. florianus* follow from Allen's hypothesis that geography, while not the ultimate arbiter of taxonomy, nevertheless strongly affects species limits: "Hence the single record from so remote a point [...] has of late seemed open to serious question" ([Allen 1890](#):192). The bioge-

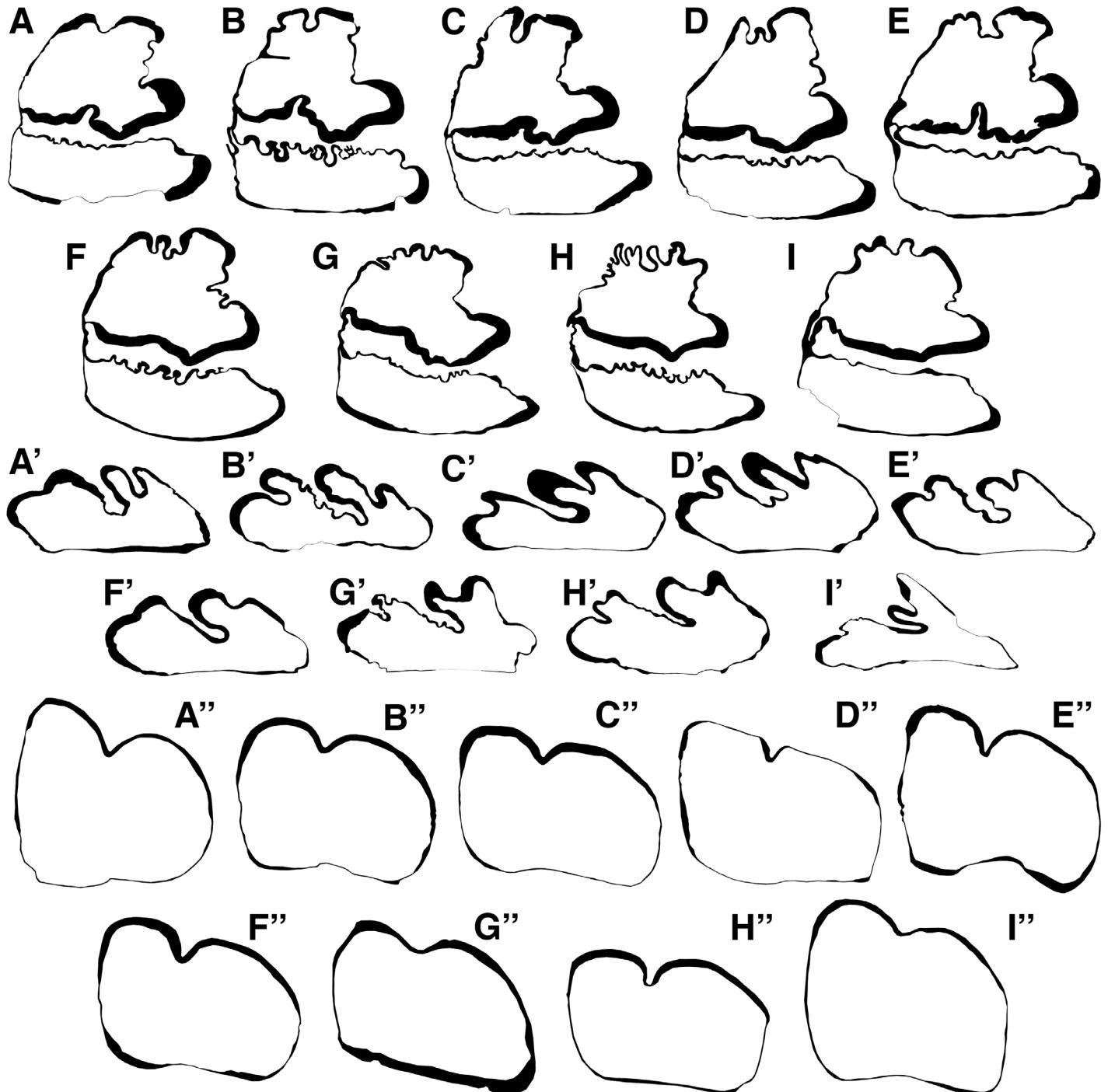


Figure 7. Crown views of the enamel structure of lower premolar 3 (upper two rows), upper premolar 2 (middle two rows), and first upper incisor (lower two rows) for the Central American taxa under consideration herein. Specimens in each triplet are, A: *Sylvilagus f. florianus*, holotype, AMNH 1890/1155 (♀); B: *S. f. costaricensis*, holotype, UMMZ 65232 (♀); C: *S. f. honurensis*, holotype, USNM 257062 (♂); D: *S. f. aztecus*, holotype, AMNH 3116/2438 (♂); E: *S. f. chiapensis*, holotype, USNM 75953 (♀); F: *S. f. yucatanicus*, holotype, USNM 37772 (♀); G: *S. g. gabbi*, lectotype, USNM 11371/37794 (♂); H: *S. dicei*, holotype, UMMZ 64043 (♀); I: *S. brasiliensis surdaster*, holotype, MNH 1901.6.5.16 (♀). Some images were rotated horizontally in order for all perspectives to be the same; all images are scaled to the same width so as to show differences in proportion rather than in size. In each image, rostral is to the top of the figure, labial is to the right of the figure.

graphic breaks in Central and South America, reflected in the taxonomy of numerous taxa, are likewise reflected in *Sylvilagus*. In South America, rivers have been implicated in speciation events in small mammals ([da Silva and Patton 1998](#); [Matocq et al. 2000](#); [Patton et al. 2000](#)), primates ([Wallace 1852](#); [Boubli et al. 2015](#)), and birds ([Naka and Brumfield 2018](#)) alike. *Sylvilagus* are similarly affected by vicariant effects. In the instance of *Sylvilagus*, the effects of strong ecological change brought about by the xeric conditions at the Isthmus of Tehuantepec also appear important.

From a biogeographic perspective, the patterns of speciation revealed by our taxonomic framework are congruent with those of other taxa. For example, *Bassariscus astutus* is restricted to the north and west of the Isthmus of Tehuantepec, and its sister species *B. sumichrasti*, while somewhat overlapping the range of *B. astutus* in coastal Guerrero and Oaxaca, México, largely is restricted to the east and south of the isthmus. Similarly, taxa in the *Reithrodontomys sumichrasti* species complex (Rodentia: Cricetidae: Neotominae) show an analogous distribution and hypothesized relationships ([Hardy et al. 2013](#)) as we propose here for *Sylvilagus*. In the case of mice of the genus *Habromys* (Rodentia: Cricetidae: Neotominae), six of the seven species in the genus are restricted to the north and west of the isthmus, and only one species, *H. lophurus*, is restricted to the south and east of the isthmus ([León-Paniagua et al. 2007](#)). This pattern of sister taxa of mammals exclusively distributed to one or the other side of the Isthmus of Tehuantepec is a repeating evolutionary and biogeographic motif ([Sullivan et al. 2000](#); [Rogers et al. 2007](#)).

One result of the integration of distinct data streams to assess taxonomic relationships is the stark difference in taxonomic information content that is brought about by using morphometric (continuously variable measurement data) versus discrete character data. Our principal components analysis (Figure 2) shows that there is substantial overlap in morphology among the distinct taxa of *Sylvilagus* when these are subjected to morphometric analysis. Of note, the principal components analysis is an a posteriori test, thus there is no prior hypothesis imposed on the ensuing result. In contrast, an a priori test such as a discriminant function analysis essentially “forces” the output to conform to the a priori hypothesis (*i. e.*, predict group—species—membership) because it describes a function that will distinguish among the *predefined* samples groups (*i. e.*, presumptive taxa). As a result, a posteriori tests are preferable in taxonomy because they do not impose a hypothesis on the data, rather the results derived from the data are a reflection of the presumptively true nature of the underlying taxonomic reality. In the present instance, however, the two statistically significant principal components only accounted for 7.9 % of the morphological variation among the groups. That is to say, conversely, that 92.1 % of the mensural variation went unaccounted for. Thus, either a posteriori or a priori tests would be on tenuous grounds in terms of establishing—or even testing—a robust taxonomic hypothesis, no doubt

because of the morphologically conservative, or strongly homomorphic nature of cranial morphology in *Sylvilagus*, and indeed, in Leporidae in general. Because of this, and based on the results of our morphometric analysis, taxa clearly distinguished in the analysis (*e. g.*, *gabbi*, *dicei*, *yucatanicus*) are hypothesized to be definitively distinct; however, taxa in our sample that overlap in multivariate space are not definitively demonstrated to be the same, *i. e.*, subject to Type II error. It is in these circumstances that inspection of character data becomes increasingly valuable: assessment of discretely variable characters in morphologically conservative taxa, particularly when such characters may be discretely distinct in morphometrically indistinguishable groups, can result not only in identification and discrimination of different taxa but also in the possibility of inferring evolutionary relationships among the groups or taxa in question. Character data (qualitative) can be useful for identifying and classifying organisms, while morphometric data (quantitative) may under certain circumstances be useful for identifying organisms, as well as for studying the physical (mensural) characteristics of organisms and their variation. Excessive reliance on either, particularly morphometric data, may result in erroneous taxonomic hypotheses.

Unanswered, however, remains the question of: why are there so many species of *Sylvilagus* present in Costa Rica? We hypothesize that the present biodiversity is a combination of the ecological heterogeneity of Costa Rica, along with its location. We have previously documented, using molecular approaches ([Ruedas et al. 2017](#)), that there were multiple invasions of South America by *Sylvilagus*. Some of the remaining biodiversity of Costa Rican *Sylvilagus* may be essentially remnants of these multiple invasions: taxa that resulted from populations that remained in place as other populations continued to expand the dispersal front. As remnant populations, their conservation therefore becomes ever more imperative.

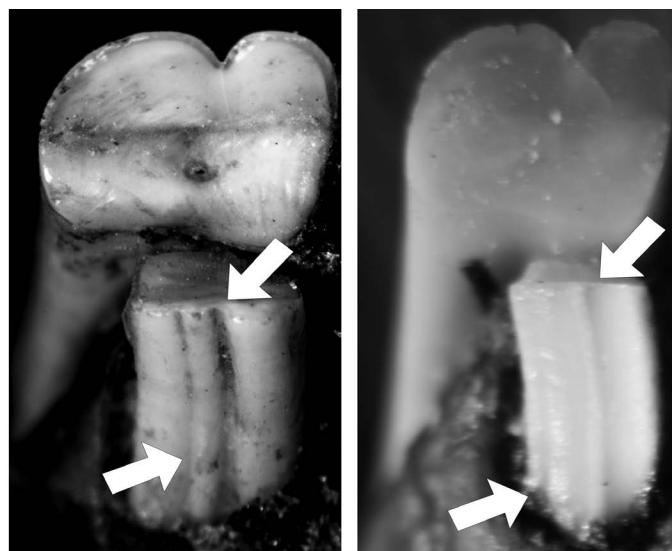


Figure 8. Occlusal perspective of the first and second right upper incisors of *S. f. costaricensis* (left) and *S. f. hondurensis* (right). Arrows mark the two grooves on the caudal aspect of I2. Note the unusual triangular cross section of I2, rather than the almost universal condition for *Sylvilagus* of a circular cross section for this tooth.

Taxonomic Conclusions. On the basis of the foregoing, we recognize the following taxa in Central America south of the Isthmus of Tehuantepec to the Panama–Colombia border: *Sylvilagus dicei*, *S. gabbi*, and *S. hondurensis*.

Sylvilagus hondurensis
Honduras cottontail

Sylvilagus floridanus hondurensis Goldman, 1932:122. Type locality, "From Monte Redondo, about 30 miles northwest of Tegucigalpa, Honduras (altitude about 5,100 feet [1554 m])." The village of Monte Redondo lies at ca. 860 m rather than, as indicated by Goldman, at 1,554 m. Roads lead NW from Monte Redondo to higher elevations. The 1,554 m contour on a road emanating from Monte Redondo is at ca. 14° 18' 42" N, 87° 18' 24" W. We speculate that Goldman referred to the higher elevations today contained within the Reserva de Vida Silvestre Corralitos (Francisco Morazán, Honduras), just NW from the village of Monte Redondo. Holotype: USNM 257062.

Sylvilagus floridanus costaricensis Harris, 1933:3. Type locality, "from Hacienda Santa María, Province of Guanacaste, Costa Rica, altitude 3,200 feet" (975 m). The Hacienda Santa María ranger station, inside Guanacaste National Park is located at 10° 45' 52" N, 85° 18' 11" W, 844 m, thus corresponding fairly closely with Harris' description. Holotype: UMMZ 65232.

Sylvilagus yucatanicus
Yucatan cottontail

Lepus aquaticus: Allen, 1877:365 (part). Not *Lepus aquaticus* Bachman, 1837. Allen noted that "In the collection are quite a number of specimens from the provinces of Vera Cruz and Yucatan in Southern México. These differ from specimens from Mississippi and Louisiana in no very marked degree." He later revised his opinion ([Allen 1890b](#)) and transferred these specimens to *Lepus sylvaticus* [= *S. floridanus*].

Lepus sylvaticus aztecus: Allen, 1890:191, from "Merida, Yucatan"; not Allen 1890:188, from "Tehuantepec City".

Lepus floridanus yucatanicus Miller, 1899:384. Type locality, "Merida, Yucatan" (correctly spelled "Mérida, Yucatán" by [Hall 1951](#):159). Holotype, USNM 11441/37772.

Sylvilagus floridanus yucatanicus: Lyon, 1904:336. Name combination.

Acknowledgments

This paper honors the life work of Alfred "Al" Lunt Gardner. Many of the specimens examined here were done so with permission granted by Al, before and after fascinating discussions with him on taxonomy and biogeography of rabbits and American mammals in general. Much of the work was inspired, influenced, and illuminated by Al's wisdom and phenomenal breadth of knowledge, all of which he generously shared and continues to share with all who visit the

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Appendix 1

Specimens examined:

The taxa below are listed under their original names, with the currently accepted synonym following in square brackets. Latitude and longitude coordinates are provided in datum WGS84. Museum abbreviations as follows, AMNH: American Museum of Natural History, New York; MCZ: Museum of Comparative Zoology, Harvard University; MVB: Museum of Vertebrate Biology, Portland State University, Portland, Oregon; TTU: Natural Science Research Laboratory, The Museum, Texas Tech University, Lubbock, Texas; UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Michigan; USNM: United States National Museum—Smithsonian Institution, Washington, D.C.

***Sylvilagus daulensis* J. A. Allen, 1914:199** [= *Sylvilagus brasiliensis surdaster*; following circumscription of *S. brasiliensis* to the Pernambuco Endemism Center (Ruedas et al. 2017), we hypothesize that this taxon is unlikely to be conspecific with *S. brasiliensis*]. Ecuador: (Guayas Prov.); Daule [ca. 1° 51' 42" S, 79° 58' 44" W, ~8 m]: holotype, AMNH 34671 (♀).

***Sylvilagus (Tapeti) fulvescens* J. A. Allen, 1912:75** [= *S. fulvescens*; see Ruedas et al. 2019]. Colombia: Departamento de Cauca: "Belén (alt. 6000 ft.) Western Andes" [Lawrence (1993) noted that the label incorrectly gave the altitude as 6,000 feet, and that the actual collecting locality was "Colombia: Cauca; Belén, west of Papayan [sic.], 10,000 ft (3050 m)." There is a town named Belén (Municipio de Inzá) ca. 2° 28' 11" N, 76° 02' 21" W, ~1,705 m, some 65 km airline distance from Popayán (ca. 2° 27' 05" N, 76° 36' 46" W, ~1,725 m) with nearby elevations in the range noted by Lawrence; the eminence closest to Belén of that elevation (~8 km W) is ca. 2° 27' 40.7" N, 76° 06' 22.1" W; the AMNH database lists Belén as Municipio Guapí; however, the Belén in Mpo. Guapí is at ca. 2° 30' 28" N, 77° 35' 49" W, and more pointedly at ~72 m, approximately 173 km (airline distance, bearing 271°) from Belén, Inzá, Cauca]: holotype, AMNH 32360 (♀).

***Sylvilagus kelloggi* Anthony, 1923:9** [*S. b. kelloggi*; following circumscription of *S. brasiliensis* to the Pernambuco Endemism Center (Ruedas et al. 2017), we hypothesize that this taxon is unlikely to be conspecific with *S. brasiliensis*]. Ecuador: Loja Province; Cordillera Occidental, Guachanamá, east of Alamor and northeast of Celica, 9,050 ft (2,760 m), headwaters of the Río Chira [ca. 4° 25' 42" S, 79° 13' 19" W]: holotype, AMNH 60515 (♂).

***Sylvilagus chillae* Anthony, 1923:12** [*S. b. chillae*; following circumscription of *S. brasiliensis* to the Pernambuco Endemism Center (Ruedas et al. 2017), we hypothesize that this taxon is unlikely to be conspecific with *S. brasiliensis*]. Ecuador: El Oro Province; trail between Salvias and Zaraguro, 6,000 ft (1,830 m) SW flank Cordillera de Chilla [ca. 3° 37' 2" S, 79° 30' 12" W; the AMNH catalog lists as locality for this specimen: "Ecuador, Salvias". Salvias is a rural "parroquia" (administrative subdivision) in Sector

Oriental of Cantón Zaruma, El Oro province]: holotype, AMNH 60511 (♀).

***Sylvilagus (Tapeti) salentus* J. A. Allen 1913:476** [= *S. salentus*; see Ruedas et al. 2019]. Colombia: Caldas; Salento, at head of Río Quindío, west of Mount Tolima, western Quindío Andes, 7,000 ft [~2,135 m; ca. 4° 38' 31.6" N, 75° 33' 30.6" W; AMNH catalogue lists as Dept. Chocó, however, Salento currently is in Depto. Quindío; the Depto. Caldas is north of Quindío and separated from the latter by Depto. Risaralda]: holotype AMNH 33050 (♂).

***Sylvilagus dicei* Harris, 1932:1** [*S. dicei*; see Diersing, 1981]. Costa Rica: [San José Prov., Cantón de Dota]: El Copey de Dota [ca. 9° 38' 50" N, 83° 55' 05" W, ~1,850 m]: holotype, UMMZ 64043 (♀). Costa Rica: Provincia de Cartago; 9° 33' 12.3" N, 83° 41' 24.8" W, 2,830 m: TTU 163828 (♂). Puntarenas: Cedral de Miramar, 10° 12' 46.38" N, 84° 40' 34.28" W, MVB 5036 (JMM-001-2018; ♀). Heredia: Los Cartagos, Santa Bárbara, 2,080 m, 10° 08' 55.7" N, 84° 09' 11.6" W: MVB 5065 (JMM-001-2017; ♂). Heredia: Varablanca, 1,700 m, 10° 11' 05.31" N, 84° 09' 18.17" W: MVB 5037 (JMM-002-2017; ♀).

***Lepus sylvaticus aztecus* J. A. Allen, 1890b:188** [= *S. floridanus aztecus*]. México: Oaxaca; Tehuantepec City [ca. 16° 20' N, 95° 14' W, ~50m]: holotype, AMNH 3116/2438, ♂; AMNH 143454, 143455, 143457, 143458 (all ♀), 2439, 2440, 2441, 142550, 143456, 143459, 145166 (all ♂). México: Oaxaca; Dist. Tehuantepec, Las Tejas, AMNH 143460 (♂). México: Oaxaca; Juchitán [ca. 16° 26' N, 95° 01' W, ~25m]: AMNH 186409 (♀). México: Oaxaca; Juchitán, Palomares [possibly ca. 17° 08' 17" N, 95° 03' 45" W, ~120 m], AMNH 254522 (sex unknown).

***Sylvilagus boylei* J. A. Allen, 1916:84** [*S. f. superciliaris*]. Colombia: Departamento del Atlántico; La Playa, near Barranquilla, 150 ft [46 m; La Playa was originally a "corregimiento" (Puerto Colombia) and is currently a district of Barranquilla better known as "Eduardo Santos"; an elevation of ca. 46 m in the vicinity of La Playa could be ca. 11° 01' 04.6" N, 74° 51' 52.6" W]: holotype, AMNH 37794 (♀). [Allen (1916:84) noted that the "skull appears to have been lost in transit." However, Lawrence (1993) subsequently reported that the holotype was constituted by a skin and skull; we examined a *Sylvilagus* with the number corresponding to the holotype of this taxon and characteristics definitively identifying it as a South American species.]

***Lepus floridanus chiapensis* Nelson, 1904:106** [= *S. f. aztecus*]. México: Chiapas; San Cristobal [ca. 16° 43' 57" N, 92° 38' 44" W, ~2,160 m. Fisher and Ludwig (2015) noted that E. W. Nelson and E. A. Goldman, collectors of the holotype (Nelson 1904), listed "8,200 ft" (2,499 m) in their field catalogue]: holotype, USNM 75953 (♀). Guatemala: Dpto. Totonicapán: Momostenango [ca. 15° 02' 42.5" N, 91° 24' 29" W, ~2,210 m]: AMNH 69275 (♂). Guatemala: Jutiapa Dept.; Municipalidad de Moyuta, Colonia Montúfar, Aldea El Paraíso [Moyuta: ca. 14° 2' 19" N, 90° 4' 51" W, ~1,276 m]: AMNH 243827 (♀). México: Chiapas: 3.5 mi S of Comitán; [ca. 16° 12' 28" N, 92° 06' 40" W, ~1,595 m], AMNH 175078 (♂).

***Lepus floridanus connectens* Nelson, 1904:105** [*S. f. connectens*]: México: Veracruz; Chichicaxtle [we located two localities of this name in Veracruz, only ca. 9.5 km distant from each other: at ca. 19° 21' 24.9" N, 96° 22' 43.2" W, ~30 m, and 19° 20' 32.3" N, 96° 28' 02.7" W, ~127 m]: holotype, USNM 63660 (♂).

***Sylvilagus floridanus costaricensis* Harris, 1933:3** [*S. hondurensis costaricensis*; this paper]. Costa Rica: Provincia de Guanacaste: Hacienda Santa María, 3,200 ft [975 m] ("a large ranch just within the cloud forest on the western slope of the Cordillera de Guanacaste, 22 miles northeast of Liberia") [ca. 10° 45' 53" N, 85° 18' 11.8" W, ~845 m]: holotype, UMMZ 65232 (♀). Costa Rica: Provincia de Guanacaste: Parque Nacional Palo Verde, Bagaces, 15 m. 10° 20' 40.46" N, 85° 20' 21.83" W: MVB 5066 (MVB JMM-003-2016; ♀). Costa Rica: Provincia de Puntarenas: Chomes, 11 m. 10° 02' 35.91" N, 84° 54' 32.77" W: MVB 5056 (JMM-015-2017; ♂). Costa Rica: Provincia de Puntarenas: Chomes, 7 m. 10° 02' 26.77" N, 84° 54' 35.55" W: MVB 5067 (JMM-016-2017). Costa Rica: Provincia de Guanacaste: close to Parque Nacional Rincón de la Vieja, 724 m. 10° 46' 15.87" N, 85° 21' 30.78" W: MVB 5057 (JMM-017-2017). Costa Rica: Provincia de Guanacaste: close to Parque Nacional Rincón de la Vieja, 720 m. 10° 46' 05.77" N, 85° 21' 21.87" W: MVB 5058 (JMM-018-2017). Costa Rica: Provincia de Guanacaste: Cañas, 57 m. 10° 24' 52.71" N, 85° 06' 33.91" W: MVB 5059 (JMM-019-2017). Costa Rica: Provincia de Cartago: El Silencio, La Suiza, Turrialba, 897 m. 9° 52' 27.75" N, 83° 36' 50.4" W: MVB 5048 (JMM-020-2017; ♀). Costa Rica: Provincia de Guanacaste: Cañas, 61 m. 10° 25' 17.43" N, 85° 06' 35.91" W: MVB 5068 (JMM-021-2017). Costa Rica: Provincia de Guanacaste: Cañas, 68 m. 10° 24' 02.23" N, 85° 06' 06.67" W: MVB 5060 (JMM-022-2017; ♂). Costa Rica: Provincia de Guanacaste: Cañas, 43 m. 10° 24' 10.84" N, 85° 07' 12.45" W: MVB 5061 (JMM-023-2017; ♀). Costa Rica: Provincia de Guanacaste: main road, 50 m before the entrance to Parque Nacional Rincón de la Vieja, 797 m. 10° 46' 25.22" N, 85° 20' 58.20" W: MVB 5062; JMM-024-2017 (♂).

***Lepus sylvaticus floridanus* J. A. Allen, 1890a:160** [= *Sylvilagus floridanus floridanus*]. United States: Florida: Brevard Co., San Sebastian River, near Micco [ca. 27° 50' 04" N, 80° 30' 24.2" W, ~2 m]: holotype, AMNH 1890/1155 (♀). United States: Florida: Brevard Co.; Micco, Oak Lodge, topotype: USNM 70870 (♀). United States: Florida: Brevard Co.; Micco, topotypes: USNM 77114 (♀), 76711, 77113, 77115 (all ♂). United States: Florida: Seminole and Volusia counties; Lake Harney [ca. 28° 46' 36" N, 81° 03' 19" W, ~1 m]: USNM 78756, 78757, 80334, 80335 (all ♀), 78754, 78755 (all ♂).

***Sylvilagus floridanus hondurensis* Goldman, 1932:122** [*S. hondurensis hondurensis*; this paper]. Honduras: [Departamento de Francisco Morazán]: Monte Redondo, about 30 miles northwest of Tegucigalpa (altitude about 5,100 feet) [the bearing and distance from Tegucigalpa and elevation suggest this locality may more likely be located in the Reserva de Vida Silvestre Corralitos, perhaps ca. 14° 18' 46" N, 87° 18' 18" W]: holotype, USNM 257062 (♂). Honduras: Francisco Morazán: Distrito Central; Comayaguela [ca.

14° 06' 38" N, 87° 13' 57" W, ~1205 m]: AMNH 123378 (sex unknown). Honduras: Francisco Morazán; Orica, El Caliche Cedros [Orica is at ca. 14° 42' 56" N, 86° 56' 36.5" W, ~860 m. We were able to locate a nearby locality called Cedros, some 23 km, bearing 235°, at ca. 14° 35' 44" N, 87° 07' 08" W, ~950 m]: AMNH 127564 (♂). Nicaragua: Departamento de Managua; Managua, Laguna de Jiloá [ca. 12° 12' 31.5" N, 86° 18' 14" W, ~52 m]: AMNH 176699 (♀). Honduras: Francisco Morazán; Las Flores, Archaga [[Goodwin \(1942:110\)](#) specified that "Las Flores Archaga" corresponded to La Flor Archaga, "(4500-5000 ft.), a small village on the Talanga road east of Archaga." Archaga is located ca. 14° 17' 7" N, 87° 13' 45" W, ~865 m; Talanga is at ca. 14° 23' 55" N, 87° 04' 57" W, ~810 m]: AMNH 126144, 126145, 126146, 126147 (all ♂). Honduras: Departamento Intibucá; La Florida [specimen label reads "La Flor Intibuca" but [Goodwin \(1942:110\)](#) listed a locality in Intibucá as "La Florida"; La Florida is ca. 14° 11' N, 87° 56' W, ~1,800 m; notwithstanding, [Goodwin \(1942:150\)](#) did not list any *Sylvilagus* with that locality, but did list 8 with a provenance of "La Flor Archaga"]: AMNH 126203 (♂). Honduras: Departamento Intibucá; El Horno [we could only find "Cerro El Horno", a 1,516 m mountain, in Intibucá at ca. 14° 03' 13" N, 88° 12' 26" W; [Goodwin \(1942:109\)](#) listed a locality with the name of El Horno as being "(4000 ft.), Dept. La Paz, 5 miles north of Marcala." That would situate this locality at ca. 14° 13' 48" N, 88° 02' 36" W, ~1,345m]: AMNH 126205 (♀), 126206 (♂). Nicaragua: Departamento de Chontales: AMNH 28482 (♀). Nicaragua: Departamento de Jinotega; San Rafael del Norte [ca. 13° 12' 46" N, 86° 06' 39" W, ~1085 m]: AMNH 29229 (♀); 29230 (♂). Nicaragua: Departamento de León; León [ca. 12° 26' 06" N, 86° 52' 44" W, ~105 m]: AMNH 28325 (♂). Nicaragua: Departamento de Nueva Segovia; Jalapa [ca. 13° 55' 01" N, 86° 07' 37" W, 685 m]: AMNH 29228 (♂).

***Lepus margaritae* G. S. Miller, 1898:97** [= *S. f. margaritae*]. Venezuela: Nueva Esparta; Isla Margarita [Isla Margarita is a ca. 1,020 km² island off the coast of Venezuela, centered at ca. 10° 56' 11" N, 64° 02' 17" W, rising to 920 m, and containing highly varied terrain; it is unclear where, beyond "Isla Margarita," the type locality might be]: holotype, USNM 63217 (♂).

***Lepus (Sylvilagus) russatus* J. A. Allen, 1904:31** [= *S. f. russatus*]. México: Veracruz; Pasa Nueva [= Paso Nuevo, *fide* [Lawrence \(1993\)](#), ca. 18° 36' 22.8" N, 96° 34' 35.3" W, ~167 m]: holotype, AMNH 17203 (♂).

***Lepus (Sylvilagus) superciliaris* J. A. Allen, 1899:196** [= *S. f. superciliaris*]. Colombia: Departamento de Magdalena: Distrito de Santa Marta; Bonda [ca. 11° 14' 05" N, 74° 07' 32" W, ~65 m]: holotype, AMNH 15428 (♂), 15426, 15429 (all ♂), 23569 (♀), 14634 (sex unknown). "Colombia, S[outh]. A[merica]." [likely near Bonda, "250 ft" (76 m)] AMNH 14848 (♀).

***Lepus floridanus yucatanicus* G. S. Miller 1899:388** [= *S. yucatanicus*; this paper]. México: Yucatán; Mérida [environs of ca. 20° 58' 01.5" N, 89° 37' 25.5" W, ~14 m]: holotype, USNM 37772 (♀).

***Lepus brasiliensis* var. *gabbi* J. A. Allen, 1877:349** [= *S. g. gabbi*; see Ruedas and Salazar-Bravo, 2007]. Costa Rica: Talamanca. Further defined by [Hershkovitz \(1950\)](#) as: "Talamanca (= Sipurio, Río Sixaola, near the Caribbean coast), Costa Rica." [Sipurio is located ca. 9° 32' 3" N, 82° 56' 58" W, ~71 meters, but Puerto Viejo de Talamanca, ca. 7.5 Km N/NE of the Sixaola River at its closest, is at ca. 9° 39' 20" N, 82° 45' 13" W, ~5 m]: lectotype, USNM 11371/37794 (♂). Heredia: Isla Verde, Chilamate, Sarapiquí, 103 m, 10° 26' 38.83" N, 84° 05' 16.16" W: MVB 5069 (JMM-001-2016; ♀). Heredia: Isla Verde, Chilamate, Sarapiquí, 102 m; 10° 26' 38.83" N, 84° 05' 16.59" W: MVB 5041 (JMM-002-2016; ♂). Heredia: Chilamate, Sarapiquí, 101 m, 10° 26' 39.69" N, 84° 05' 16.53" W: MVB 5042 (JMM-003-2017; ♂). Heredia: Chilamate, Sarapiquí, 95 m, 10° 26' 48.00" N, 84° 05' 21.05" W: MVB 5043 (JMM-004-2017; ♂). Heredia: Chilamate, Sarapiquí, 101 m, 10° 26' 39.75" N, 84° 05' 16.40" W: MVB 5044 (JMM-005-2017; ♀). Alajuela: Guacalito, Las Armenias, Upala, 509 m, 10° 48' 45.4" N, 85° 06' 34.8" W: MVB 5049 (JMM-012-2017; ♂). Alajuela: Esterito, Poco Sol, San Carlos, 10° 38' 57.28" N, 84° 29' 57.32" W, MVB 5050 (JMM-013-2017; ♂). Alajuela: Esterito, Poco Sol, San Carlos, 10° 39' 48.30" N, 84° 32' 20.51" N, MVB 5051 (JMM-014-2017; ♀).

***Lepus (Tapeti) incitatus* Bangs, 1901:633** [= *S. incitatus*; see [Ruedas et al. 2019](#)]. Panamá: Archipiélago de las Perlas; San Miguel Island [= Isla del Rey; this island, centered at ca. 8° 21' 20.4" N, 78° 55' 58" W, covers ca. 234 km², with elevations ranging from sea level to ~212 m; [Bangs \(1901\)](#) provided no additional information as to the provenance of what remains the only specimen of the taxon]: holotype, MCZ, Bangs Collection no. 8441 (♀).

***Sylvilagus gabbi messorius* Goldman, 1912:13** [= *S. g. messorius*]. Panama: Darién; [Santa Cruz de] Cana, altitude 1,800 ft [549 m], eastern mountains of Panama. [ca. 7° 45' 25" N, 77° 41' 02" W]: holotype, USNM 179569 (♂).

***Lepus truei* J. A. Allen, 1890b:192** [= *S. g. truei*]. México: Veracruz; Mirador [the exact location of Mirador in Veracruz has never been able to be ascertained: there are numerous locations with that name in Veracruz; it is not our desire in this work to speculate]: holotype, USNM 6357/34878 (sex undetermined) [[Allen \(1890b\):194](#) listed the number of the skull of the type specimen as 25953; [Fisher and Ludwig \(2015\):30](#) pointed out that Allen's identification was due to a cataloguing error and that the correct number for the skull is 34878, as listed here].

***Sylvilagus surdaster* Thomas, 1901:543** [= *Sylvilagus surdaster*; see [Ruedas et al. 2019](#)]. Ecuador: Esmeraldas; Río Bogotá, Carondelet, 20 m [ca. 1° 07' 26.6" N, 78° 45' 45.4" W]: holotype, MNH 1901.6.5.16 [not listed in original description but so designated, presumably by Thomas, in the MNH collection: data in specimen tags match those in the original description].