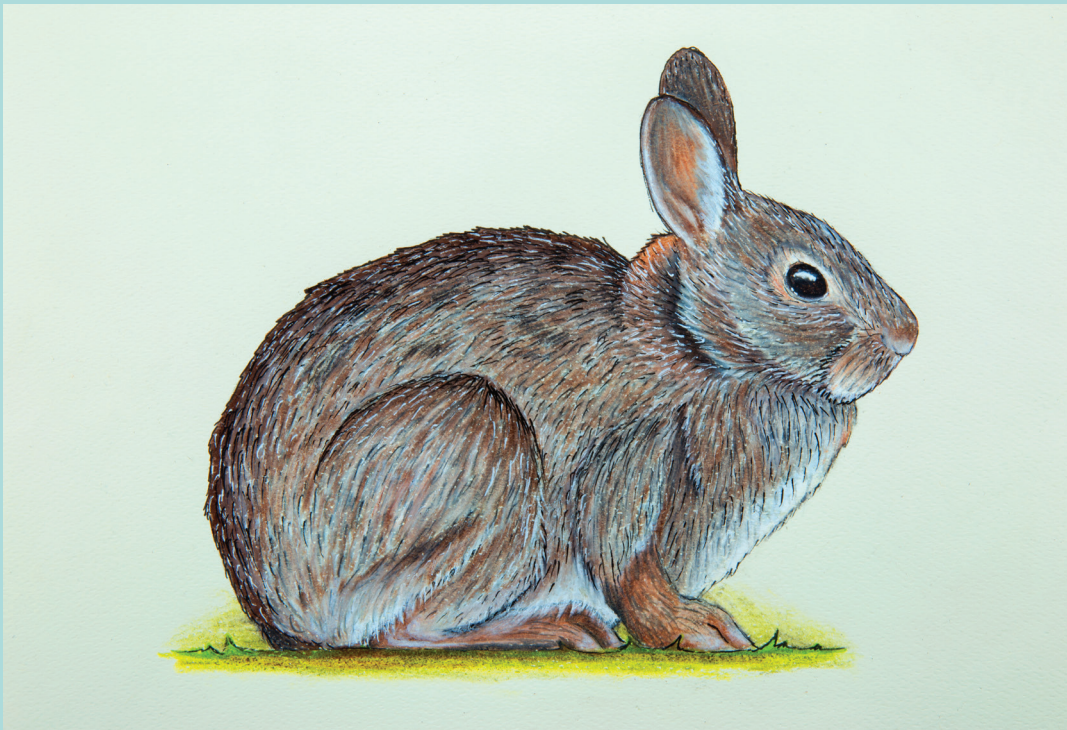


**A PROLEGOMENON TO THE SYSTEMATICS OF SOUTH  
AMERICAN COTTONTAIL RABBITS (MAMMALIA,  
LAGOMORPHA, LEPORIDAE: SYLVILAGUS): DESIGNATION  
OF A NEOTYPE FOR *S. BRASILIENSIS* (LINNAEUS, 1758), AND  
RESTORATION OF *S. ANDINUS* (THOMAS, 1897)  
AND *S. TAPETILLUS* THOMAS, 1913**

**LUIS A. RUEDAS, SOFIA MARQUES SILVA, JOHNNIE H. FRENCH,  
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AND CODY W. THOMPSON**



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**MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 205**

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Ann Arbor, February 9, 2017  
ISSN 0076-8405

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COVER FIGURE— Interpretation of the possible appearance of a *Sylvilagus brasiliensis* in life, drawn from the neotype, Universidade Federal de Pernambuco no. 1740, by Jessica Szabo, 2017

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BY

**LUIS A. RUEDAS**

Department of Biology and Museum of Natural History  
Portland State University  
Portland, OR 97207–0751 U.S.A.

**SOFIA MARQUES SILVA**

CIBIO—Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto,  
InBIO Laboratório Associado, Campus Agrário de Vairão, R. Padre Armando Quintas, 4485–661  
Vairão, Portugal

**JOHNNIE H. FRENCH**

Department of Biology and Museum of Natural History  
Portland State University  
Portland, OR 97207–0751 U.S.A.

**ROY NELSON PLATT II**

Department of Biological Sciences  
Texas Tech University  
Lubbock, TX 79409–3131 U.S.A.

**JORGE SALAZAR–BRAVO**

Department of Biological Sciences  
Texas Tech University  
Lubbock, TX 79409–3131 U.S.A.

**JOSÉ M. MORA**

Instituto Internacional en Conservación y Manejo de Vida Silvestre (ICOMVIS)  
Universidad Nacional  
Heredia, Costa Rica

**CODY W. THOMPSON**

Department of Ecology and Evolutionary Biology and Museum of Zoology  
University of Michigan  
Ann Arbor, Michigan 48109–1079, USA



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BY

Luis A. Ruedas<sup>1</sup>, Sofia Marques Silva<sup>2,3</sup>, Johnnie H. French<sup>1</sup>, Roy Nelson Platt II<sup>4</sup>, Jorge Salazar-Bravo<sup>4</sup>,  
Jose M. Mora<sup>5</sup>, and Cody W. Thompson<sup>6</sup>

Abstract

A critical issue with species names derived from Linnaeus' 10<sup>th</sup> edition of the *Systema Naturae* is the lack of holotypes, which in many instances has led to taxonomic confusion and uncertainty, as well as an unstable taxonomy. In the particular case of the South American cottontail, currently known as *Sylvilagus brasiliensis*, Linnaeus listed the type locality as "America Meridionali," or South America. As a result, *S. brasiliensis* was ascribed a widespread distribution in North and South America, over an area estimated as approximately  $1.09 \times 10^7$  Km<sup>2</sup>, and containing upwards of 37 named subspecies. In order to stabilize the taxonomy and initiate the process of illumination of evolutionary and biogeographic relationships among the South American cottontails, we designate herein a neotype for *S. brasiliensis*. Because the original description by Linnaeus was based on the posthumously published 1648 work of Georg Marcgraff, we restrict the type locality of *S. brasiliensis* to coastal Pernambuco State, near Recife, where Marcgraff largely was based. We select and describe a neotype from that area, specifically from a forest fragment in the Pernambuco Endemism Center of the Atlantic Forest Biome, collected at ca. 7°50'38.4"S, 35°6'7.3"W, elevation: ca. 137 m. Niche modeling suggests that *S. brasiliensis* as thus defined may have a much more restricted range of 500–700 Km<sup>2</sup>, in a narrow distributional band along northern Atlantic coastal Brazil. We compare the neotype of *S. brasiliensis* to holotype material of *S. andinus* and *S. tapetillus* and find sufficient distinction in characters and measurements between *S. brasiliensis*, *S. andinus*, and *S. tapetillus*, to retain the latter two as valid species level taxa. Molecular phylogenetic analyses based on a limited number of sequences from the mitochondrial 12S rRNA and cytochrome-*b* genes support the distinction between *S. andinus* and *S. brasiliensis*. Genetic distances also support the lack of close relationship between the two taxa, with cytochrome-*b* showing a patristic distance between the two of ca. 15%, the largest interspecific distance among *Sylvilagus* species previously examined for that locus. Our analysis of Lineages Through Time suggests that the vast unreported taxonomic diversity among Tropical *Sylvilagus* is based on high speciation rates in the genus, combined with unusually low extinction rates. Episodes of explosive speciation in *Sylvilagus*, hypothesized to be ecologically driven, have been coeval with cooling events at the Miocene–Pliocene transition and following the Piacenzan Warm Period (Late Pliocene) into the Pleistocene; warm periods have in contrast slowed down speciation rates. The status of all described subspecies of *S. brasiliensis* will require careful scrutiny and comparison with the neotype to ascertain and establish species limits. Because of a lack of specimens of Neotropical *Sylvilagus* in collections, our study suffers from a typological schema, however, our approach from first principles—examination of holotypes—not only serves to establish a more stable taxonomic framework for Neotropical *Sylvilagus*, but also further suggests that many of the existing taxa currently subsumed as subspecies within *Sylvilagus brasiliensis* likely are valid species in their own right.

**Key words:** Neotropics, taxonomy, biogeography, Andes, Ecuador, Páramo, conservation

<sup>1</sup>Portland State University, Portland, OR 97207, USA

<sup>2</sup>Museu Paraense Emílio Goeldi / Universidade Federal do Pará, Brasil CEP 66077

<sup>3</sup>Universidade do Porto, Vairao, Portugal

<sup>4</sup>Texas Tech University, Lubbock, TX 79409, USA

<sup>5</sup>Universidad Nacional, Heredia, Costa Rica

<sup>6</sup>University of Michigan, Ann Arbor, MI 48109, USA

## INTRODUCTION

The South American cottontail, or Tapetí, *Sylvilagus brasiliensis*, was among the species enumerated by Linnaeus in the 1758, 10<sup>th</sup> edition of the *Systema Naturæ* (Linnaeus 1758). The history of that inclusion is of some interest. Indeed, in the 10<sup>th</sup> edition, the species is included as one of the varieties of *Lepus*, the 24<sup>th</sup> of 39 genera distributed among eight orders; in this instance, in the order Glires. In that edition, *Lepus* included the species (in order): *L. timidus* (p. 57), *L. cuniculus* (= *Oryctolagus cuniculus*, p. 58), *L. capensis* (p. 58), and *L. brasiliensis* (= *S. brasiliensis*, p. 58). The diagnosis provided for the genus was: two upper incisors, the interior pair smaller than the exterior pair, whence we can infer that the taxonomic level of genus was at the time equivalent to that of the modern order Lagomorpha, as that diagnosis defines the modern concept of the order Lagomorpha.

Inclusion of this remarkable creature may have begun as a historical accident of linguistic ability. The Holy Roman Emperor Charles V, (also King Charles I of Spain), was born in Ghent and spoke many of the languages of the Low Countries. In contrast, his son Philip II, in favor of whom Charles V abdicated in 1556, spoke little if any of those languages. The inability to communicate with his northern subjects (both in person and due to the time then involved for written communication on account of the distances), along with the unpopular imposition of Catholicism and the Spanish Inquisition (whom nobody expects), were among the factors that led to the Eighty Years' War (1568–1648), during which the Netherlands became independent and, more specifically as far as the present circumstances are concerned, established colonial outposts in what is now Brazil, most notably Mauritsstad (now Recife) in New Holland, or Dutch Brazil, an endeavor that lasted from 1581 to 1654. Georg Marcgraff von Liebstadt was one of the scientists in the employ of Count Johann Moritz von Nassau–Siegen, the German–born Dutch governor from 1636 to 1644. Marcgraff authored the groundbreaking *Natural history of Brazil*, published posthumously in 1648 (Marcgraff 1648), where “the various species of Brazilian rabbits” are discussed starting on page 223. The only true lagomorph included in the series is Marcgraff’s “*Tapeti brasiliensibus*,” one of whose principal recognizable characteristics in the written description was the absence of a tail (Fig. 1). The description is quite explicit for 1648, and better than many species descriptions from the 18<sup>th</sup> and 19<sup>th</sup> centuries.

John Ray (1693) repeated almost verbatim, in his synopsis of the quadrupeds (Ray 1693:205–206), Marcgraff’s description of the Tapetí. That characteristic, the lack of a tail (“*cauda nulla*”), must have been so remarkable relative to the known European lagomorphs of the time that it was the precise character that Linnaeus seized upon in distinguishing *S. brasiliensis* from other lagomorphs. And so the matter may have rested, were it not for a detail also noted by Linnaeus:



Figure 1— Illustration of the Tapetí in Marcgraff’s work (1648:224); although described in Marcgraff’s text as tailless (“*nullam habet caudam*”), it is more realistically illustrated with a diminutive tail.

that the range of *S. brasiliensis* was South America (“*Habitat in America meridionali*”). With that stroke of the pen, and the authority of the mere name of Linnaeus, *S. brasiliensis* assumed a distribution from Veracruz, México, in the north, to Argentina in the south, and from sea level on the Atlantic coast of Brazil to well above 4000–4500 meters in the Peruvian, Ecuadorian, Colombian, and Venezuelan Andes of western South America, and back down to the Pacific coast of South America in Peru, Ecuador, and Colombia. Such a broad geographic distribution—among the largest of any described mammal species, and almost certainly the largest of any small to medium mammal species—encompassing such a wide variety of ecotypes and habitats should immediately be considered suspect at best when applied to an allegedly singular species of the biological characteristics habitually ascribed to species in the lagomorph genus *Sylvilagus* (cf. Palacios *et al.* [2008] for similar comments with respect to *Lepus capensis*).

Possibly the only attempt at remedying this question was undertaken by Thomas (1911), who correctly noted that Linnaeus’ locality data were “for the most part too vague to be of any use, while accepting them literally would sometimes lead to grotesque errors...” (Thomas 1911:123). Initially, Thomas (1901a:535) suggested that “since even [ca. 1640] Rio Janeiro [sic.] was the chief settlement in this part of Brazil, it would seem best to consider the Rio animal as representing [*S. brasiliensis*].” However, in attempting to ascertain the type localities of Linnaean taxa for his 1911 work, he modified that opinion based on the notion that Marcgraff had collected primarily in the environs of Recife, Pernambuco. In addition, the specimen from Rio de Janeiro (Porto Real, near Rezende, ca. 22°24′40.53″S, 44°19′14.72″W, NHMUK no. 1892.11.24.3) was unusually small compared to “*S. brasiliensis*” from throughout the range, and most particularly, in comparison to a series collected in Lamarão, Bahia, which Thomas took to be “true” *S. brasiliensis*. Thomas (1913) would describe the Rio specimen as *S. tapetillus*. In search of taxonomic stability,

Thomas therefore fixed the type locality of *S. brasiliensis* as “Pernambuco” (Thomas 1911:146). It also is possible that Thomas was using Pernambuco as an earlier name for Recife, rather than for the state of Pernambuco. Underscoring the ambiguous nature of Thomas’ decision, A. Langguth (*in litt.*) suggested that because animals described by Marcgraff (1648) could have come from anywhere between the Brazilian state of Sergipe and that of Ceará, Pernambuco always should be understood as the region, rather than the city of Recife. Thomas’ decision as to type locality (Thomas 1911:146) was based on his assessment that “the sole quotation [in Linnaeus’ 10<sup>th</sup> edition] is Ray” (incorrect) “whose account is taken from Marcgrave” (correct). Marcgraff is in fact the first citation in Linnaeus’ few lines on *S. brasiliensis*. Additional justification as to type locality was further provided by Thomas (1911:124), who noted that Marcgraff “stayed at “Moritzstadt,” [sic] now Recife, most of his time, 1640–1644, while even his excursions were limited to the coast region between 5°45’ and 11°11’S, thus taking in little more than from Rio Grande do Norte to Alagoas, a region at the center of which Pernambuco lies.” (Fig. 2).

While an attempt to fix a type locality was a good start, the Brazilian state of Pernambuco is unfortunately quite large geographically and extremely heterogeneous ecologically, with an area of 98,312 Km<sup>2</sup>, and a length of ca. 730 Km E to W. A ca. 700 Km transect drawn along the center of the state shows marked topographical relief (Fig. 2) and numerous po-

tential geographic barriers to species presumptively adapted to local microhabitats, as *Sylvilagus* species tend to be. Besides the obvious topographic barriers described in Fig. 2, Feijó and Langguth (2013) pointed out that the coastal municipalities of Pernambuco are constituted by Mata Atlântica (Atlantic Rainforest) biome, whereas the interior consists of Caatinga biome. Thus, extensive topographical barriers exist between eastern and western regions of Pernambuco, potentially hampering movement among *Sylvilagus* populations, particularly between coastal, coastal montane, and interior habitats. In addition, radically different biomes with starkly distinct internal ecoregions further underscore the potential for the presence of distinct species of *Sylvilagus* within Pernambuco alone, let alone Brazil and South America at large.

A final thorn in the bed of complacency wherein the taxonomy of *S. brasiliensis* long has lain has to do with the extensive morphological variation to be found in the taxon. There are some 32–37+ subspecific taxa currently associated with *S. brasiliensis* (Tate 1933, Hershkovitz 1950, Hoffmann & Smith 2005, this paper), we have examined most of the holotypes associated with *S. brasiliensis* and Central and South American *Sylvilagus* species. Based on that examination, we can definitively state that as currently construed, what is considered a single species, *Sylvilagus brasiliensis* Linnaeus, 1758, with a vast geographical distribution across North and South America, is in fact constituted by multiple, distinct, species-level taxa. To suggest otherwise would be absurd

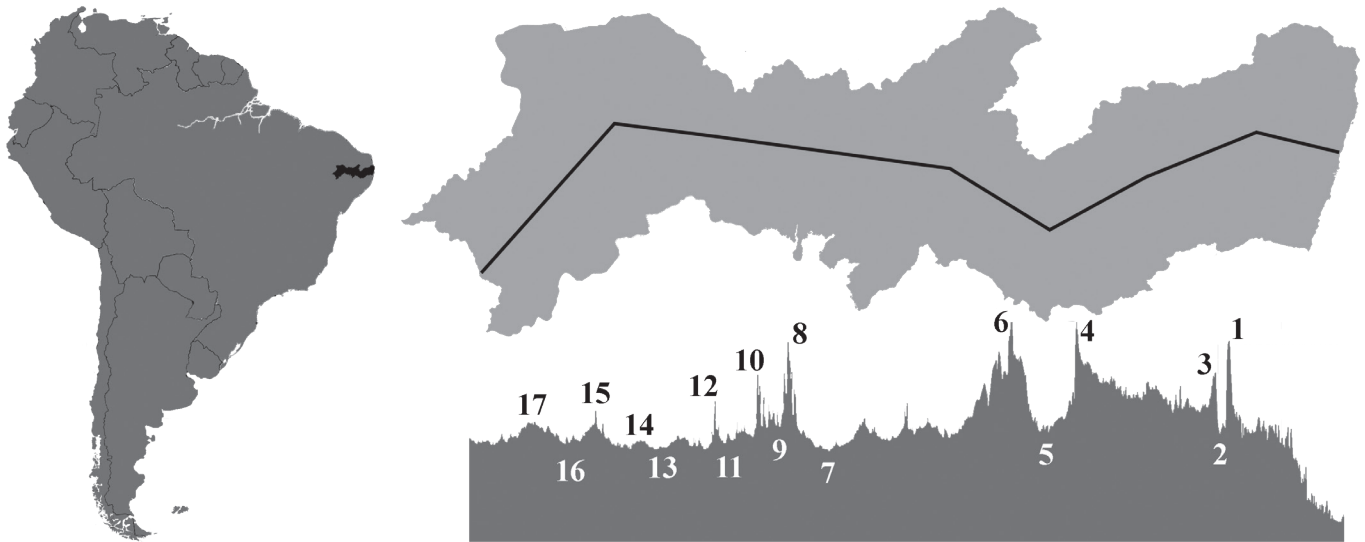


Figure 2— Left: The Brazilian state of Pernambuco (in black) in South America. Upper right, outline map of Pernambuco with the approximate line of a ca. 700 Km transect drawn through the center of the state. The elevational section, lower right, shows the elevation (data from Google Earth) along the transect. Potential altitudinal breaks and reference points include: 1. 965 m, ca. 8°11'13"S, 35°47'27"W; 2. 444 m, ca. 8°11'S, 35°51'W; 3. 756 m, ca. 8°11'50"S, 35°52'40"W; 4. 1115 m, ca. 8°36'18"S, 36°47'W; 5. 450 m, ca. 8°41'S, 35°58'17"W; 6. 1035 m, ca. 8°35'50"S, 37°13'10"W; 7. 361 m, ca. 8°18'40"S, 38°30'8"W; 8. 914 m, ca. 8°16'48"S, 38°47'W; 9. 485 m, ca. 8°16'17"S, 35°50'20"W; 10. 748 m, ca. 8°15'17"S, 39°W; 11. 400 m, ca. 8°13'46"S, 39°13'52"W; 12. 705 m, ca. 8°13'12"S, 39°17'7"W; 13. 364 m, ca. 8°13'10"S, 39°44'W; 14. 420 m, ca. 8°13'S, 39°50'13"W; 15. 577 m, ca. 8°20'21"S, 40°06'10"W; 16. 402 m, ca. 8°30'16"S, 40°15'48"W; 17. 513 m, ca. 8°39'19"S, 40°24'32"W.



and fly in the face of reason. Further, an examination of the *Sylvilagus* material at the National Museum of Brazil, Rio de Janeiro, suggests that there may exist specific variation from North to South even within the Mata Atlântica, and certainly that there exist numerous species-level taxa within "*Sylvilagus brasiliensis* (Linnaeus, 1758)" east of the Andean foothills.

The principal hurdle in assessing and adequately describing this geographic and taxonomic variation is, however, the lack of a holotype for *S. brasiliensis*, habitual in many species described by Linnaeus. Further, there are no existing syntypes from which a potential lectotype could be selected. There are in fact no name-bearing type specimens associated with this species (*sensu stricto*, although numerous subspecies were named in the 19<sup>th</sup> and early 20<sup>th</sup> centuries). A name-bearing type being necessary to objectively define *Sylvilagus brasiliensis* to ascertain the species limits and taxonomy, in accordance with Article 75 of the International Code of Zoological Nomenclature (ICZN 1999), the purpose of the present work is to establish a suitable neotype, and begin the process of excision of valid biological species from a more naturally circumscribed *S. brasiliensis*.

#### MATERIALS AND METHODS

Morphological data: continuous characters—Cottontails of the genus *Sylvilagus* tend to be relatively homogeneous morphologically, and the range of intraspecific phenotypic variation in cranial characters among members of the genus so broad as to overlap interspecifically (Ruedas 1998). Hence, we undertook analyses of mensural characters both on cranial and mandibular measurements as well as on mensural characters of lower premolar 3, a key dental feature in delineating species boundaries among *Sylvilagus* species (Ruedas 1998, White 1987). Most of the measurements recorded were defined by Ruedas (1998), and White (1987); those that were not, or are modified, are defined below (terminology generally follows Wible 2007). Characters were: GLS, greatest length of skull; POSTORB, width of postorbital constriction; BROSTR and DEPROSTR, breadth and depth (height) of rostrum—these were listed by Ruedas (1998) as being measured at plane of extremity of anterior zygomatic process but following the terminology of Wible (2007) would be modified to be measured at the anterior extremity of the masseteric spine on the maxillary portion of the zygomatic arch; BBRAIN, breadth of braincase; ZYGO1, greatest width across the masseteric (=zygomatic) spine on the maxillary portion of the zygomatic arch; ZYGO2, zygomatic breadth; LZYG0, length of zygomatic arch from anteriormost portion of masseteric spine on the maxillary portion of the zygomatic arch to posteriormost extension of jugal spine; 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,

from ventralmost point of ectotympanic to dorsalmost point of external auditory meatus; CONDL, condylopremaxillary length of cranium; LPALFOR, WPALFOR, length and width of incisive foramina; PALONG, palatal length: from posterior edge of I2 alveolus to posterior extremity of palatal bridge; PALBRDGE, greatest anteroposterior dimension of palatal bridge; BASIOC, anteroposterior length of basioccipital; WIDBULL, width of auditory bulla, measured perpendicularly to the longest axis of the bulla (at approximately a 45° angle to the long axis of the skull), across its broadest dimension from the most external portion of the ectotympanic to the suture between ectotympanic and exoccipital, about even with the middle of the occipital condyle; ANTBULL, 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; CHOANA, breadth of choanae—we measured this at the posterior narial opening, at the level of the second molar, hence this is technically the nasopharynx; 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 on mandibular body; MANDEP, depth of mandibular body below m1; P3M3, greatest alveolar length of p3–m3 in mandibular body; HMAND, height of the mandible from ventral aspect of angular process (labial to pterygoid shelf) to most dorsal aspect of condyloid process (articular facet); HPTT, distance from ventral aspect of angular process (labial to pterygoid shelf) to most dorsal aspect of pterygoid tuberosity; BCON, breadth of condyloid process, below articular facet; LMAND, length of mandibular body, from anterior edge of incisive alveolus to posteriormost aspect of angular process. Dental characters recorded from the third lower premolar included: wpostlof, greatest width of the posterior loph of pm3, wpm3, greatest width of pm3, aplpostl, greatest anteroposterior length of posterior loph of pm3, wantlof, greatest width of anterior loph of pm3, lantlof, greatest anteroposterior length of anterior loph of pm3, lpm3, greatest anteroposterior length of pm3, antlofar, area circumscribed by enamel in the anterior loph of pm3, pstlofir, area circumscribed by enamel in the posterior loph of pm3.

Statistical analyses were performed using the Statistical Analysis System (SAS) software, version 6.03 (SAS Institute 1988a, 1988b), generally following Ruedas (1995, 1998). Significance in all analyses was set at  $\alpha = 0.05$ ; however because of the restricted sample size,  $0.10 \geq \alpha > 0.05$  also are reported (Moyé 2000). Similarly, no attempt 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, given small sample sizes, could affect results of multivariate analyses (Reyment *et al.* 1984). Univariate statistics (mean, standard deviation) were calculated using the UNIVARIATE procedure of SAS. Two series of multivariate analyses were undertaken, the first only comparing specimens of *S. andinus* with *S. brasiliensis*, the second including those two species as well as *S. tapetillus*. In each instance, a principal component analysis (SAS procedure PRINCOMP) was carried out first on the correlation matrix of the raw (untransformed) cranial data of complete specimens in the species under consideration measured in all the focal species: *S. andinus* and *S. brasiliensis* in the first analysis, then those two taxa as well as *S. tapetillus*, in order to determine whether any group separation occurred using the measurements taken. Such a posteriori grouping methods are preferred over a priori grouping methods (multiple range tests, canonical discriminant analysis) because there is no prior hypothesis as to the putative identity of specimens examined. We undertook the principal components in a stepwise manner because we undertook the comparisons in a stepwise manner. For the initial comparison between *S. andinus* and *S. brasiliensis* only, given that the analysis is sample dependent, having included samples potentially ascribable to other taxa (*S. tapetillus*) could have confounded the resulting variation in multivariate space in the direction of an added sample that was not germane to the particular comparison. We were interested first only in assessing whether there was any overlap by *S. brasiliensis*, of which we currently know of only the neotype (see below, results), with other putative taxa. In the first instance, that was *S. andinus*, for which we had a broader sampling for morphological variation. The second, more complete series of principal component analyses, on all three focal taxa of this work, were carried out on the correlation matrix of raw (untransformed) data recorded only from specimens deemed adult based on ossification of occipital sutures and tooth wear, and for which a complete suite of measurements would assure inclusion in the principal component analysis.

Morphological data: Discrete characters—Drawings of p3 crown enamel patterns 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. Among leporids, p3 generally constitute the most informative dental elements for taxonomic and systematic purposes (Dalquest 1979, Dalquest *et al.* 1989, Hibbard 1963, Palacios & López Martínez 1980, Ruedas 1998, White 1987, White 1991, White & Morgan 1995, Winkler & Tomida 2011). White (1987) further noted that although P2 (among others) eventually might prove to be diagnostic, adequate descriptive work was lacking for that tooth. 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 are described in Appendix I of Ruedas (1998); the presumed plesiomorphic condition is

exhibited by *Lepus californicus*, in the genus hypothesized as sister to *Sylvilagus* (Halanych & Robinson 1997, White 1991, White & Morgan 1995). Additional characters useful in distinguishing among lagomorph species were extracted from Palacios (1996), Palacios *et al.* (2008), and Erbayeva (1988).

Morphological data: Cladistic analysis of morphological characters—We analyzed the morphological data in order to assess the utility of the characters in evolutionary analyses, as well as to determine the distribution of character states across resulting trees. Cladistic analyses were carried out in PAUP\* 4.0b10 (Swofford 2003), specifying *Lepus californicus* as the outgroup. We used the heuristic search algorithm with stepwise addition to obtain starting trees for branch swapping, specifying the tree bisection–reconnection algorithm to be used for branch swapping, with the addition sequence used in the stepwise addition set to random, and using 100 random–addition–sequence replications. Bootstrap and jackknife explored 10,000 replications using the same specifications except for the use of 10 random–addition–sequence replications at each search, holding a single tree at each search.

An initial analysis was undertaken using the dental characters employed by Ruedas (1998), absent characters xix–xxiii, which are characters of the third upper premolar and were not surveyed in the South American taxa under consideration herein, and one additional character not used by Ruedas (1998): character xxiv, lacunar remnant of p3 paraflexid (sometimes called anterointernal reentrant) present (0) or absent (1). It may be unclear in certain species whether the lacuna on the lingual side of p3, in the area of the metaconid, is in fact formed by a fusion of the anterior and posterior lophes of p3, usually at the central angle, causing the lingual portion of the hypoflexid to become pinched off and perhaps reduced. For example, the latter could certainly be the case in the instance of some of the specimens illustrated by White (1991), including †*Alilepus hibbardi*, (White 1991: Fig 4B6), †*A. vagus*, (White 1991: Fig 4C2–4), †*Alilepus* sp. (White 1991: Fig 4D), †*A. wilsoni*, (White 1991: Fig 4E2), †*A. browni*, (White 1991: Fig 4F3), †*Pratilepus kansansensis*, (White 1991: Fig 4J2–3), †*Aluralagus bensonensis*, (White 1991: Fig 4K1), †*Nekrolagus progressus*, (White 1991: Fig 9A2–5), †*Aztlatonolagus agilis*, (White 1991: Fig 9G), and *Romerolagus diazi*, (White 1991: Fig 4M1–4). However, in the specific instance of the character as we describe herein, the specimen of *Lepus californicus* that we examined had a distinct enamel-ringed lacuna cranial to a fully developed hypoflexid extending from labial to lingual sides of p3, hence is inferred to be a remnant of paraflexid, rather than the lingual aspect of the hypoflexid. We further note that this character may not be present in all specimens of *L. californicus* (e.g., White 1991: Fig 10).

In the first instance, we combined the taxa from the analysis of Ruedas (1998) as well as those examined in the present manuscript. That analysis resulted in an unresolved polytomy among *Sylvilagus* species. We then reduced the taxa

to include *S. andinus*, *S. brasiliensis*, *S. tapetillus*, *S. dicei*, and *S. floridanus*, rooted by *L. californicus*. Ancestral state reconstruction was carried out in Mesquite (v. 3.03, build 702). Once it was demonstrated that this analysis had some resolving ability (see “Cladistic Analysis of Morphological Data” below), a subsequent, expanded analysis was undertaken that included additional taxa (*S. cunicularius*, *S. nuttallii*, and *S. palustris*) and in particular, included the cranial morphological characters used in the diagnoses of *S. andinus*, *S. brasiliensis*, and *S. tapetillus*. The additional characters, again polarized with respect to *L. californicus*, are as follows: xxv, braincase pitting (character 6 of Wible 2007), absent (0), present (1). xxvi, antorbital process present (0), absent (1). This character can be considered synonymous with characters 5 of Wible (2007) and 130 of Asher *et al.* (2005): supraorbital notch absent (0) or present (1), given that a supraorbital notch depends on the presence of an antorbital process. xxvii, postorbital process fused to cranium (0), free (1); we note that although we scored this as plesiomorphic in *Lepus*, that is the condition exhibited by *L. californicus*: other species of *Lepus* (e.g., *L. townsendii*) display this character in its derived condition, thus additional paleontological material should be examined in order to indubitably ascertain the polarity and distribution of this character in modern and extinct lagomorphs. xxviii, caudal aspect of postorbital process rounded (0), or sharply pointed (1). Our characters xxvii and xviii are dependent on character 4 of Wible (2007), which is equivalent to character 129 of Asher *et al.* (2005): postorbital process present (0) or absent (1); we did not use this character because a postorbital process is present in all the Leporidae we examined, hence has no information content. xxix, zygomatic fossa present (0), absent (1). This is the character 19 of Wible (2007) and 119 of Asher *et al.* (2005). However, those authors scored it as absent (0) or present (1). In the present analysis, because a zygomatic fossa, the depression in the anterior zygoma for the lateral masseter, was present in our outgroup, *L. californicus*, the plesiomorphic condition in the analysis was presence rather than absence. xxx, frontoparietal suture interdigitated (0), smooth (1). We considered for this character any amount of interdigitation along the frontoparietal suture as character state (0): some of the individuals we examined had a smooth frontoparietal suture in the medial half of either suture line, and an interdigitated suture for the lateral portion of either suture (as illustrated e.g. for *Romerolagus*, Fig. 1 of Wible 2007). xxxi, frontonasal suture sharp, or V-shaped (0), broader, or U-shaped (1); it is likely that this character may be found, upon broader taxonomic sampling, to constitute extremes of a continuum. For the taxa under consideration herein, however, this character is consistently binary. xxxii, nasal process of frontal long (0) or short (1). In species of lagomorphs, there is variation in a process extending facially from the frontal bone between the posterodorsal process of the premaxillae and the nasal bones. This nasal process may be short or absent (as illustrated for *Ochotona* and *Romerolagus*

in Fig 1 of Wible 2007), or extremely long, up to a third of the length of the nasal bone. xxxiii, single (0) or multiple (1) foramina in the basisphenoid bone. In the plesiomorphic condition, the basisphenoid bone is pierced by a single aperture, the craniopharyngeal canal (e.g., Wible 2007, Fig. 4; foramen cavernosum of Bensley 1948:182 and 173: Fig. 87). The craniopharyngeal canal, a developmental remnant of the connection between the roof of the pharynx and the developing pituitary gland (J. R. Wible, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, *in litt.*, 27 October 2015), can be identified by its orientation: running obliquely in a posteroventral to anterodorsal direction, and is generally the only opening present in the basisphenoid of lagomorph species, or the principal opening. Additional openings in the basisphenoid, possibly fenestrae rather than foramina, may be present and appear to be consistent at the intraspecific level. J. H. Wahlert (American Museum of Natural History, N.Y., N.Y., *in litt.*, 18 May 2016) noted with respect to this character that the more anterior perforations also have been identified as the craniopharyngeal canal (as detailed e.g. in Gray 1966:191, “The craniopharyngeal canal, through which the hypophyseal diverticulum is connected with the buccal ectoderm in fetal life, occasionally persists between the presphenoid and postsphenoids.”). The precise identity of the perforations in the basisphenoid therefore bear further scrutiny. Lastly, character xxxiv: premolar foramen absent (0), present (1); this character is extensively detailed in the main text of the present work.

Morphological data: specimens examined—*Lepus californicus*: USA: Oregon: Morrow Co., 2 mi E, 1 mi N Morrow, ca. 45°51'10.65"N, 119°39'43.51"W (WGS84), elev. ca. 97 m, Portland State University Museum of Vertebrate Biology (PSUMVB) 1676, ♂. *Sylvilagus andinus*: Ecuador: Pichincha Prov., Eastern Cordillera, W. slope of Mt. Cayambe, 4000 m. Est. coordinates: 0°1'47.24"N, 78°01'26.89"W (WGS84), The Museum of Natural History (NHMUK) 1897.11.7.54, ♀ (holotype). Ecuador: Pichincha Prov., Cayambe, near Cangagua. Est. coordinates: 0°04'33.88"N, 78°05'37.32"W (WGS84), elev. ca. 3525 m, University of Michigan Museum of Zoology (UMMZ) 77072, ♀, 77073, ♂, 77075, ♂, 77076, ♀, 77077, ♀, 77078, ♂, 77079, ♂, 77080, ♂, 77082, ♀. Ecuador: Imbabura, Rio Chota Valley, below Pimampiro, San Nicolás. Est. coordinates: 0°33'56.8"N, 77°56'9.61"W (WGS84), elev. ca. 2000 m, UMMZ 77061, ♀ (holotype of *S. brasiliensis chotanus* Hershkovitz, 1938). Ecuador: Carchi Prov., foot of the páramos of Boliche, ca. 5 mi SW San Gabriel, Montúfar. Est. coordinates: 0°25'13.61"N, 77°46'20.6"W (WGS84), elev. ca. 2900 m, UMMZ 77062, ♀ (holotype of *S. b. carchensis* Hershkovitz, 1938). *Sylvilagus brasiliensis*: Brazil: state of Pernambuco, Municipality of Paudalho, Mata da Privativa, forest fragment Centro de Instrução Marechal Newton Cavalcanti, 7°50'38.4"S, 35°6'7.3"W, elevation: ca. 137 m. Universidade Federal de Pernambuco (UFPE) 1740 (neotype). Brazil: Pernambuco,

Municipality of Rio Formoso, Estação Experimental Florestal de Saltinho, (as of 1983: Reserva Biológica de Saltinho), coll. A. G. de Miranda Coelho, 5 Sept. 1974. Est. coordinates: 8°43'14.7"S, 35°10'44.6"W (WGS84), elev. 104 m. Sex unknown. UFPE 427. *Sylvilagus cunicularius*: Mexico: Oaxaca: Oaxaca; purchased at the market, reputedly from nearby Oaxaca. *Sylvilagus nuttallii*: USA: Oregon: Jefferson Co., 8½ mi South, 2¼ mi E Madras, ca. 44°30'40.47"N, 121°04'43.7"W (WGS84), elev. ca. 940 m, PSUMVB 855, sex unknown. *Sylvilagus palustris*: USA: South Carolina: Colleton Co.; Bear Island Wildlife Management Area; 17 mi E. Green Pond, ca. 32°43'47"S, 80°21'24"W, ca. 12 m, ♂. *Sylvilagus tapetillus*: Brazil: Rio de Janeiro, Porto Real, Rio Paraíba, near Rezende. Est. coordinates: 22°24'40.53"S, 44°19'14.72"W, ca. 390 m (WGS84). NHMUK 1892.11.24.3 (holotype). Brazil: Rio de Janeiro, Porto Real. Naturalis (Leiden), two uncatalogued specimens, coll. H. du Dréneuf, 1890 (adult, skull in skin), coll. H. du Dréneuf, 1892 (juvenile, skull in skin).

**Molecular data**—The analyses are based on sequences from the mitochondrial 12S ribosomal and cytochrome *b* loci as used in previous studies investigating the phylogeny of Leporidae (e.g., Halanych & Robinson 1999, Matthee *et al.* 2004, Berkman *et al.* 2009). DNA was extracted from the neotype described below of *Sylvilagus brasiliensis*, Universidade Federal de Pernambuco no. 1740, using approximately 30 mg from a sample of tissue preserved in 95% ethanol. Total genomic DNA was extracted using a DNeasy Blood & Tissue extraction kit (Qiagen), following the manufacturer's recommendations. Primers used for amplifying and sequencing 12S rRNA were 12C (5'–AAA GCA AAR CAC TGA AAA TG–3') and 12G (5'–TTT CAT CTT TTC CTT GCG GTA C–3'), and for *cyt-b* were CytB1F (5'–CAT CGT TGT TTT CAA CTA TAA GAA CC–3') and CytB5R (5'–GGC CAG GGT AAT GAA TTA TAC TAC T–3', Tursi *et al.* 2013). 12S rRNA polymerase chain reaction (PCR) program consisted of an initial denaturation of 94°C 3 min., followed by 35 cycles of 94°C 40 sec., 42°C 2 min. and 72°C 3 min, ramping 1°C/sec, and final extension 72°C for 30 min. Amplifications were carried out in a total volume of 50 µL with about 30 ng of DNA, 10X buffer, 6 ng/µL of each primer, 0.5 mM of dNTPs, 5 mM of MgCl<sub>2</sub> and 1.25 U of *Taq* DNA polymerase (Life Technologies). PCR program for amplification of *cyt-b* fragment comprised an initial denaturation 94°C 3 min., followed by 40 cycles of 94°C 45 sec., 52°C 30 sec., and 72°C 1.5 min, and final extension 72°C for 10 min. PCR was undertaken in a final volume of 25 µL with about 30 ng of DNA, 10X buffer, 4 ng/µL of each primer, 0.1 mM of dNTPs, 5 mM of MgCl<sub>2</sub> and 1 U of *Taq* DNA polymerase (Life Technologies). PCR products from both reactions were purified using 20% polyethylene glycol (PEG)/2.5 M NaCl solution. Sequencing products were precipitated in an ethanol/EDTA solution, re-suspended in Hi-Di formamide and sequenced with BigDye 3.1 Terminator

kit (Applied Biosystems) in an ABI PRISM 3730 Genetic Analyzer (Applied Biosystems). Both strands were sequenced to improve accuracy of base calling. Sequence chromatograms were visually inspected and manually corrected using Chromas Lite, v.2.1.1 ([www.technelysium.com.au](http://www.technelysium.com.au)).

DNA also was harvested from dried skin clips (4 mm x 4 mm x 1 mm) for one specimen, *Sylvilagus andinus* UMMZ 77075, using a modified version of the Fulton *et al.* (2012) and Moraes–Barros & Stenghel Morgante (2007) extraction protocols. Hair and the outer dermal layer were scraped from the sample using a sterile scalpel. The skin clips were then sterilized in a 0.5% bleach solution for 30 seconds before three, 1–minute rinses with UltraPure™ distilled water (Invitrogen, Grand Island, NY). The sterilized skin clips were then cleaned and initially rehydrated in 1 mL of UltraPure™ distilled water at room temperature for seven days. The water was replaced each day. After seven days in water, the sample was fully rehydrated in 1 mL of TE buffer for two days with replacement of the TE buffer each day. At the end of the two–day rehydration period, the sample was washed three times in a 0.5 M EDTA solution. Finally, DNA was isolated from the sample using the standard Qiagen (Valencia, CA) DNeasy instructions with the following modifications. Initial digestion conditions included 180 µL buffer ATL, 20 µL of Proteinase K, and 20 µL of 1M DTT. After the ethanol washes, the column bound DNA was eluted into 50 µL of H<sub>2</sub>O. 12S and *cyt-b* were amplified in 150–350 bp overlapping fragments using primers developed in Primer3 (Koressaar & Remm 2007, Untergrasser *et al.* 2012). *Cyt-b* primers were as follows: SylvF (5'–ATG ACC AAC ATC CGT AAA ACC–3'), Sylv247F (5'–CAT GCT AAC GGA GCA TCAA T–3'), Sylv423F (5'–AGG CGC AAC CGT AAT CAC TA–3'), Sylv747F (5'–ACTTGGCGATCCAGACAAC–3'), Sylv905F (5'–CCA TTA TTC CCC TCC TCC AT–3'), Sylv298R (5'–GGC CGA CGT GTA TGT AAA GG–3'), Sylv590R (5'–AAG TGA ACT ATA ACT AGG GCT GCA A–3'), Sylv850R (5'–TAG AGC GTA GAA TGG CGT AGG–3'), Sylv1012R (5'–TGC TAC CTG TCC AAT GGT GA–3'), and SylvR (5'–CCT TCA TTT GAG GAT TTT GTT C–3'). 12S primers were as follows: 12sSylvF (5'–CCC TCC CCA GTG AGA ATG C–3'), 12sSylv305F (5'–AAA CAA AAA TAA ACA ACG AAA GTG A–3'), 12sSylv535F (5'–CCA CTC TTT GCC AAT TCA GC–3'), 12sSylv232R (5'–CGC CGG GTG TTT ATT AGT TT–3'), 12sSylv663R (5'–GCC CAT TGC TTT CCA CTC TA–3'), and 12sSylvR (5'–AAA TCC TCC TTT GGC CTC T–3').

Amplifications of each fragment were performed in 12.5 µL aliquots using the following conditions: (6.25 µL 2x HotStarTaq Master Mix [Qiagen, Valencia CA], 0.75 µL Primer 1 (0.5 µM), 0.75 µL Primer 2 (0.5 µM), 3.75 µL H<sub>2</sub>O, 1 µL DNA (3 ng/µL)). Thermal conditions were as follows: 95 °C for two minutes, 40 cycles of 95°C for 30 seconds, 45°C for 45 seconds, and 72°C for 45 seconds, followed by a final 72°C, 5–minute elongation. Prior to loading, the thermal cycler was heated to 80°C per the requirements of



the HotStarTaq. Approximately 2  $\mu$ L of PCR product was visualized on a 1.5% agarose gel electrophoresed at 300 volts for 20 minutes. Successful reactions were purified via QiaQuick PCR purification kits (Qiagen, Valencia CA) eluted into 50  $\mu$ L of H<sub>2</sub>O. Eleven  $\mu$ L of purified PCR product and 4  $\mu$ L of the appropriate sequencing primer (10  $\mu$ M) were mixed and sequenced using the Power Read service provided by Eurofins Genomics (Huntsville, AL).

Sequences derived from the complete mitochondrial genomes of the domestic rabbit, *Oryctolagus cuniculus* (GenBank no. NC001913, Gissi *et al.* 1998) and collared pika, *Ochotona collaris* (Lagomorpha, Ochotonidae, GenBank no. NC003033, Lin *et al.* 2002) were used as references to align our sequences. Reference sequences were 961 and 956 nt (*Oc. collaris* and *Or. cuniculus* 12S rRNA), and 1139 nt (*Oc. collaris* and *Or. cuniculus* cyt-*b*). We also included new and GenBank sequences as follows, for 12S rRNA: *Bunolagus idahoensis*, AY292695, U58921, *S. floridanus*, AY012126, AY292698, new, Texas A&M AK11178, AK114511, *S. gabbi* (?), new, Angelo State University Natural History Collections nos. 2328, 2329, 2330, *S. obscurus*, U63887, new, Texas A&M AK11516, *S. transitionalis*, new Texas A&M AK11525, *S. audubonii*, AY292696, *S. nuttallii*, AY292697, U63886, *S. aquaticus*, AY292700, *S. palustris*, AY292701, U63885. For cyt-*b*: *B. idahoensis*, AY292721, *S. floridanus*, AY292724, *S. obscurus*, AY292725, *S. transitionalis*, AF034256, *S. aquaticus*, AY292726, *S. palustris*, AY292727, *S. nuttallii*, AY292723, *S. audubonii*, AY292722. Chimeric 12S+cyt-*b* sequences used the following: *B. idahoensis*, AY292695 + AY292721, *S. floridanus*, AY292698 + AY292724, *S. obscurus*, AK11516 + AY292725, *S. transitionalis*, AK11525 + AF034256, *S. palustris*, AY292701 + AY292727, *S. aquaticus*, AY292700 + AY292726, *S. audubonii*, AY292700 + AY292726, *S. nuttallii*, AY292697 + AY292723. To adequately date cladogenic events within Leporidae, for the analysis undertaken in BEAST, we added to the chimeric sequences noted above the following chimeric sequences: *Lepus americanus*, AY292707 + AY292733, *L. brachyotis*, AB058613 + AB058616, *L. californicus*, AY292705 + AY292731, *L. capensis*, AY292706 + AY292732, *L. europaeus*, AJ421471 + AJ421471, *L. saxatilis*, AY292704 + AY292730, *L. timidus*, AB058610 + AB058607, *L. townsendii*, AY292703 + AY292729, *Oryctolagus cuniculus*, NC001913 + AY292717. GenBank accession numbers for the new sequences generated for this paper are listed in Table 1.

Initial alignments were produced using Clustal X, version 2.0 (Larkin *et al.* 2007) and its default values for alignment parameters. The 12S rRNA gene alignment was further refined following the two-dimensional structure model of stems and loops proposed by Springer *et al.* (1995). Final alignments were adjusted in Mesquite 3.02, build 681 (Maddison & Maddison 2015). Best-fit selection of nucleotide substitution models was based on the Bayesian Information Criterion (BIC), as implemented in jModelTest2 version 2.1.6 (Darriba

*et al.* 2012, Guindon & Gascuel 2003). Genetic distances, uncorrected (p) and model corrected, were calculated in PAUP\* 4.0b10 (Swofford 2003). Maximum likelihood (ML) analyses were undertaken on 12S and cyt-*b* separately, then combined; each analysis used a separate model of evolution elucidated as described above. The ML analyses were conducted using RAxML v. 8.2.4 (Stamatakis 2014), which uses a GTR model of evolution. The dataset was initially partitioned for the different loci in order to assess the complementarity between the two data sets: while the 12S rRNA gene shows strong phylogenetic signal among Leporidae, the utility of cyt-*b* has been questioned at the intergeneric level (Halanych & Robinson 1999). We ran 1000 replicate ML searches, assessing clade confidence with 1000 bootstrap pseudoreplicates using the thorough bootstrapping algorithm. Phylogenetic analyses of *Sylvilagus* taxa were rooted using *Brachylagus idahoensis*, the presumed sister taxon to *Sylvilagus* (Matthee *et al.* 2004).

Bayesian analyses were undertaken using MrBayes 3.2.4 (Ronquist *et al.* 2012). We ran four independent Markov chain Monte Carlo (MCMC) analyses, each with eight Metropolis-coupled chains, an incremental heating temperature of 0.1, and an exponential distribution with a rate parameter of 25 as the prior on branch lengths. Analyses were run for 100 million generations, with parameters and topologies sampled every 1000 generations. We assessed stationarity and convergence by plotting the -ln L per generation in the program Tracer 1.6 (Rambaut *et al.* 2013), and dropped samples prior to achieving -ln L asymptote as burn-in. We assessed whether the four analyses reached stationarity at a similar likelihood score and that the topologies were similar, and used the resultant trees to calculate posterior probabilities on a 50% majority rule consensus tree.

For molecular dating methods (time to most recent common ancestor), we used fossil based dates of divergence coupled to a relaxed molecular phylogenetics technique as implemented in the program BEAST, v.1.8.1 (Drummond *et al.* 2012), which simultaneously estimates phylogeny and divergence times among the sampled taxa. We used an uncorrelated lognormal relaxed molecular clock model (Drummond *et al.* 2006, Ho 2007) and a Yule prior on the tree to simulate the process of speciation (Yule 1925). Operators were tuned in successive runs of BEAST under the chosen model of evolution, with slight changes to the scaling factors until the Effective Sample Size (ESS) for each parameter exceeded 200 (Drummond & Rambaut 2007). When optimum operator scaling was achieved, we re-ran the analysis for 20 million generations. Burn-in was assessed based on having reached a stable negative log likelihood (asymptote), and trees prior to reaching an asymptote discarded from the beginning of the run; all samples were examined in Tracer (Rambaut *et al.* 2013) to verify an effective sample size exceeding 200 for all parameters being estimated. We initially calibrated our molecular clock analyses using a divergence estimate, derived using fossils, of 47.6 MYA between Ochotonidae and

Leporidae. This date was suggested by Benton *et al.* (2014) based on the rationale that the fossil material described by Rose *et al.* (2008) was referable to Leporidae. This latter taxonomic assignment we feel is not justified at this time: the robust Shanghuang taxon is located within the Rose *et al.* (2008) phylogeny based on a single calcaneus, resulting in six characters being represented in a data matrix of 228 characters, or 2.6% representation; their gracile Shanghuang and Vastan lagomorphs' taxonomy is based on two calcanea and a single talus resulting in the presence of 20 of 228 characters, or 8.8% representation in the data matrix (Rose *et al.* 2008). Notwithstanding, the first occurrence of Ochotonidae is definitively documented in the Eocene, specifically the Uintan North American faunal stage, 42–46.2 MYA (Storer 1984), based on a record of †*Desmatolagus vusillus* from the Swift Current Creek fauna of Saskatchewan. Besides the Rose *et al.* (2008) fossils, the earliest documented unequivocal Leporidae otherwise likely date from the late Barstovian (ca. 13 MYA) of North America (Voorhies & Timperley 1997), and †*Litolagus*, 33.9 MYA (Fostowicz-Frelik 2013).

Given the foregoing uncertainties, combined with the long branches and rate variation in the matrix, as well as the fact that we were fundamentally interested in timing cladogenic events within *Sylvilagus*, the final analyses in BEAST were conducted using *Sylvilagus*, *Brachylagus idahoensis*, and *Oryctolagus cuniculus*, with *Lepus* as the outgroup. The 19 taxon analysis relied on two fossil calibration points: basal diversification of *Sylvilagus* at 4.4 million years ago ( $\sigma = 0.255$ , 95% confidence interval = 3.9 – 4.9 MYA), and basal diversification of *Lepus* at 4.5 MYA ( $\sigma = 0.250$ , 95% CI = 4.0 – 5.0 MYA). Justification for assigning that age to *Sylvilagus* is presented below [see: Restoration of *Sylvilagus andinus* (Thomas, 1897)]. Assignment of *Lepus* to that age is more controversial. The oldest undisputed *Lepus* fossils date from the Blancan to Irvingtonian transition in North America (Pajak *et al.* 1996, <0.6 MYA) and Middle Pleistocene of Kenya (Potts *et al.* 1988, 0.70 – 0.56 MYA). Dawson (1981) listed a fossil record for *Lepus* of Pleistocene (11.7 KYA – 2.59 MYA) of Eurasia, North America, and Africa, with possibly a Mid-Pleistocene origin from †*Nekrolagus*. Older assignments remain problematic: a Barstovian age, for example, is based on a single astragalus “similar to that of *Lepus*” (J.C. Merriam 1919:471) in the Rosamond Series of the Upper Miocene (Baker 1911, ca. 5.3 – 7.2 MYA). Given the chromosomal uniformity of *Lepus* (Robinson *et al.* 1983a) in stark contrast to *Sylvilagus* (Robinson *et al.* 1983b, 1984), it may be even more likely that *Lepus* is more recent than *Sylvilagus* (Ge *et al.* 2013 suggested a basal diversification of <2.5 MYA based on molecular data). Notwithstanding, we opted for the conservative fossil dates of ca. 4.5 MYA, also supported by some molecular analyses (Yamada *et al.* 2002), which could explain the current almost worldwide distribution of the genus.

Molecular data: specimens examined—GenBank accession numbers for all sequences used in this paper are listed in Table 1.

Niche modeling—We developed the initial ecological niche models for *S. brasiliensis sensu lato* (as currently construed) and *sensu stricto* (this paper), as well as for *S. andinus*, to estimate their current distributions. Known occurrence data were retrieved from the Global Biodiversity Information Facility (GBIF 2014), which allows free access to records of many different natural history museum specimens. Certain specimens that were doubtful with respect to identification, or that fell outside their predicted range, were examined in order to indubitably ascertain their identity (Maldonado *et al.* 2015). Records without latitude/longitude points were excluded from this range assessment. We also included some specimens from museum collection databases not accessible to search engines and georeferenced by us. The occurrence data with latitude and longitude were then georeferenced in ArcMap 10.2 (ESRI 2013) to ensure plotted points corresponded to the original locality descriptions. Duplicate records were removed to avoid a highly skewed output. We retrieved 19 environmental variables available in WorldClim (Hijmans *et al.* 2005) and a total of 35 (including WorldClim's original 19) available in CliMond (Kriticos *et al.* 2012), together with elevation and vegetation, the latter derived from Data Basin (2014). The bioclimatic layers used represent a range of climate conditions including temperature, isothermy, seasonality, precipitation, solar radiation, and moisture index. We used ArcMap 10.2 to mask the environmental layers to our spatially proscribed study area. We then used MaxEnt v. 3.3.3k (Phillips *et al.* 2006) to run the ecological niche models in order to estimate current range based on museum data for *S. brasiliensis* as a whole as well as individual taxa currently subsumed therein as subspecies (Appendix 1). MaxEnt is based on the maximum-entropy principle developed by Jaynes (1957) and has proven to be a reliable method for determining species distributions (Rissler & Apodaca 2007). In addition we used two scenarios for predicted global climate change from the special report on emissions developed under the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC 2007) to assess potential range expansion or contraction for the individual subspecies (Appendix 1). IPCC (2007) scenario A1B hypothesizes a mean increase of 2.8°C by 2100 (range 1.7°–4.4°), while scenario A2 hypothesizes a mean increase of 3.4°C (2.0°–5.4°).

Niche modeling: specimens examined—These analyses are based on more individuals than can be listed herein. Interested individuals may download their own data from GBIF or request the files from authors LAR or JHF.

## RESULTS

*Sylvilagus brasiliensis* (Linnaeus, 1758)

Figs. 5–11

**Neotype.** Stuffed skin, skull, and almost complete skeleton of an adult male, collected by Paulo H. Asfora on 13

TABLE 1— GenBank identification numbers, tentative identification (see molecular results for alternative interpretations), locality (when available), and decimal latitude and longitude (when available) of the individuals used in the molecular analyses described herein.

GenBank Number	Tentative Species Identification	Locality	Latitude	Longitude
AF038019	<i>Sylvilagus audubonii</i>	No data		
AY012126	<i>Sylvilagus floridanus</i>	No data		
AY012126	<i>Sylvilagus floridanus</i>	No data		
AY292695	<i>Brachylagus idahoensis</i>	USA: Utah: Cache Co.; no specific locality		
AY292696	<i>Sylvilagus audubonii</i>	USA: Wyoming: Carbon Co.; no specific locality		
AY292697	<i>Sylvilagus nuttallii</i>	USA: Utah: Cache Co.; no specific locality		
AY292698	<i>Sylvilagus floridanus</i>	USA: Maryland: Allegheny Co.: LaVale		
AY292699	<i>Sylvilagus obscurus</i>	No data		
AY292699	<i>Sylvilagus obscurus</i>	No data		
AY292700	<i>Sylvilagus aquaticus</i>	USA: Louisiana: Cameron Parish; Rockefeller Refuge		
AY292701	<i>Sylvilagus palustris</i>	USA: North Carolina: Halifax Co.; no specific locality		
GQ387162	<i>Sylvilagus aquaticus</i>	No data		
GQ387163	<i>Sylvilagus aquaticus</i>	No data		
GQ387164	<i>Sylvilagus aquaticus</i>	No data		
GQ387165	<i>Sylvilagus floridanus</i>	No data		
GQ387166	<i>Sylvilagus floridanus</i>	No data		
GQ387167	<i>Sylvilagus floridanus</i>	No data		
GQ387168	<i>Sylvilagus floridanus</i>	No data		
KU057207	<i>Sylvilagus brasiliensis andinus</i>	Ecuador: Guamaní; Cordillera Oriental	-0.33	-78.53
KU057208	<i>Sylvilagus floridanus</i>	México: Oaxaca; Santiago Tamazola, 7 km NE Santiago Tamazola	17.664	-98.226
KU057209	<i>Sylvilagus floridanus</i>	México: Jalisco; La Rosa Amarilla, 10 KM NW, 2 KM E La Manzanilla	20.084183	-103.152454
KU057210	<i>Sylvilagus floridanus</i>	México: Michoacán; 10 km N of San Jose de Gracia	20.0786	-103.0303
KU057211	<i>Sylvilagus floridanus</i>	México: Jalisco; 6.5 km E Mazamitla	19.91556	-102.9606553
KU057212	<i>Sylvilagus audubonii minor</i>	México: Durango; Reserva de la Biosfera Mapimí, 140 km NE of Gomez Palacio		
KU057213	<i>Sylvilagus audubonii minor</i>	México: Durango; Reserva de la Biosfera Mapimí, 140 km NE of Gómez Palacio	26.67513	-103.74986
KU057214	<i>Sylvilagus mansuetus</i>	México: Baja California Sur; Zona Oeste de la Isla San José	24.972651	-110.655137
KU057215	<i>Sylvilagus mansuetus</i>	México: Baja California Sur; Zona Oeste de la Isla San Jose	24.972651	-110.655137
KU057216	<i>Sylvilagus floridanus</i>	México: Tabasco; 3.8 km SW ruinas Acalán, sea level	17.74315833	-91.30466944
KU057217	<i>Sylvilagus floridanus</i>	México: Tabasco; 3.8 km SW ruinas Acalán, sea level	17.74315833	-91.30466944
KU057218	<i>Sylvilagus floridanus</i>	México: Tabasco; 3.8 km SW ruinas Acalán, sea level	17.74315833	-91.30466944
KU057219	<i>Sylvilagus brasiliensis</i>	Costa Rica: Heredia; San Rafael: Monte de la Cruz, elev. 1863m	10.06588056	-84.07658333
KU057220	<i>Sylvilagus floridanus</i>	Costa Rica: Guanacaste; Palo Verde	10.35	-85.35
KU057221	<i>Sylvilagus floridanus</i>	Costa Rica: Guanacaste; Palo Verde	10.35	-85.35
KU057222	<i>Sylvilagus brasiliensis</i>	Costa Rica: Heredia; Sarapiquí, Isla Verde	10.371	-84.02
KU057223	<i>Sylvilagus brasiliensis</i>	Costa Rica: Heredia; Sarapiquí, Isla Verde	10.371	-84.02
KU057224	<i>Sylvilagus brasiliensis</i>	Costa Rica: Heredia; Sarapiquí, Isla Verde	10.371	-84.02
KU057225	<i>Sylvilagus brasiliensis</i>	Costa Rica: Heredia; Sarapiquí, Isla Verde	10.371	-84.02
KU057226	<i>Sylvilagus brasiliensis</i>	Costa Rica: Heredia; Sarapiquí, Isla Verde	10.371	-84.02
KU057227	<i>Sylvilagus brasiliensis nivicola</i>	Ecuador: Pichincha; Mt. Antisana	-0.48	-78.2
KU057228	<i>Sylvilagus brasiliensis</i>	Ecuador: Pichincha; Peñas Blancas, elev. 3720m	-0.3028	-78.24
KU057229	<i>Sylvilagus floridanus</i>	Venezuela: Cojedes; Finca Hidra, 30 km S de San Carlos	9.3778	-68.583
KU057230	<i>Sylvilagus floridanus</i>	Venezuela: Cojedes; Finca Hidra, 30 km S de San Carlos	9.3778	-68.583



TABLE 1— GenBank identification numbers, continued.

GenBank Number	Tentative Species Identification	Locality	Latitude	Longitude
KU057231	<i>Sylvilagus floridanus holzneri</i>	USA: Arizona; Mansfield Canyon, Santa Rita Mts., 10 mi W of Patagonia. 4500feet	31.6267	-110.8222
KU057232	<i>Sylvilagus gabbi</i>	Panamá: Los Santos; Estancia “La Catalina,” 5.7 mi east of Tonosí, elev. 34m	7.45	-80.37
KU057233	<i>Sylvilagus gabbi</i>	Panamá: Los Santos; Estancia “La Catalina,” 5.7 mi east of Tonosí, elev. 34m	7.45	-80.37
KU057234	<i>Sylvilagus floridanus holzneri</i>	USA: New México; Animas Mts., Horse Thief Tank; T32s, R19w, Sec 34	31.4811085	-108.7616855
KU057235	<i>Sylvilagus floridanus</i>	México; Oaxaca; Temazcal, Piscifactoria Temazcal. Elev ca. 60m	19.2642	-96.4233
KU057236	<i>Sylvilagus brasiliensis</i>	Ecuador; Parque Nacional Yasuni, 5KM S of Pompeya Sur. Elev 250m	-0.4123	-76.4425
KU057237	<i>Sylvilagus audubonii</i>	México; Tamaulipas; 1 mi SW Rancho Los Carricitos. Elev. ca. 700m	24.594	-99.0476
KU057238	<i>Sylvilagus bachmani ubericolor</i>	USA: California; 8 mi N, 1.5 mi E Arcata	40.98604	-124.05086
KU057239	<i>Sylvilagus bachmani macrorhinus</i>	USA: California; Moraga, Moraga Rd. near Rheem Blvd.	37.86315	-122.15303
KU057240	<i>Sylvilagus brasiliensis</i>	Bolivia: Beni; 4 km N Yacuma	-15.1	-67.06667
KU057241	<i>Sylvilagus brasiliensis</i>	Paraguay: Alto Paraguay; 3 km E Destacamiento Militar “Gabino Mendoza.” Elev. 340m	-20.0737	-61.8873
KU057242	<i>Sylvilagus brasiliensis chacarius</i>	Paraguay: Amambay; Parque Nacional Cerro Cora, elev 280m.	-22.652778	-56.011167
KU057243	<i>Sylvilagus brasiliensis peruanus</i>	Peru: Amazonas; vicinity of Huampami (Aguaruna village), Rio Cenepa	-4.47	-78.17
KU057244	<i>Sylvilagus floridanus</i>	USA: New México; 0.5mi N of I-40 on NM Hwy 14	35.091837	-106.3809643
KU057245	<i>Sylvilagus floridanus holzneri</i>	USA: New México; Animas Mts., 1 mi N San Luis pass. Elev. ca. 1700m	31.4107604	-108.7598116
KU057246	<i>Sylvilagus floridanus</i>	USA: New York: Westchester Co.; 0.4 mi N, 0.9 mi W Armonk, Louis Calder Conservation and Ecology Center of Fordham University	41.1301	-73.7309
KU057247	<i>Sylvilagus obscurus</i>	USA: West Virginia: Grant Co.; Dolly Sods Scenic Area (Monongahela National Forest), 0.96 km N, 0.35 km E Red Creek Campground. Elev. 1220m	39.0412	-79.3117
KU057248	<i>Sylvilagus obscurus</i>	USA: Virginia: Bath Co.; Bald Knob, 5.25 mi S, 1.5 mi W Hot Springs	37.924	-79.856
KU057249	<i>Sylvilagus palustris</i>	USA: South Carolina; Colleton Co.; Bear Island Wildlife Management Area, 17 mi E Green Pond. Elev. 12m	32.563	-80.3567
KU057250	<i>Sylvilagus transitionalis</i>	USA: New Hampshire: Strafford County; Dover: Dover Industrial Park	43.187	-70.903
KU057251	<i>Sylvilagus dicei</i>	Costa Rica; Punta Arenas, Loma Linda	8.73473	-82.9218
KU057252	<i>Sylvilagus floridanus</i>	Colombia: Córdoba; Berastegui, ca. 10 km east of Cerete. Elev. 11 m	8.8802	-75.6883
KU057253	<i>Sylvilagus floridanus</i>	Colombia: Córdoba; Estancia “Las Chispas,” 12 Km E of Montería, on the rd to Planeta Rica	8.65	-75.78
KU057254	<i>Sylvilagus brasiliensis</i>	Brazil: Pernambuco; Garanhuns Municipality, Cavaquinho	-8.8907	-36.49656
KU057256	<i>Sylvilagus dicei</i>	Costa Rica: Cartago	9.55338	-83.6903
KU057258	<i>Sylvilagus brasiliensis nivicola</i>	Ecuador: Pichincha; Mt. Antisana	-0.48	-78.2
U58921	<i>Brachylagus idahoensis</i>	No data		
U63885	<i>Sylvilagus palustris</i>	No data		
U63886	<i>Sylvilagus nuttalli</i>	No data		
U63887	<i>Sylvilagus obscurus</i>	No data		

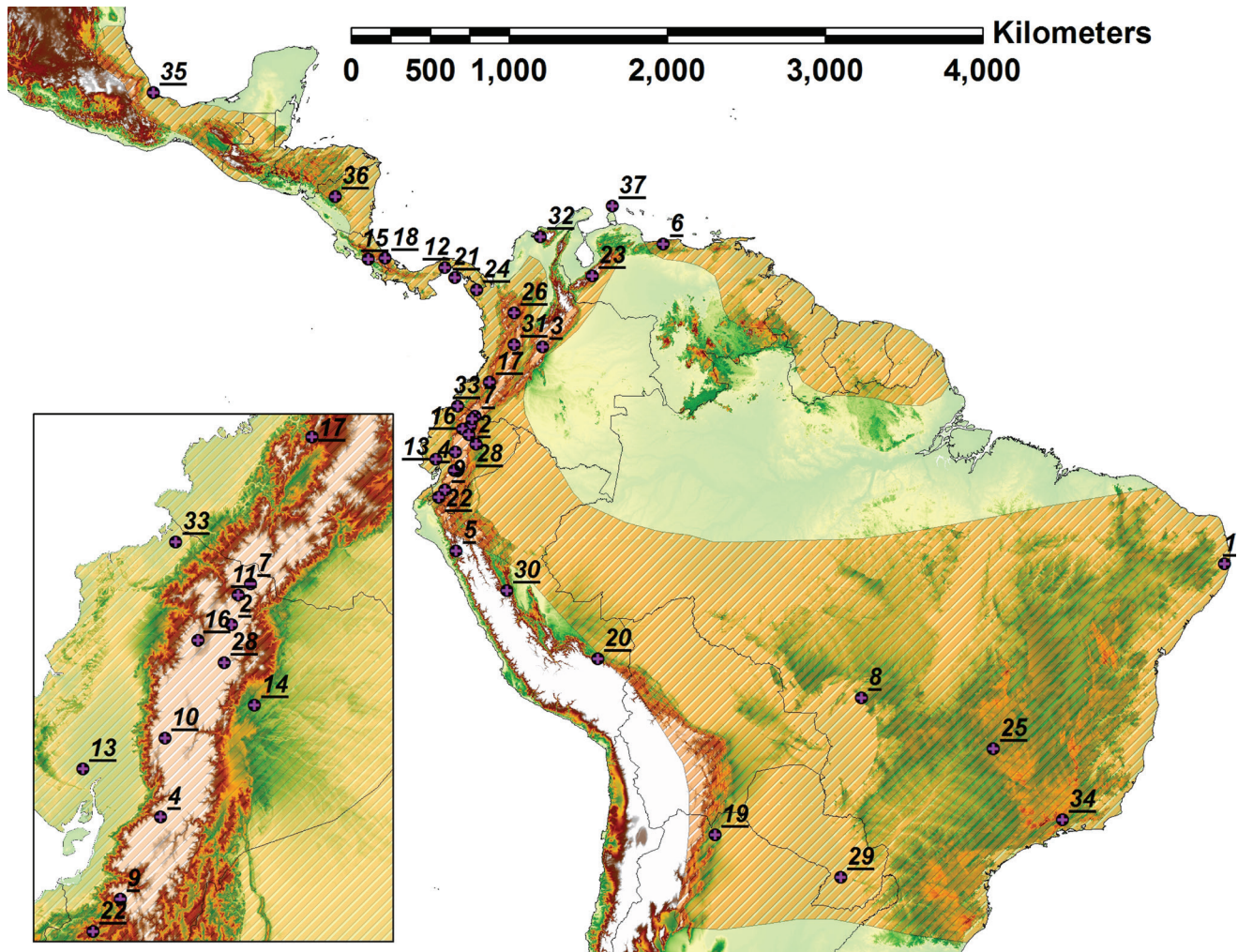


Figure 3— Alleged current distribution of *Sylvilagus brasiliensis* based on 1,852 occurrences of museum record data downloaded from the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)). We present the data as is, fully aware of the fact that there are numerous errors contained therein. For example, it is somewhat dismaying that ten years on, there still is no recognition in that database of *S. gabbi* as a valid species exclusive of *S. brasiliensis* (Ruedas and Salazar-Bravo, 2007). Exclusion of data from some collections with large numbers of specimens significantly affects the distribution. In addition, a museum specimen from Fordlândia (Aveiro, Pará, Brazil, 3°41'35"S, 55°27'44"W, 70m), falls in the center of otherwise unoccupied Amazonia; there are other similar omissions, e.g.: records from the mainland and islands at the mouth of the Amazon (de Sousa e Silva Júnior *et al.* 2005), which otherwise is also shown as an area devoid of cottontails. Inset map, lower left, shows Ecuador separately for clarity, with the taxa described therefrom. Numbered points refer to taxonomic designations as follows: 1. *Sylvilagus brasiliensis*, this paper; 2. *S. b. andinus*; 3. *S. b. apollinaris*; 4. *S. b. canarius*; 5. *S. b. capsalis*; 6. *S. b. caracasensis*; 7. *S. b. carchensis*; 8. *S. b. chapadae*; 9. *S. b. chillae*; 10. *S. b. chimbanus*; 11. *S. b. chotanus*; 12. *S. b. consobrinus*; 13. *S. b. daulensis*; 14. *S. b. defilippi*; 15. *S. dicei*; 16. *S. b. ecaudatus*; 17. *S. b. fulvescens*; 18. *S. gabbi*; 19. *S. b. gibsoni*; 20. *S. b. inca*; 21. *S. b. incitatus*; 22. *S. b. kelloggi*; 23. *S. b. meridensis*; 24. *S. b. messorius*; 25. *S. b. minensis*; 26. *S. b. nicefori*; 27. *S. b. nigricaudatus*; 28. *S. b. nivicola*; 29. *S. b. paraguensis*; 30. *S. b. peruanus*; 31. *S. b. salentus*; 32. *S. b. sanctamartae*; 33. *S. b. surdaster*; 34. *S. b. tapetillus*; 35. *S. gabbi truei*; 36. *S. g. tumacus*; 37. *S. b. nigronuchalis*.

July 2008 (field number PHA 246). Housed at the Laboratório de Mastozoologia, Departamento de Zoologia, Universidade Federal de Pernambuco, under catalogue number UFPE 1740. Tissue sample preserved in ethanol, housed in a freezer in the same location.

**Diagnosis.** *Sylvilagus brasiliensis* is distinguished from other species of *Sylvilagus* by the following combination of characters: cranially, presence of pitting on the dorsal

surface of the cranium, particularly the parietal and caudal surface of frontal bones, with pits clear and evident; pitting extending to frontal bone only along frontoparietal suture, and posteromedial margin of supraocular shelf; antorbital process absent; relatively long postorbital process ending in a broadly rounded terminus that is tightly fused to the frontal, on the tuberculum frontoparietale, which is slightly projecting from the frontal bones near the angulus sphenoidalis of the

parietal bones; zygomatic arch dorsoventrally robust, with a strongly marked zygomatic fossa for attachment of the lateral masseter muscle; strongly interdigitated frontoparietal suture, in places fused rather than clearly visible, somewhat broadly U-shaped, between each frontal and parietal bone; frontonasal suture shallow U-shape; process between posterodorsal process of premaxillae and nasal bones extremely short; single craniopharyngeal foramen in basisphenoid; and premolar foramen absent. Crown enamel pattern of third lower premolar relatively simple, with single or double, extremely shallow anteroflexid invagination into rostral aspect of anterior lobe; deep, simple (not crenellated) paraflexus and inconspicuous hypoflexus in second upper molar.

**Type locality.** The specimen described above was collected in: Brazil, state of Pernambuco, Municipality of Paudalho, Mata da Privativa, a forest fragment located in CIMNC (Centro de Instrução Marechal Newton Cavalcanti), 7°50'38.4"S, 35°6'7.3"W, elevation: ca. 137 m. The rationale for establishing this as the type locality is that there is a specimen associated with the locality (UFPE 1740), the locality is close to Recife, and although it is unlikely that Marcgraff collected precisely there, it fits within the Atlantic coastal plain that he did sample. This locality lies within the Pernambuco Endemism Center (hereafter PEC), a unit of the Atlantic Forest Biome generally acknowledged to begin north of the São Francisco River (separating the states of Sergipe and Alagoas), and encompassing most of eastern Alagoas, coastal segments of the states of Pernambuco and Paraíba, and a narrow coastal band in eastern Rio Grande do Norte (Asfora & Pontes 2009). The Atlantic Forest biome was assessed as a biodiversity hotspot (Myers *et al.* 2000) based on endemism in plant and vertebrate species. The Atlantic Forest has been reduced to between only 5–7% of its original area over the last 500 years (Asfora & Pontes 2009, Brown & Brown 1992, Viana *et al.* 1997, Tabarelli *et al.* 2005). The São Francisco River, one of the longest rivers in South America, constitutes an important biogeographic barrier to the regional fauna (Nascimento *et al.* 2013). For the PEC component, the equivalent figure is a loss of between 94% (Mendes Pontes *et al.* 2013) to as much as 98% (Brown & Brown 1992, Viana *et al.* 1997, Asfora & Pontes 2009, Y. L. R. Leite *et al.* 2011). The conservation importance of the PEC is undoubted: at least 35 species or subspecies of birds are endemic (of at least 435 present, Silveira *et al.* 2003, Stotz *et al.* 1996, Roda *et al.* 2003, Lobo–Aráujo *et al.* 2013), and even medium-sized mammals are still routinely discovered (e.g., the porcupines *Coendou speratus* Mendes Pontes *et al.* 2013, *C. baturitensis* Feijó and Langguth, 2013, and the red-rumped agouti *Dasyprocta iacki* Feijó and Langguth, 2013). Stattersfield *et al.* (1998) identified this region an area of bird endemism that they considered among the most endangered in South America, and having the highest endemism based on unit area. da Silva *et al.* (2004) similarly singled out the uniqueness of the PEC (based on cladistic analysis of presence absence data from passerine

birds), as well as other units (areas of endemism) contained within the Atlantic Forest biome.

The CIMNC, established in 1944, covers 7,324 Ha of forest remnants, making it the largest block of Atlantic Forest north of the Rio São Francisco (Guimarães 2008). Moreover, just within the CIMNC, 119 bird species were documented in the course of a two day survey (Pereira 2009); two of the species are restricted to Atlantic Forest (*Touit surdus* [Psittaciformes: Psittacidae], and *Ramphocelus bresilius* [Passeriformes: Thraupidae]), and four have subspecies, listed as Vulnerable by IUCN, also restricted to the PEC (*Picumnus exilis pernambucensis* [Piciformes: Picidae], *Thamnophilus caerulescens pernambucensis* [Passeriformes: Thamnophilidae], *Conopophaga lineata cearae* [Passeriformes: Conopophagidae], *Xenops minutus alagoanus* [Passeriformes: Furnariidae]). We stress the biological significance of this area of endemism to underscore the possibility that, like the novel species of porcupine listed above, the neotype of *Sylvilagus brasiliensis* will be found to represent a geographically restricted species, as we hypothesize below.

**Distribution.** *Sylvilagus brasiliensis* as heretofore understood has potentially the broadest geographic distribution of any small or medium sized terrestrial mammal (barring the red fox, *Vulpes vulpes*), extending from Veracruz, México, in the North to Argentina in the South, and from the Atlantic coast of Brazil in the East to the Pacific coast of South America in Peru and Ecuador in the West, and including elevations upwards of 4000–4500 m in Peru, Ecuador, Colombia, and Venezuela (Fig. 3). Using ArcGIS and the currently available data through GBIF we estimated the potential area covered by that broad conception of the species *S. brasiliensis* as approximately  $1.09 \times 10^7$  Km<sup>2</sup>. It is highly unlikely that the potential range shown in Fig. 3 represents any form of biological reality for the species whose neotype we are describing herein. Vieira (1953) suggested that *S. b. brasiliensis* were restricted to northern and northeastern Brazil, and that other subspecies (*S. b. minensis*, *S. b. paraguensis*, and *S. b. tapetillus*) occupied the remainder of Brazil. A more punctilious ecological niche modeling approach based on the existing locality data from Pernambuco suggests instead a much more restricted fundamental niche of 500–700 Km<sup>2</sup> (Fig. 4), the true range (realized niche), a narrow distributional band along Atlantic coastal Brazil, likely is even smaller. This hypothesized range is congruent with the PEC within the Atlantic Forest Biome, a particularly endangered ecosystem (Buckley & de Vasconcellos Pegas 2014, Haddad *et al.* 2015) wherein lies Recife. At least one sigmodontine rodent species, *Hylaeamys oniscus*, and to some extent a second, *Wiedomys pyrrhorhinos*, overlap in distribution the range of *S. brasiliensis* as restricted herein (Weksler *et al.* 2006, Brennand *et al.* 2013, Bonvicino 2015). It is likely that only a careful revision of *S. brasiliensis* as broadly understood, including further, more detailed morphological, chromosomal, and molecular assessments, will yield a



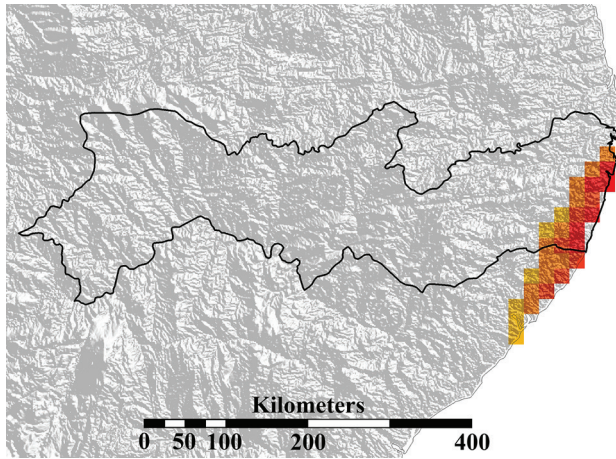


FIGURE 4—Map of the putative range of *Sylvilagus brasiliensis* as defined herein, based on a niche modeling approach, derived using ArcGIS, and using the locality data from the neotype and a second specimen of *S. brasiliensis* from UFPE, no. 427, from ca. 8°43'14.7"S, 35°10'44.6"W, elev. 104m. The black outline marks the geographic border of the state of Pernambuco. Note the tight correspondence of the modeled distribution with the Pernambuco Endemism Center, with a southern boundary at the São Francisco River (see "Type locality" above).

true picture of its taxonomic diversity and geographic scope.

**Description of the neotype.** External appearance (Figs. 5–6)—Body measurements (from fresh specimen): Head and body, 375 mm, tail length, 20 mm, hind foot, 83 mm, ear length, 58 mm, mass, 950 grams. Pelage (Fig. 5) habitual for forest *Sylvilagus* species. Colors assessed by direct comparison with Smithe (1975). Nuchal patch Orange Rufous to Mahogany Red in general appearance, hair approximately 0.8 mm in length, with fine black underfur and sparser, bicolored emergent hairs Buff throughout the length of the shaft with a Black tip. Mid-dorsal fur approximately 22–25 mm in length, with thick, fine, white to gray underfur approximately 10 mm in depth, emergent hair coarse and agouti with basal band above underfur black, approximately 4 mm in length, central band, between Chamois and Buff Yellow with hints of Orange Yellow and approximately 3 mm in length, and distal tip black, 4–5 mm in length. Midventral hair approximately 22 mm in length, with thick, primarily gray underfur constituting basal 10–12 mm. Remaining emergent fur consisting of coarse white hair. Fur from border between ventral and lateral aspects transitioning ventrally from region with thick, fine, gray underfur, 5–7 mm thick, with emergent all white hair, merging to (more laterally) thick, fine, gray underfur 4–6 mm thick, with a mixture of uni- and bicolored hair, unicolored hair mostly White, with some close to Cream, bicolored hair mostly White with some Buff–Yellow, with distal 3–6 mm Black, total length ca. 20 mm. Mid-lateral fur approximately 22–28 mm thick, basal layer about 10 mm thick, consisting of thick, fine, gray underfur, emergent hair bicolored, proximal

portion of shaft Pale Horn, distal 3–6 mm Black. Fur in gular area about 20 mm in length, basal portion consisting of thick, fine, gray underfur, emergent hair Cream to Pale Horn, with a transition zone about 1 mm to the distal Jet Black band, 0.8–2 mm in length, with some hairs showing as much as 3 mm of Black. Hair from tail 15–18 mm thick, basal 7 mm consisting of thick, fine, gray underfur transitioning distally to Warm Buff, emergent hair bicolored, distal band Jet Black, 2–4 mm in length, proximal portion of shaft Warm Buff.

External pinnae (Fig. 6) relatively densely furred externally for basal 25 mm, then remainder of length lightly furred, with skin visible, internal aspect lightly furred in Orange Rufous transitioning to mixture of Buff and primarily White on the interior edge of the pinnae. Hind foot primarily White dorsally, with some Pale Pinkish Buff beneath, particularly between the phalanges.

Skull and mandibles (Figs. 7–8)—Skull medium-sized to large within *Sylvilagus*: greatest length of skull, 71.4 mm, basilar length, 57.4, zygomatic breadth, 34.6 mm. Generally longer and narrower than other species in the genus: longer than *S. audubonii*, *S. bachmani*, *S. floridanus*, *S. mansuetus*, *S. nuttallii*, and *S. transitionalis*, overlapping *S. insonus*, and smaller than *S. aquaticus* and *S. palustris*. Zygomatic breadth narrower than most remaining *Sylvilagus* species, being larger than *S. bachmani* and *S. nuttallii*, equal to *S. audubonii*, and smaller than *S. aquaticus*, *S. floridanus*, *S. graysoni*, and *S. transitionalis* (data from Cervantes 1997, Cervantes & Lorenzo 1997, Chapman 1974a, 1974b, 1975, Chapman & Feldhammer 1981, Chapman & Willner 1978, 1981, Chapman *et al.* 1980, Lowery 1974, Orr 1940, Thomas & Best 1994; data on *S. transitionalis*, obtained from Chapman [1975], presumably includes—or indeed, may exclusive refer to—individuals of *S. obscurus*, between which species he was unable to distinguish). From a dorsal perspective (Fig. 7), paired nasal bones flare caudally, extending most caudally (greatest antero-posterior length: 31.2 mm [l] and 31.6 mm [r]) midway to the lacrimal tubercle when viewed dorsally. Lacrimal tubercles prominent, extending 2.5 mm (l) to 2.8 mm (r) from lacrimal and maxillary bones. Maxillary heavily fenestrated, or latticed (latticed area ca. 61 mm<sup>2</sup>), on dorsal half, starting ca. 6 mm above the palate and extending from premaxillary–maxillary suture to the lacrimal. Nasals start diverging approximately 9 mm from their caudal end, with a broadly blunt triangle separating the nasal bones formed by an anterior inclusion of the frontals (V-shaped frontal articulation, character 1, state 2, of Wible 2007). The posterodorsal processes of the premaxillae extend posteriorly subequally with the nasal bones, but extending just past (ca. 0.3–0.5 mm) the caudal extremity of the nasal bones. Antorbital process completely absent, postorbital process tightly fused to frontal over a length of ca. 1.6 mm, such that posterior supraorbital incisures have become foramina rather than incisures. Frontals generally smooth anteriorly, but increasingly pitted in their posterior half, toward the frontoparietal suture. Frontoparietal suture heavily crenellated,



FIGURE 5— Neotype of *Sylvilagus brasiliensis* (UFPE 1740). From left to right, dorsal, left lateral, and ventral perspectives of the skin. Scale bar equals 300 mm.





FIGURE 6— Details of pinna and hind foot of the neotype of *S. brasiliensis* (UFPE 1740). Left pair of images: exterior (left) and interior (right) of pinna. Right couplet: dorsal (upper) and ventral (bottom) aspect of hindfoot; scale bar equals 100 mm.



FIGURE 7— Views of the cranium of the neotype of *Sylvilagus brasiliensis* (UFPE 1740): dorsal (left), lateral (center), and ventral (right). Scale bar equals 80 mm; greatest length of skull, 71.42 mm, zygomatic breadth, 34.63 mm.





FIGURE 8— Views of the dentaries and articulated jaw of the neotype of *Sylvilagus brasiliensis* (UFPE 1740); maximum height of left ramus, 35.1 mm, maximum height of right ramus, 36.5 mm, alveolar length of left maxillary tooththrow 14.8 mm (right, 14.5 mm).

with strong interdigitation between frontal and parietal bones, as well as between parietal and squamosal bones. Parietal bones heavily pitted (character 6, condition 1, of Wible 2007).

From a lateral perspective, the rostrum is constituted by the premaxilla and maxilla, as the nasal bones only have a shallow bow to them (ca. 2.9 mm height at the anterior point of separation between nasal and premaxillary bones). The root of first incisor does not appear to extend to the maxilla, originating instead just anterior to the premaxillary–maxillary suture. The dorsolateral portion of the premaxilla is fenestrated, but the lower half is not. Supraocular shelf projecting slightly (ca. 1 mm) above dorsal aspect of skull. Zygomatic arch is robust, with a substantial dorsoventral deepening approximately medial from facial and caudal aspects thickening (depth of zygomatic arch at this point: 4.8 mm), which, being constituted by the zygomatic fossa, is apparently due to a massive lateral masseter muscle, or medial portion of the *m. masseter*, suggesting a robust masticatory apparatus in this species. Zygomatic fossa prominent and large, with origin posterior to masseteric spine of zygoma, approximately 8.75 mm caudal from anterior (maxillary) portion of spine, immediately caudal to three small foramina; the most caudal of these is presumably the zygomatico-orbitale, although it is not located in the zygomatic fossa itself. Wible (2007) speculated that these foramina may be equivalent to the human zygomaticofacial and zygomaticotemporal foramina. Entopterygoid crest of pterygoid prominent, projecting ventrally, with large hamulus (ca. 2 mm anteroposterior length) recurved caudally. Slight parietal crest present along squamoso–parietal suture, from insertion point of posterior postorbital process into parietal to terminus of suture at supraoccipital. Auditory bulla

relatively small: greatest length measured from just caudal to paraoccipital process of petrosal to suture between squamosal and auditory bulla, 9.5 mm, width measured on ventral surface from stylomastoid foramen to jugular foramen, 9.3 mm.

Ventrally, the perspective is dominated the incisive foramina, these are long (17.2 and 17.8 mm, left and right respectively), and broad (6.5 mm across the widest point). The incisive foramina extend caudally to a point marked by an imaginary line between the distal hypercones of the second upper premolar. The palatal bridge, formed by the maxillary and palatine bones, extends from the aforementioned line to another linking the anterior lochs of the first upper molars. Premolar foramen absent, major palatine foramen relatively small and inconspicuous. The craniopharyngeal canal is relatively evident, approximately 1.3 mm in anteroposterior dimension, 0.9 mm in width. Foramen ovale and piriform fenestra small, jointly measuring 3.5–4 mm in greatest linear dimension.

Mandibles (Fig. 8) largely unremarkable. Diastema long, ca. 15.2 and 14.9 mm (right and left ramus, respectively), and dorsoventrally shallow, somewhat concave rostrally, becoming flatter caudally. Mental foramen shallow, somewhat inconspicuous, ca. 1.4 mm (left) and 2.1 mm (right) in anteroposterior dimension. Coronoid process inconspicuous from a labial perspective, but somewhat acute and recurved in a lingual direction when viewed from dorsal or facial perspectives, reaching halfway over the sulcus ascendens. Condylar process relatively long and narrow dorsally at the articular head, height of the dentary measured from anteroventral edge of masseteric fossa (incisura vasorum facialium) to articular head of condylar process, 35.1 mm, anteroposterior length at constriction below articular head

(mandibular incisure) ca. 8.4 mm. Large, prominent masseteric and pterygoid tuberosities forming caudal end of mandibular ramus, extending forward along ventral edge of the mandibular ramus as a strong masseteric line ending abruptly at the anteroventral edge of the masseteric fossa, forming a sharp distinction between the masseteric fossa and the mandibular body, at the incisura vasorum facialium. Both mandibles have a fenestra in the inferior masseteric fossa, dorsal to the masseteric line and facial to the pterygoid tuberosity: on right mandible, 2.7 mm (vertical) by 2 mm (horizontal), on left mandible, 4 mm by ca. 2.3 mm (not symmetrical, see Fig. 8).

#### DENTAL MORPHOLOGY (FIGS. 9–11)

The standard terminology (after Palacios & López Martínez 1980) in the principal teeth used to differentiate among species of lagomorphs (third lower and second upper premolars) is illustrated in Fig. 9. The key features in these teeth are detailed below. Dental formula is standard for *Sylvilagus*: I 2/1, C 0/0, P 3/2, M 3/3.

*Third lower premolar* (Fig. 10)—*Anteroflexid* (Palacios & López Martínez 1980), anterior reentrant (White 1991). This was character (ix) in Ruedas (1998), scored as multiple (0), single (1), or absent (2). In the neotype of *S. brasiliensis* under consideration, the anteroflexid is present and multiple (condition 0), a smaller lingual and a larger labial pocket. The enamel of the anteroflexid is of varying thickness but generally thicker throughout (Ruedas 1998: character x, condition 1). The depth of the larger anteroflexid from the external surface of the enamel to an imaginary line drawn between the labial and lingual anteroconids is 0.3 mm, or approximately 12% of the anteroposterior length of the rostral loph.

*Paraflexid* (Palacios & López Martínez 1980), anterointernal reentrant (White 1991). This was character (xi) in Ruedas (1998), scored as absent (0), or present (1). This character is largely absent (condition 0), but its putatively homologous location is marked by a slight labially oriented depression of the lingual surface of the enamel into the rostral loph.

*Protoflexid* (Palacios & López Martínez 1980), anteroexternal reentrant (White 1991). This feature comprises characters (xii) and (xiii) in Ruedas (1998), scored in (xii) as having a single (0), or multiple reentrants (1), and in (xiii) as thin (0) or thick (1) enamel. The protoflexid of the neotype is simple and broadly U-shaped, showing little evidence of crenellation. This represents condition (0) of character (xii) in Ruedas (1998). The enamel thickness tapers gradually from the labial anteroconid and the protoconid to the deepest point of the protoflexid, where it is at its thinnest, with respect to character (xiii) of Ruedas (1998), this is ambiguously represented in the neotype.

*Hypoflexid* (Palacios & López Martínez 1980), posteroexternal reentrant (White 1991). This feature is comprises characters xiv–xviii of Ruedas (1998). Character

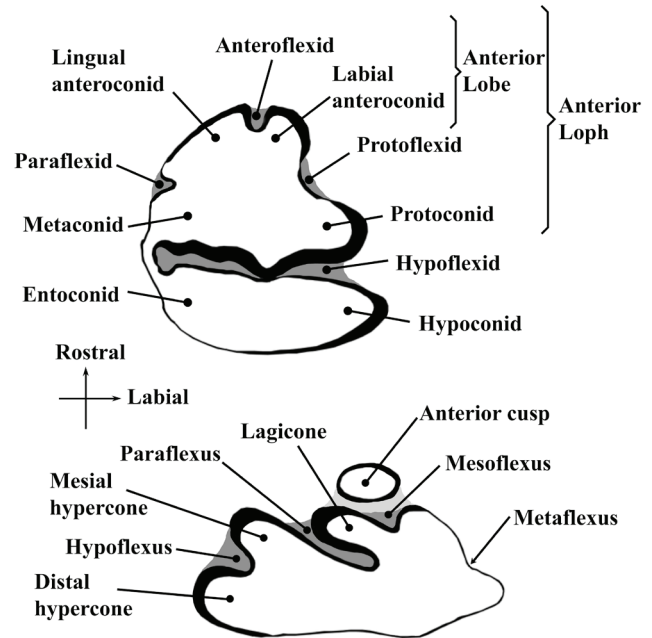


FIGURE 9— Standard nomenclature for dental features of leporid lagomorphs' third lower premolar (top) and second upper premolar (bottom), adapted from Fig. 1 of Palacios & Torres Martínez (1980:62). The term "anterior loph," preferred herein, was used interchangeably with "trigonid" by Hibbard (1963).

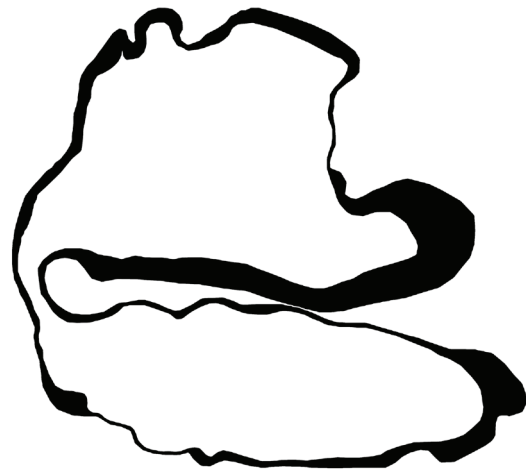


FIGURE 10— Third lower premolar of the neotype of *Sylvilagus brasiliensis* (UFPE 1740).

xiv is: rostral wall of hypoflexid constituted by continuous layer of thick enamel (0), or thick enamel layer discontinuous (1). The neotype of *S. brasiliensis* has a continuous layer of thick enamel (0), although there appears to be some diminution of the thickness in the lingual lacuna. Character xv concerns the central angle of the hypoflexid: reflected rostrally relative to main axis of hypoflexid (0), vs. not highly reflected (1). The neotype of *S. brasiliensis* has a minimally developed central

angle (1). Character xvi describes the central angle of the hypoflexid, referring to whether the central angle is angled such that an isolated lacuna is formed in the medial portion of the hypoflexid (0), vs. no lacuna formed by central angle in hypoflexid (1). While the central angle is shallow, it does get close to the caudal surface of the hypoflexid, notwithstanding, it is not so sharp as to form a lingual lacuna in the third lower premolar, as is the case for example in †*Nekrolagus progressus* (e.g., Hibbard 1963:3, Fig. 1e–f). Character xvii describes the enamel in the rostral wall of the hypoflexid: smooth (0) versus crenellated (1). The neotype of *S. brasiliensis* has a smooth rostral enamel wall in the hypoflexid. Finally, character xviii has to do with the condition of enamel in caudal wall of hypoflexid: enamel crenellated (0) versus smooth (1). The neotype of *S. brasiliensis* has little relief on the caudal margin of the hypoflexid, which is almost uniformly smooth: there is nothing besides an intimation of some undulations on the rostro–labial margin of the hypoconid.

*Second upper premolar* (Fig. 11)—*Mesoflexus* (Palacios & López Martínez 1980), external anterior reentrant (White 1991). Character i of Ruedas (1998, as anteroexternal reentrant): deep (0), shallow (1), or absent (2). This character relatively deep (condition 0) and narrow in the neotype: 0.4 mm when measured to an imaginary line between the lagicone and labial anterocone, and it is surrounded by thin enamel on the labial side and thick enamel tapering to thin enamel

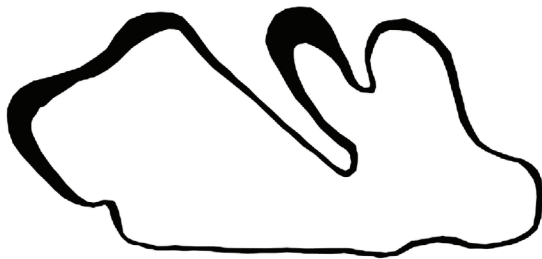


FIGURE 11— Second upper premolar of the neotype of *Sylvilagus brasiliensis* (UFPE 1740).

caudally on the lingual side. With respect to character ii, therefore, this character is ambiguous. This character was polarized by Ruedas (1998) by outgroup comparison with *Lepus californicus*, representing the presumed sister genus to *Sylvilagus* (Halanych & Robinson 1997, White 1991, White & Morgan 1995, Matthee *et al.* 2004); in *L. californicus*, the mesoflexus is deep. However, depth compared to the presumed primitive condition as expressed for example in †*Nekrolagus progressus* (e.g., Hibbard 1963:3, Fig. 1a), shows that the mesoflexus may primitively be expressed as a shallow, open, V-shaped depression between the lagicone and labial anterocone. In comparison to the holotype of *S. f. floridanus* (AMNH 1890/1155, illustrated in Ruedas 1998:1358, Fig. 1, as anteroexternal reentrant), which has an almost imperceptible

depression representing this character, the mesoflexus of the neotype of *S. brasiliensis* is much deeper.

*Paraflexus* (Palacios & López Martínez 1980), main anterior reentrant (White 1991). The feature comprises characters iii–vi of Ruedas (1998). Character iii is: paraflexus, labial aspect enamel: enamel thick (0), or thin (1). In UFPE 1740, the enamel on the labial side, as it ascends the lagicone, is thick, condition 0. Character iv concerns the gross morphology of the labial aspect of the paraflexus: enamel smooth (0), or crenellated (1). In this character, the neotype displays smooth enamel (0). Character v describes the enamel of the lingual aspect of the paraflexus as thin (0) or thick (1). The neotype displays condition (0) in this character. The final character listed by Ruedas (1998) for the paraflexus is character vi, gross morphology of the lingual aspect, with enamel crenellated (0) or smooth (1). In this character, the neotype unequivocally displays condition 1. It is of note that with respect to the complexity (crenellation) expressed in the paraflexus other taxa of *Sylvilagus* (e.g., North American *Sylvilagus*, Ruedas 1998:1363, Fig. 3), the paraflexus of the neotype of *S. brasiliensis* is quite simple and almost identical to that of †*Nekrolagus progressus* (Hibbard 1963:3, Fig. 1a) and *Lepus* (Palacios & López Martínez 1980).

*Hypoflexus* (Palacios & López Martínez 1980), internal anterior reentrant (White 1991), anterointernal reentrant (Ruedas 1998). This feature comprises characters vii–viii of Ruedas (1998). Character vii describes the depth, deep (0), shallow (1), or absent (2). The neotype of *S. brasiliensis* displays condition (2), absent. A barely perceptible depression is present on the exterior of the enamel in the presumed location of the hypoflexus, and the interior enamel is flat and featureless. In comparison to other *Sylvilagus* where this feature was illustrated (Ruedas 1998:1363, Fig. 3), it is most similar to the condition—also scored as absent by Ruedas (1998)—displayed by *S. nuttallii pinetis* (holotype AMNH 9041/7336) although in this latter, the depression is clear, and expressed both in external and internal surfaces of the enamel. All other North American taxa of *Sylvilagus* examined by Ruedas (1998) had an evident and clear hypoflexus (condition 2). With respect to the enamel in the hypoflexus (character viii of Ruedas 1998), the neotype fairly homogeneously displays thick enamel throughout the presumed location of the hypoflexus, hence character state 1 (thick enamel throughout the hypoflexus).

*Metaflexus* (Palacios & López Martínez 1980), not considered by White (1991) or Ruedas (1998). The metaflexus is present as a shallow depression, as shown by Palacios & López Martínez (1980). This depression is present in certain individuals of certain species of *Lepus* (e.g., *L. granatensis*, Palacios & López Martínez 1980:71, Fig. 6.1), but is certainly not a universal feature across leporids. It is absent from †*Nekrolagus progressus* (Hibbard 1963:3, Fig. 1a) and variably present as a depression (*S. cognatus*, *S. robustus*) or absent in North American species of *Sylvilagus* (Ruedas 1998:1363, Fig. 3).



## ADDITIONAL REFERRED SPECIMEN

Universidade Federal de Pernambuco, no. 427, from locality: Brazil: Pernambuco; Municipality of Rio Formoso, Estação Experimental Florestal de Saltinho, (as of 1983: Reserva Biológica de Saltinho, 475.2 Ha), collected by Arthur Galileu de Miranda Coelho on 5 Sept. 1974. Estimated coordinates: 8°43'14.7"S, 35°10'44.6"W (WGS84), elev. 104m.

Restoration of *Sylvilagus andinus* (Thomas, 1897)

*Sylvilagus andinus*: Taxonomic summary—On 2 July 1897, it likely would have been a clear day at 4000 m in elevation, in the upper reaches of the Rio Blanquillo, a small glacial stream flowing from the western slopes of Mt. Cayambe. Located in the Cayambe Canton of Pichinche Province, Mt. Cayambe, at 5,790 m, is the third highest mountain in Ecuador, and is only about 65 Km northeast of Quito. As such, it would have made an attractive target for late Victorian naturalists and collectors, not the least of whom was William Frederik Henry Rosenberg, of 48a Charing Cross Road, on Leicester Square, London. The traveller–naturalist, as he billed himself in the back matter of volume 3, issue 3, of the *Journal of Molluscan Studies* for 1898, was an accomplished collector, and spent his time in Ecuador effectively. For example, George Albert Boulenger (1898) listed 78 different species collected by Rosenberg from only five localities, including 23 new species—with two named after the collector. Only five of Boulenger's 23 species described in that work have not withstood the test of time (including a coral snake named after Rosenberg: *Elaps rosenbergi*, synonymized under *Micrurus ancoralis*).

The preponderance of Rosenberg's herpetological collections originated from Paramba (1070 m) and Cachabé (ca. 150 m), we can surmise some frustration on the part of the intrepid traveller–naturalist, as he only collected some *Atelopus ignescens* in Cayambe. Perhaps this was his rationale for the trip to the higher elevations. Given that Rosenberg, then aged 29, covered (on horseback) the 70 or so kilometers from Quito to Cayambe in a day and a half (Boulenger, 1898:108), we can also surmise that this might therefore have been but a day trip for him, given that it is no more than about 17 Km along the Rio Blanco from Cayambe, at 2820 m, to the Puna habitat around the 4000 m contour. The 4000 m elevation contour indeed intersects the Rio Blanco in the very upper reaches of the river valley, as stated on the label of a specimen of *Sylvilagus* that Rosenberg collected, approximately at coordinates 0°01'47.24"N, 78°01'26.89"W (datum: WGS84; Fig. 12). That specimen would become the holotype (British Museum of Natural History no. 1897.11.7.54) of *Sylvilagus andinus*, described as a then novel species of cottontail rabbit—albeit as a *Lepus*—by Thomas (1897:551). Thomas (1897:552) noted this species differed from ordinary *S. brasiliensis*: it “is clearly not that species [*S. brasiliensis*], than which it is very much

larger. Probably it is most allied to *L. gabbi* and *L. sylvaticus*, but may be distinguished by its more dingy coloration.”

In the intervening years, there has been scant critical attention given to members of the *andinus* complex of *Sylvilagus*. Thomas (1913:212–214) considered *S. andinus* a species complex that he called the *Sylvilagus andinus* group, which he recognized as consisting of: *S. andinus* Thomas, 1897, *S. a. chimbanus* Thomas, 1913, *S. a. canarius* Thomas, 1913, *S. capsalis* Thomas, 1913, and *S. nivicola* Cabrera, 1913 (*S. nivicola* would not be published for another two months; Thomas (1913:217) listed the taxon as “a fifth [form], very different from any [*S. andinus*], is now being described by Sr. Cabrera.”). By the date of this mini–review of the *andinus* group, Thomas had available to him an extensive series of “true” lowland *S. brasiliensis* collected by Alphonse Robert in May and June of 1903 from Lamarão, in the state of Bahia (Lamarão: Bahia, 291 m, on railroad, 140 km NW of Salvador, eastern Bahia, midway between the towns of Água Fria (south) and Serrinha (north), 11°45'S, 38°53'W; Coimbra-Filho *et al.* 2006). This series of specimens constituted the standard for comparison between lowland and highland *Sylvilagus* at the very least, and indeed, had been prepared by Thomas himself, hence were intimately known to Thomas. It thus would have been quite straightforward for Thomas to assess the similarities and differences between lowland *S. brasiliensis* and highland *S. andinus*.

Cabrera (1913, published 30 April 1913), in describing *Sylvilagus nivicola*, examined variation in some of the South American highland *Sylvilagus*, using external characters (coloration primarily) to distinguish, using a dichotomous key, among *S. capsalis* Thomas, 1913, *S. andinus* Thomas, 1897, *S. a. chimbanus* Thomas, 1913, *S. a. canarius* Thomas, 1913, *S. meridensis* Thomas, 1904, and *S. nivicola* Cabrera, 1913. Cabrera (1913:4) described *S. nivicola*, placing the species in the “*andinus* group,” ascribing the group to Thomas for having named the first species of the group: *S. andinus*. Cabrera (1913:6) further defined the group as being constituted by “high elevation species characterized by their stocky shapes, extremely hairy limbs, and relatively long ears, longer than other South American species of the same genus.” Besides augmenting the size of the group (from four to six) by formally adding his new species and Thomas' *S. meridensis*, Cabrera had few additional definitive or even hermeneutical comments on the *andinus* group.

In his 1933 summary of the taxonomic history of Neotropical hares, Tate (1933) summarized the highland Andean *Sylvilagus*, what one might tentatively construe as the *andinus* group, as being constituted by *S. capsalis*, *S. kelloggi* Anthony, 1923, *S. chillae* Anthony, 1923, *S. andinus*, *S. a. canarius*, *S. a. chimbanus*, *S. nivicola*, *S. salentus* J. A. Allen, 1913, *S. fulvescens* J. A. Allen, 1912, *S. apollinaris* Thomas, 1920, *S. purgatus* Thomas, 1920, *S. nicefori* Thomas, 1921, and *S. meridensis*. Although from an Andean valley, *S. purgatus* may be misplaced in this group: insofar as we have

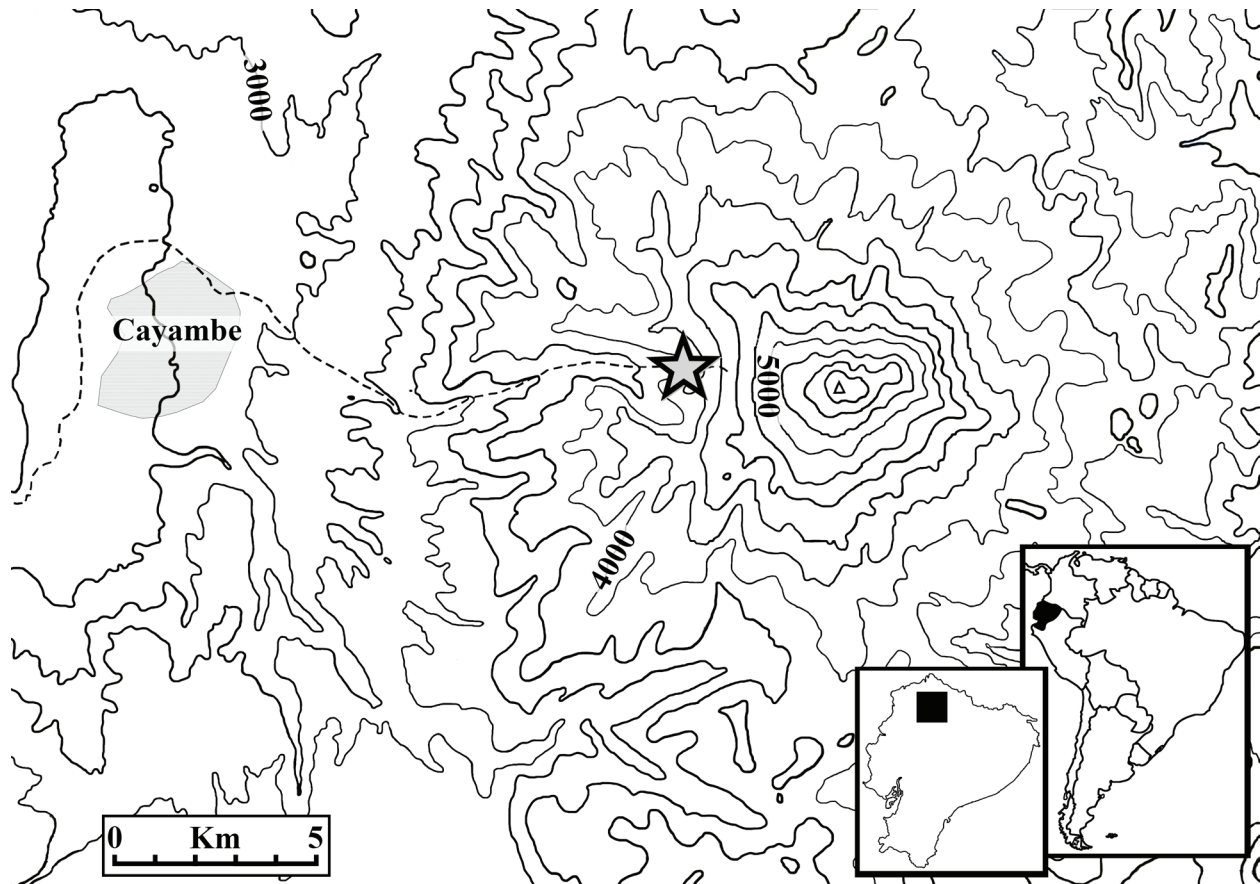


FIGURE 12— Type locality (star) of the holotype of *Sylvilagus andinus* Thomas, 1897 (NHMUK 1897.11.7.54). Verbatim locality (from specimen label): Cayambé Mt. Ecuador (Rosenberg). Verbatim locality, from Thomas (1897:552): "W. slope of Cayambé Mountain, Eastern Cordillera of Ecuador, and altitude 4000 metres." Coll. W. F. H. Rosenberg, 2nd July, 1897. Inferred latitude and longitude (WGS84): 0°01'47.24"N, 78°01'26.89"W. Smaller inset map: location of detailed map (black square) within Ecuador (outline). Larger inset map: location of Ecuador (solid black area) within South America (outline, with country boundaries). The gray circle, center left, marks the town of Cayambe, 0°02'25.25"N, 78°08'35.17"W, 2827 m (at the Cayambe Central Church crossing). The open triangle marks the summit of the Nevado Cayambe (also known as Volcán Cayambe), 0°1'44.4"N, 77°59'9.6"W, 5790 m. The dashed line running E–W between the town of Cayambe and the 5000 m contour of the Nevado Cayambe marks the course of the Rio Blanco.

been able to ascertain, Purificación, in the Magdalena Valley, the type locality, is at an elevation of ca. 300 m, and although potentially isolated from other lowland taxa—there are several narrow gorges along the course of the Magdalena before it empties into the Caribbean—and therefore possibly derived from an *andinus* group member, Thomas (1920) suggested the most apt comparison may have been to *S. margaritae* (Miller, 1898), from Margarita Island, Venezuela, and currently in synonymy with *S. floridanus* (J. A. Allen, 1890). We have yet to examine the holotypes of either *S. purgatus* or *S. margaritae*, therefore hesitate to venture any further opinions on the matter.

Hershkovitz (1938) described a collection undertaken between 1933 and 1937, in the course of which he collected 25 specimens of "three races of the Andean *Sylvilagus andinus*." He hypothesized that *S. andinus* group taxa were restricted to the treeless zone of the Andes, from Venezuela in the north (represented by *S. meridensis*) to Peru in the south

(*S. capsalis*). The treeless zone begins in the eastern and western zones at 3000 to 3500 m, and ends at the lower limit of the snowline somewhere in the vicinity of 4700 to 4800 m at the time of Hershkovitz's writing. In the interandean valleys, Hershkovitz suggested that they could descend to 2500 m or less (albeit at lower densities), but on the western and eastern slopes, they were stopped by the forests, occupied by rabbits of the *S. kelloggi* group to the west and *S. defilippi* to the east. Interestingly, Hershkovitz added the observation that these latter two taxa were nocturnal, but that the *S. andinus* group taxa were diurnal. Finally, he suggested that each race of the *S. andinus* group was altitudinally restricted to a band varying between 500 and 1000 m in extent. In that publication (Hershkovitz 1938), he defined the *S. andinus* group as being constituted by two novel subspecies that he named: *Sylvilagus andinus carchensis* and *S. a. chotanus*, and also included *S. a. andinus* (using the specimens detailed herein, from Hacienda

La Compañía, near Cangagua, ca. 10 mi SW Mount Cayambe, 3400 m), *S. a. nivicola*, *S. a. chimbanus*, and *S. a. canarius*.

However, Hershkovitz later revised his opinion (Hershkovitz 1950, 1969) suggesting instead that *Sylvilagus* in South America were in fact constituted by only two species: *S. floridanus* in the arid and semiarid tropical regions of Colombia and Venezuela, as well as their adjacent islands, and *S. brasiliensis* elsewhere in South America, in Tropical and Temperate Zone forests and in swamps, savannas, scrublands, and deserts. This restriction was based on the suggestion that “Characters given by the author [N.B.: Hershkovitz 1938] for distinguishing *S. andinus* from other groups now appear to be relative and in most cases intermediate between those of the *gabbi* and *brasiliensis* groups.” (Hershkovitz 1950:331–332). Based on the foregoing, Hershkovitz (1950:350) suggested that in fact, “The “*andinus* group” included *meridensis* of the Páramos of the Sierra de Merida, Venezuela, *andinus* with several subspecies named thereof, of the Ecuadorian highlands, and *capsalis* of western Peru. All names of these high Andean forms represent scattered populations of geographic races of *S. brasiliensis*.” Inexplicably for someone who would come to write what long has been considered the definitive zoogeographic treatise of South American mammals, Hershkovitz (1950:350) went on to say that “Former taxonomic separation of the “species groups” followed the convenient pattern of bestowing on the same animal a different specific name for each of its representatives on each of the American continents and on each side and slope of each mountain chain. None of the geographical features mentioned have impeded the distribution of *S. brasiliensis*.” Thus, he subsequently hypothesized (Hershkovitz 1969:24) that a single, unitary species, *S. brasiliensis*, entered South America overseas prior to the closing of the Panamá Land Bridge and “spread throughout the Brazilian Subregion from Amazonian rain forest and lowland savannas to temperate zone forests and grasslands in the Andes...” a single species of small to medium-sized organisms improbably covering innumerable biomes and a vast area.

Hershkovitz’ hypothesis that *S. brasiliensis* constitutes a single polytypic species throughout its currently accepted range in Central and South America has some contradictions that suggest it is false. Indeed, as he himself initially indicated (Hershkovitz 1938:2), there are marked ecological differences strongly suggestive of reproductive isolation: he described individuals of the *S. andinus* group, occupying the treeless Páramo habitat, as diurnal, in contrast to the exclusively nocturnal congeners inhabiting the forests below the treeline in both eastern and western sides of the range of *S. andinus* group species or individuals (although he later amended that statement without explanation [Hershkovitz 1950:329] that “In the highland páramos they are active from late in the afternoon to early in the morning.”). Similarly, although in his 1938 work, Hershkovitz considered *andinus* group and *brasiliensis* group species to be strongly distinct, by 1950

he was asserting that “It is imperative [...] to regard *andinus* and *meridensis* as collateral offshoots from a common stock of tapitis with an unbroken distribution at lower altitudinal levels” (Hershkovitz 1950:350), hence a single, polytypic but conspecific *S. brasiliensis*. However, scant—if any—evidence is adduced in support of his single polytypic *S. brasiliensis* hypothesis. Interestingly, Stone (1914:15), quoting S. N. Rhoads, the collector of his specimens hypothesized to be *S. a. chimbanus* (which he erroneously ascribed to Cabrera), similarly reported that one form was restricted to the “brush-grown pastures” (“templada”), and another to the immediately adjacent páramo, and noted that “It is quite possible that the paramo rabbit is distinct from the animal of the templada, at least subspecifically, or that there are two species, not distinguishable at a distance by a field observer.”

*Sylvilagus andinus: Biogeography and paleontology*—From a biogeographic perspective, Hershkovitz (1969) hypothesized that *S. brasiliensis* or its prototype invaded South America via the oversea route as a Stratum II faunal element. Although he did not explicitly date Stratum II, it is implied elsewhere in Hershkovitz (1969) that this element may refer to ca. the Oligocene, 23–34 MYA. Faunal Stratum II (“Old Island-hoppers”) as defined earlier by Simpson (1950) was constrained to Late Eocene (Priabonian) to Oligocene (38–23 MYA); Simpson (1950) however, restricted Stratum II in South America to caviomorph rodents and New World monkeys. The timing of the closing of the Panama Land Bridge remains controversial (Coates & Stallard 2013, Leigh *et al.* 2014, Kelt & Meserve 2014), but recent data support an older rather than newer date for that event: as old as ca. 15 MYA (Montes *et al.* 2012a, 2012b, 2015) and certainly no younger than 7.1 MYA (Coates *et al.* 2004). Regardless of the actual date of formation of the Panama Land Bridge, the oldest fossil *Sylvilagus* date from the Blancan, near the Pliocene–Pleistocene transition, or ca. 3.6 MYA (Gazin 1942). Molecular dates for the cladogenesis between the sister taxa *Lepus* and *Sylvilagus* have been hypothesized to be ca. 12 MYA, and basal diversification of *Sylvilagus* ca. 4.2–5.3 MYA (Matthee *et al.* 2004). However, these dates seem overly ancient in light of the fact that modern Leporidae, specifically, crown group taxa such as †*Alilepus* and †*Hypolagus* were still differentiating around 8 MYA (Flynn *et al.* 2013). Kelly (1998), for example, reporting on a Late Hemphillian fauna from west central Nevada (overlapping the Messinian to Zanclean boundary at the Miocene to Pliocene transition, or ca. 5.3 MYA), listed the presence of †*Lepoides* cf. *leporoides* and three species of †*Hypolagus*, but no *Sylvilagus*, further corroborating the absence of *Sylvilagus* in North America until at least the Pliocene (insofar as absence of evidence can be supportive, but not fully indicative of evidence of absence). Similarly, Mou (2011), reporting on a very finely dated Pliocene fauna from the Panaca Formation of Nevada (4.60–4.96 MYA, Late Memphillian to Early Blancan) listed four species of †*Hypolagus*, †*Pewelagus dawsonae*, and †*Lepoides*



*leporoides* (Archaeolaginae), and the leporines †*Nekrolagus progressus* and †*Pronotolagus* sp. No *Sylvilagus* were present in that fauna. Hibbard (1963) provided compelling morphological evidence for the origin of *Sylvilagus* from †*Nekrolagus* based on P<sub>3</sub>, with a geological horizon in the Rexroad Fauna. This particular element of the Blancan (4.75–1.8 MYA) Rexroad fauna is typically attributed to the Late Pliocene (equivalent to the Astian faunal stage of the Late Pliocene) and Early Pleistocene (e.g., Hibbard 1963:13), equivalent with the Villafranchian faunas of Europe (1.8–2.6 MYA, Thenius 1959). The fossil record based on pattern of P<sub>3</sub> enamel therefore suggests an origin for *Sylvilagus* in the Late Pliocene to Early Pleistocene, ca. 3.6 MYA (see also Jin *et al.* 2010), which is consistent with their fossil presence in South America (McKenna & Bell 1997). A more likely date for the origin of *Sylvilagus* would therefore be between the 3.6 and 8 MYA extremes, and likely in the lower end of range, 3.6–4.6 MYA. Stratum II of Hershkovitz (1969) is hence more consistent with †*Palaeolagus* (Duchesnean to Orellan, ca. 34 MYA, Tabrum *et al.* 1996, Boyd & Welsh 2014), †*Megalagus* (Duchesnean to Orellan, Tabrum *et al.* 1996, Boyd & Welsh 2014), and †*Hypolagus* (Arikarean of Wyoming [Harrison Formation], ca. 22–27 MYA, Schlaikjer 1935, to Blancan, ca. 2–5 MYA, Wagner *et al.* 2001), rather than *Sylvilagus*. The foregoing temporal framework therefore cannot falsify a singular origin for South American *Sylvilagus*, via an overland route over the Isthmus of Panama, within the last 4 million years, a timing more consistent with Faunal Stratum III of Simpson (late island-hoppers and immigrants), of the Late Miocene to Recent.

Hershkovitz (1950) also proposed that *S. andinus* and *S. meridensis* were “collateral offshoots” from a common stock of *S. brasiliensis*, rather than each others’ respective sister taxa, and as noted above, considered all to be conspecific within a broadly construed *S. brasiliensis*. It is not possible at this time to test this hypothesis: as noted by Thomas (1904), the holotype (NHMUK 1904.5.14.1) and referred specimens of *S. meridensis* have no skulls. A morphological comparison of dental and cranial characters must therefore depend on novel material that is currently unavailable. However, a sister relationship between the two taxa would not necessarily be precluded by the fact that “Their respective ranges are completely isolated by the length and ecological diversity of the Colombian portion of the Andean system” (Hershkovitz 1950:350). The numerous glacial cycles documented within the past million years in the Southern Hemisphere (Petit *et al.* 1999, Augustin *et al.* 2004) would certainly have enabled connectivity among latitudinally dispersed patches of Páramo habitats. A further examination of relationships among the *S. andinus* group taxa as defined by Thomas (1913), Cabrera (1913), Tate (1933), and Hershkovitz (1938), as well as among these and putative taxa constituting *S. brasiliensis* (most recently defined by Hershkovitz 1950), using both morphological and molecular approaches, certainly would be fruitful.

*Sylvilagus andinus: species concepts and theoretical framework*—We have observed extensive morphological differences between the neotype of *S. brasiliensis* and specimens of *S. andinus* including the holotype and the series collected by Hershkovitz 15 April – 1 May, 1935, near Cangagua, about 14 Km SW of Mount Cayambe, at 3400 m (Cangagua is located at 0°04′00.41″S, 78°09′59.87″W, 3213 m; absent a physical visit to the area, the locality described by Hershkovitz [1938] may be in the vicinity of 0°04′33.88″S, 78°05′37.32″W, although that location’s elevation is closer to 3500 m). These consistent morphological distinctions, together with the behavioral differences alluded to by Hershkovitz (1938—nocturnal v. diurnal), when viewed within the framework of the ecological (Van Valen 1976, Sangster 2014, but see Mayden 1997), evolutionary (Simpson 1961, Mayden 1997, Wiley 1978, Wiley & Mayden 2000, Sangster 2014), and phylogenetic species concepts (Eldredge & Cracraft 1980, Wiley & Lieberman 2011) are strongly supportive of the hypothesis that conspecificity between *S. brasiliensis* and *S. andinus* should be rejected. Ultimately, we agree that there is a want of cohesion between the philosophical and operational approaches to species (Maynard 1997, Sangster 2014). We therefore prefer to apply what Sangster (2014:210) called “methodological introgression” of species concepts applied in an operationally coherent manner to “discover, describe, and order into our classification system” (Maynard 1997) the individuals within, or constituting, the species category, independent of the properties of the species category. As Sangster (2014:212) noted, “Theoretically oriented debates over species concepts may benefit from empirical data on taxonomic practice.” An interesting such approach to the integrative framework, from both theoretical and operational perspectives, was suggested by Naomi (2011). Below, we detail some of the more salient differences between the two species-level taxa that enable one to distinguish between them.

*Sylvilagus andinus: diagnosis.* *Sylvilagus andinus* is distinguished from other species of *Sylvilagus* by the following combination of characters: cranially, absence of pitting on the dorsal surface of the cranium; antorbital process present but minute; postorbital process relatively short, ending in a sharp free from the frontal; tuberculum frontoparietale prominent and smooth, slightly projecting from the frontal bones; zygomatic arch dorsoventrally slender, zygomatic fossa barely perceptible; frontoparietal suture weakly interdigitated, clearly marked, with no fusion between the bones, straight or irregular in shaped; frontonasal suture sharply V-shape; single craniopharyngeal foramen in basisphenoid; premolar foramen present. Crown enamel pattern of third lower premolar extremely complex, with multiple, deep anteroflexid invaginations into rostral aspect of anterior lobe; rostral aspect of pm3 hypoflexid heavily crenellated from anteroconid to paraflexid; deep, complexly crenellated paraflexus, with generally conspicuous hypoflexus in second upper molar.

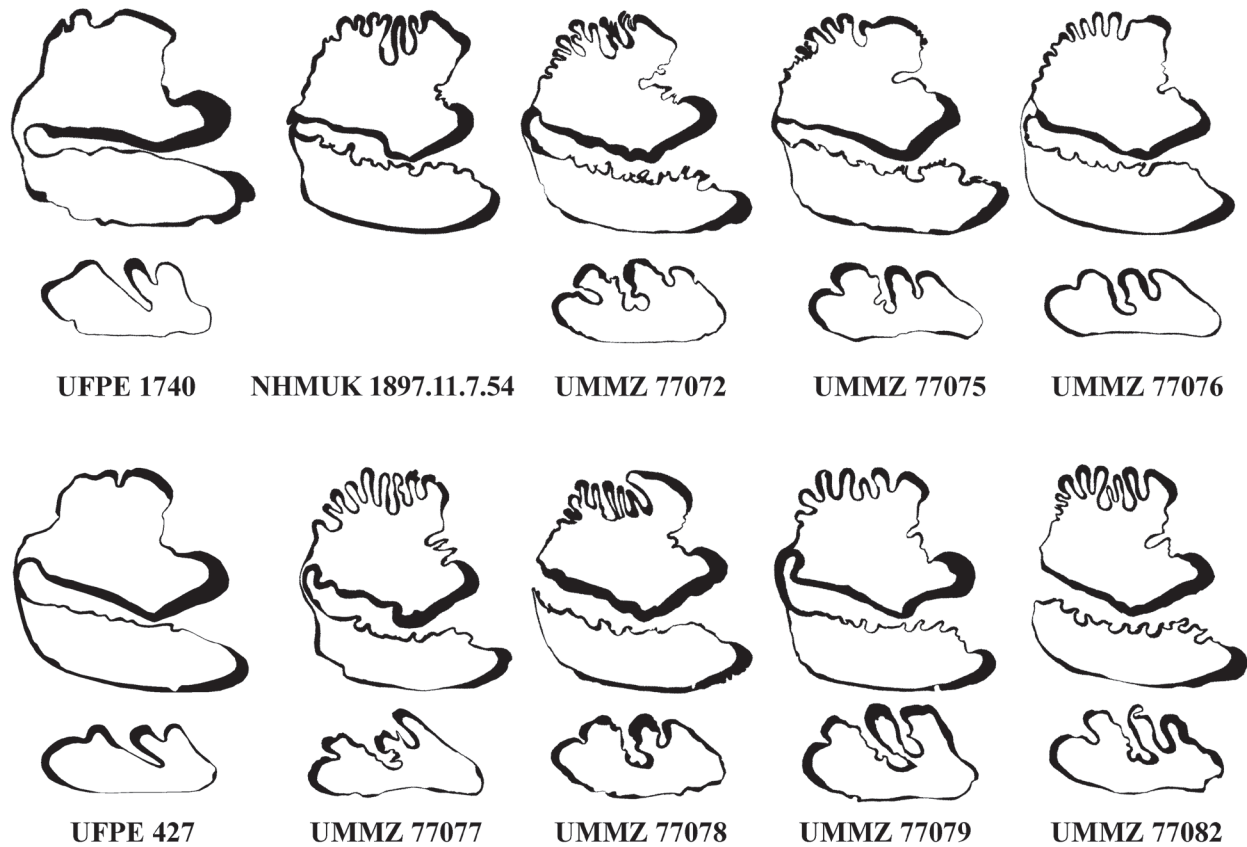


FIGURE 13— Third lower premolars (top row of each doublet) and second upper premolars of the neotype of *Sylvilagus brasiliensis*, UFPE 1740; referred specimen of *S. brasiliensis*, UFPE 427; holotype of *S. andinus*, NHMUK 1897.11.7.54; and a series of *S. andinus* at the University of Michigan Museum of Zoology, collected by P. Hershkovitz between 1933 and 1937 about 14 Km from the type locality of *S. andinus*.

Interspecific comparison of *S. brasiliensis* and *S. andinus*:  
Dental morphology (Fig. 13)

*Third lower premolar* (Fig. 13)—The region of the anteroflexid is the most distinctive feature distinguishing between the two species. The neotype of *S. brasiliensis* has a single broad, shallow anteroflexid, with a secondary narrow, shallow anteroflexid located lingual to it. The additional *S. brasiliensis* specimen, UFPE 427, has a single shallow, narrow anteroflexid. The holotype of *S. andinus*, NHMUK 1897.11.7.54, has, in contrast, two deep and multiple shallow anteroflexids. This difference is consistent in the series from near Cangagua, some of which display remarkable complexity in the anteroflexid region.

In the paraflexid, the two *S. brasiliensis* specimens exhibit a shallow, labially oriented depression of the lingual surface of the enamel into the rostral loph. In the *S. andinus* specimens, this character is somewhat more complex. The area of the paraflexid in the holotype of *S. andinus* is marked by numerous shallow depressions in the enamel. The reentrants marking the anteroflexid region are rostrocaudally oriented. In the series from Cangagua, these reentrants continue into the paraflexid

region in a labiolingually oriented direction, and as such can be tentatively associated with the paraflexid. The complexity exhibited in the anteroflexid of *S. andinus* therefore continues into the paraflexid, which in contrast is simple in *S. brasiliensis*.

The protoflexid of *S. brasiliensis* in contrast with *S. andinus* likewise is relatively simple: a large open depression in the labial margin of the anterior loph. Both UFPE 1740 and 427 have a protoflexid that begins at the rostral margin of the labial anteroconid with a marked thinning of the enamel in a caudal direction. The enamel then thickens beginning in the deepest part of the protoflexid into the labial margin of the protoconid. The specimens of *S. andinus* in contrast have a jagged margin of the protoflexid with deep to shallow invaginations in the central area of the protoflexid. The holotype displays two small invaginations, while the series from near Cangagua displays at least one deep and one or more shallow invaginations (UMMZ 77075, UMMZ 77079) or several shallow to deep narrow invaginations in the protoflexid.

The hypoflexid is most distinct in its caudal margin (rostral facies of posterior loph). In both specimens of *S. brasiliensis*, the hypoflexid has a relatively smooth caudal

margin, primarily constituted of thin enamel. All specimens of *S. andinus* have, in contrast, a heavily crenulate surface on the caudal margin of the hypoflexid, with enamel of varying thickness. The rostral wall of the hypoflexid does not appear to be diagnostic for either species. While the neotype of *S. brasiliensis* has a shallow central angle, UFPE 427 has a more developed central angle. The series of *S. andinus* may have multiple angles in the rostral wall of the hypoflexid (as the holotype of *S. andinus* displays) and a more complex pattern to the thick enamel of said rostral wall, but they can also display the more simple pattern of *S. brasiliensis*, as for example does UMMZ 77075.

*Second upper premolar*—The most obviously distinctive feature between the two species is the absence (*S. brasiliensis*) vs. presence (*S. andinus*) of a hypoflexus. There is little distinction between the distal and mesial hypercones in *S. brasiliensis*, although UFPE 427 has a somewhat better developed rostrally facing mesial hypercone. As in the neotype, UFPE 427 displays homogeneous enamel thickness in this region. In contrast, all the specimens of *S. andinus* have a relatively well-developed hypoflexus separating distal from mesial hypercones.

The paraflexus also is distinctive between the two species. In the *S. brasiliensis* specimens, this character is present as a simple and deep invagination in the rostral facies of the tooth. The lingual margin is of thin enamel and smooth, the labial margin has enamel of varying thickness but also is smooth, and the paraflexus ends as a simple narrow pocket. In contrast, the margins of the paraflexus in *S. andinus* are either both heavily crenellated or at least one margin is irregular. The paraflexus in *S. andinus* ends in either a single or double lacuna, rather than the simple, gently narrowing crevasse in *S. brasiliensis*.

Interspecific comparison of *S. brasiliensis* and *S. andinus*:  
Cranial morphology (Figs. 14–21)

*Dorsal perspective*—A comparison of the dorsal perspective of the crania of the neotype of *S. brasiliensis* and the holotype of *S. andinus* is shown in Fig. 14. In terms of overall size, both species are similar: greatest length of skull is 71.4 mm in the neotype of *S. brasiliensis* and 70.6 mm in the holotype of *S. andinus*, breadth of braincase is 26.3 and 25.8 mm, respectively. One consistent feature between the species in all specimens examined is the heavy pitting present on the dorsal surface of the skull, particularly the braincase (parietal bones) of *S. brasiliensis* in contrast to *S. andinus* (Fig. 15). This character was discussed by Wible (2007) as his character 6, braincase pitting absent or present, as a significant difference between *Ochotona* and *Romerolagus*. He also noted (Wible 2007:225) that “*Sylvilagus* has nearly as much pitting as *Romerolagus*, but the rostral half of its frontal is smooth.” In both specimens of *S. brasiliensis*, the pitting is extensive on the parietal and extends rostrally to about the middle of the supraorbital crest, whereas in

the specimens of *S. andinus*, the braincase is smooth, as in *Ochotona*. Fostowicz–Frelík (2013) described this pitting (as a “strongly marked ornamentation expressed as a series of minute concavities,” Fostowicz–Frelík 2013:35) in the nasal and frontal bones, and onto the parietal bones, primarily along the parietal–mastoid suture, of †*Litolagus molidens* (Early Orellan and Chadronian/Orellan of Wyoming, 33.3–33.9 MYA). She further noted that such ornamentation was present and well developed among extant lagomorphs only in *Romerolagus* C. H. Merriam, 1896 (Fostowicz–Frelík 2013). We undertook a direct comparison between *Romerolagus diazi* (NHMUK 84.2096) and *S. brasiliensis* as well as comparing to the cranium of *R. diazi* illustrated by Cervantes *et al.* (1990:3, their Fig. 2). *Romerolagus* do appear to display more pitting than *S. brasiliensis* on the frontal bones (the rostral half of the frontals in *S. brasiliensis* are smooth, as noted by Wible 2007), although not so on the parietal bones, on which *S. brasiliensis* has at least as much, and possibly more pitting than appears in the specimen of *Romerolagus* illustrated by Cervantes *et al.* (1990), as well as NHMUK 84.2096. The latter in particular has some rugosities—rather than pitting—along the parietal suture, whereas this area is quite pitted in the *S. brasiliensis* specimens examined (UFPE 427 and 1740). The presence of pitting in cranial bones of †*Litolagus* and *Romerolagus*, the latter an acknowledged outgroup species to *Sylvilagus*, suggests that it is primitive in Leporidae and certainly among *Sylvilagus*, reinforcing the distinctiveness between *S. brasiliensis* and *S. andinus*.

The frontonasal suture also is a character that has been employed in the identification of *Sylvilagus* species, although it has been shown to be broadly variable. The two species differ in the shape of the frontonasal suture (Fig. 16): the neotype and referred specimen of *S. brasiliensis* have a broadly rounded rostral terminus to the frontonasal suture whereas all the specimens of *S. andinus* that we have examined have a sharp, V-shaped frontonasal suture. However, this character may be variable: a larger sample is required to determine whether this character is diagnostic.

Another potentially diagnostic feature distinguishing the two species is the shape and disposition of the postorbital process (Fig. 17). The neotype of *S. brasiliensis* and the holotype of *S. andinus* differ strongly in these characters: *S. brasiliensis* has a longer postorbital process ending in a broadly rounded terminus that is tightly fused to the frontal, on a tubercle (tuberculum frontoparietale, possibly homologous with the supraorbital process of †*Rhombomylus*, Fig. 23 of Meng *et al.* 2003) slightly projecting from the frontal bones near the angulus sphenoidalis of the parietal bones. In the referred specimen, UFPE 427, the postorbital processes are damaged, therefore, we cannot verify that the condition is the same as in the neotype. However, all the specimens of *S. andinus* examined have short, sharp, V-shaped postorbital processes, the termini of which are distinctly free of contact with the frontal bones. As with the frontonasal suture, a larger





FIGURE 14— Dorsal perspective of the cranium of the neotype of *Sylvilagus brasiliensis* (UFPE 1740, left) and the holotype of *S. andinus* (NHMUK 1897.11.7.54, right). Images not to scale.



FIGURE 15— Brainscase (parietal bones and frontoparietal suture) of the neotype of *Sylvilagus brasiliensis*, UFPE 1740; referred specimen of *S. brasiliensis*, UFPE 427; holotype of *S. andinus*, NHMUK 1897.11.7.54; and the series of *S. andinus* at the University of Michigan Museum of Zoology whose teeth are illustrated in Fig. 14. Note the heavily pitted condition of the two *S. brasiliensis* specimens (leftmost column; presumed herein to be the primitive condition for *Sylvilagus*) in comparison with the smooth condition of the same bones in all specimens of *S. andinus* (derived). Images not to scale.





FIGURE 16— Frontonasal suture of the neotype of *Sylvilagus brasiliensis*, UFPE 1740; referred specimen of *S. brasiliensis*, UFPE 427; holotype of *S. andinus*, NHMUK 1897.11.7.54; and the series of *S. andinus* from UMMZ. Note the blunt rostral terminus of the frontonasal suture in *S. brasiliensis* (top and bottom left) in contrast to the sharp, V-shape of the same feature in all the specimens of *S. andinus*. Images not to scale.

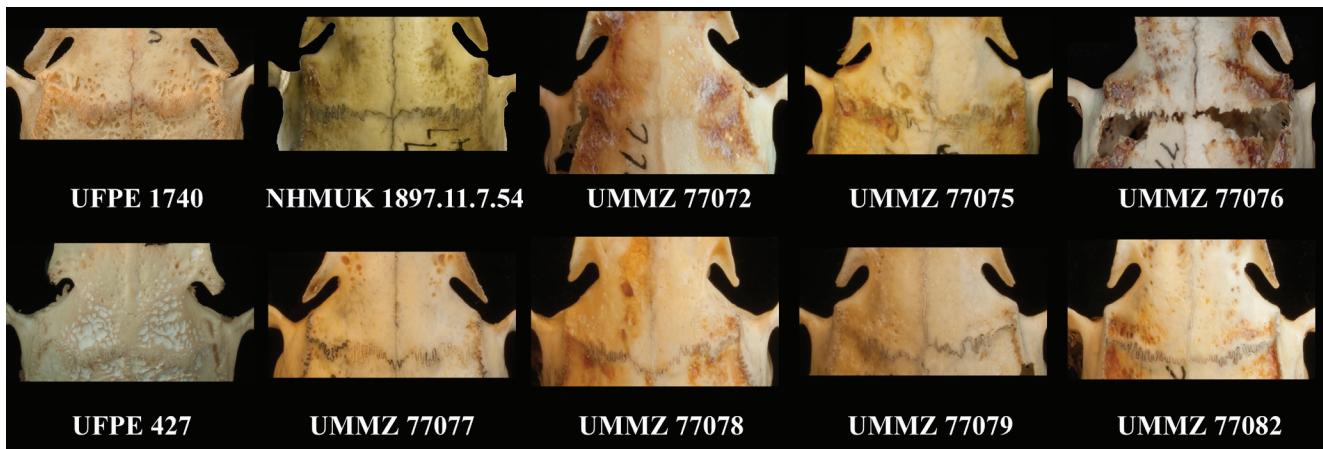


FIGURE 17— Detail of the region of the postorbital process and frontoparietal suture of the neotype of *Sylvilagus brasiliensis*, UFPE 1740; referred specimen of *S. brasiliensis*, UFPE 427; holotype of *S. andinus*, NHMUK 1897.11.7.54; and the series of *S. andinus* from UMMZ. Note the blunt rounded terminus of the postorbital process, strongly attached to the frontal bone in *S. brasiliensis* (top left) in contrast to the sharp, narrowing shape of the same feature, distinctly free of the frontal bone, in all the specimens of *S. andinus*. Specimen UFPE 427 (lower left) has broken postorbital processes. Images not to scale.

sample of *S. brasiliensis* would be useful in assessing this character for its diagnostic properties.

*Lateral perspective*—The lateral perspective of the cranium (Figs. 18–19) is largely unremarkable. One notable difference between the holotypes is in the appearance of the zygomatic arch. As noted above, the zygomatic arch of the neotype of *S. brasiliensis* is robust, with a substantial dorsoventral deepening approximately centered in the zygomatic arch, a deepening that is largely constituted by the zygomatic fossa, the zygomatic fossa itself begins some 8.75 mm caudal of the anterior portion of the zygomatic spine. In addition, the ventral surface of the zygomatic arch has a deep

inflection at this point, the angle formed by this inflection is approximately 150°. In contrast, the zygomatic arch of the holotype of *S. andinus* is relatively straight and slender. The zygomatic fossa is only vaguely defined, appearing to begin some 6.5 mm caudal of the anterior portion of the zygomatic spine, which itself projects more rostrally in *S. andinus* than in *S. brasiliensis* (Fig. 14). Another fossa, presumably created by the zygomatic portion of the deep layer of the *m. masseter*, also is larger on *S. brasiliensis* (length, 15.2 mm, to 14.3 mm in *S. andinus*). Mensurally, the zygomatic arches of both specimens are otherwise identical in length, at 31.4 mm. The zygomatic length of UFPE 427 is 31.7 mm, those of adults from the series



FIGURE 18— Lateral perspective of the cranium of the neotype of *S. brasiliensis*, UFPE 1740 (top) and holotype of *S. andinus*, NHMUK 1897.11.7.54 (bottom).

from near Cangagua housed at UMMZ average  $28.37 \pm 1.06$  mm (range: 27.20–30.4). The greatest dorsoventral depth of the zygomatic arch of the neotype is 4.9 mm; that of the referred specimen, UFPE 427, 4.7 mm; that of the holotype of *S. andinus*, 4.3 mm; those of adults from the series from near Cangagua housed at UMMZ average (range: 4.0–4.9).

*Ventral perspective*—In the ventral perspective of the cranium (Figs. 20–21), the neotype of *S. brasiliensis* and the holotype of *S. andinus* broadly resemble each other. However, one foramen definitively distinguishes both holotypes from each other, as it does remaining specimens of either species from each other: the premolar foramen (character 34 of Wible [2007], character 8 of Corbet [1983], as “posterior palatine foramina,” *foramen premolare* of Bohlin [1942]).

On the holotype of *S. andinus*, this foramen is located on the palatal bridge, just lingual to the caudal loph of PM3, the second tooth in the maxillary toothrow. The presence or absence of this foramen is of sufficient significance that it has

been used in discriminating among families in Lagomorpha (Bohlin 1942). For example, Storer (1984) suggested that †*Procaprolagus* and †*Desmatolagus* “are clearly separate genera, and based on the presence [†*D. gobiensis*] or absence [†*P. vetustus*] of the premolar foramen appear referable to different families” (Storer 1984:120), that is: Leporidae for †*Procaprolagus* and Ochotonidae for †*Desmatolagus*; these two genera were, however, synonymized by Meng & Hu (2004). Corbet (1983), in undertaking a survey of 59 characters in Leporidae, and retaining 21 as “most useful,” carefully considered this character across a broad spectrum of extant Leporidae. Within *Sylvilagus*, he scored the premolar foramen as present and clear to an extreme degree in the species that he examined, *S. brasiliensis*, *S. aquaticus* (Bachman 1837), and *S. palustris* (Bachman 1837), within what is traditionally construed as constituting the subgenus *Tapeti*, Gray, 1867. With respect to the subgenus *Tapeti*, Gureev (1964) treated *Tapeti* as including *S. brasiliensis*, *S. gabbi* Allen, 1877, *S. aquaticus*, *S.*





FIGURE 19— Comparison of the lateral perspective of the cranium of specimens under consideration in the text. Left column, top to bottom: neotype of *S. brasiliensis*, UFPE 1740; holotype of *S. andinus*, NHMUK 1897.11.7.54; *S. andinus* UMMZ 77075, 77077, and 77079. Right column top to bottom: referred specimen of *S. brasiliensis*, UFPE 427; *S. andinus* UMMZ 77072, 77076, 77078, 77082.

*palustris*, and *S. insonus* Nelson, 1904. Hoffmann & Smith (2005), following Hershkovitz (1950), removed *S. insonus*, but added *S. varynaensis* Durant and Guevara, 2001. The remaining species of *Sylvilagus* examined by Corbet (1983), *S. floridanus* (J. A. Allen, 1890) and *S. bachmani* (Waterhouse,

1839), did not exhibit a premolar foramen. Fostowicz-Frelik & Meng (2013), in an even broader survey of this foramen across extinct and extant taxa of Lagomorpha, noted that 67 of 99 *S. brasiliensis* specimens they examined displayed this foramen, underscoring the likely multispecies nature of *S.*



FIGURE 20— Ventral perspective of the cranium of the neotype of *S. brasiliensis* (UFPE 1740, left) and the holotype of *S. andinus* (NHMUK 1897.11.7.54, right). Images not to scale (nor, apparently, in the exact same horizontal plane: the anteroposterior length of both specimens' zygomatic arch is identical measured on the specimen itself). Note the distinctive premolar foramina lingual to the caudal loph of premolar 3 of the holotype of *S. andinus*, and its absence in the neotype of *S. brasiliensis*.

*brasiliensis* as currently understood. No other species showed such a disparity between presence and complete absence, although presence and absence was not always homogeneous. Interestingly for such a phylogenetically informative character, the other taxon showing the greatest amount of variation (present in 25 of 202 specimens examined, 12.4%) in the study by Fostowicz-Frelik & Meng (2013) was *S. floridanus*, another taxon that likely encompasses multiple species.

The presence or absence of the premolar foramen is split among the holotypes of *Sylvilagus* species from South America at the NHMUK, London, and certainly not “present and clear,”

as Corbet (1983) indicated for *S. brasiliensis*. Interestingly, however, the holotype of *chimbanus*, which was originally described by Thomas (1913) as a subspecies of *S. andinus*, displays premolar foramina: on the left it is located just lingual to the rostral loph of PM3, on the right side, just lingual to the space between PM2 and PM3. Another taxon originally described as a subspecies of *S. andinus* by Thomas (1913), *canarius*, has a prominent premolar foramen on the right side, but none on the left. The holotypes of taxa wherein it is absent include *capsalis*, *cumanicus*, *inca*, *nicefori*, *surdaster*, and *tapetillus*. Those wherein it is present include *apollinaris*





FIGURE 21— Comparison of the ventral perspective of the cranium of non-type specimens under consideration in the text; individual images not to scale. Top row, left to right: *S. brasiliensis* UFPE 427; *S. andinus* UMMZ 77072, 77075–76; bottom row, left to right: *S. andinus* UMMZ 77077–79, 77082.

(minute, present on right only, lingual to, and between, PM2 and PM3), *gibsoni* (lingual to and between PM3 and PM4), *minensis* (lingual to the caudal loph of PM3), topotypes of *nivicola*, where it is variously located rostrocaudally in the lingual immediacy of PM3 and who display little evidence of major palatine foramina, *paraguensis* lingual to caudal loph of PM3 on right side and lingual to, and between PM3 and PM4 on the left), and *purgatus* (present on left only, lingual to PM3).

If it is indeed the case that the premolar foramen is of the taxonomic importance that the authors cited in the foregoing discussion have indicated, then the foregoing distribution

of presence or absence strongly supports our contention that *S. brasiliensis* is in fact constituted by a number of species level taxa. And certainly, the presence of the premolar foramen in *S. andinus*, and its absence in the neotype and referred specimen of *S. brasiliensis*, strongly supports our hypothesis that *S. andinus* and *S. brasiliensis* are distinct, species level taxa. We caution, however, that broader intraspecific sampling may show variation that could diminish the significance of this foramen at the species level.

A second foramen-like feature that may also potentially be distinctive is the craniopharyngeal canal, a single large opening in the basisphenoid bone. This opening is highly

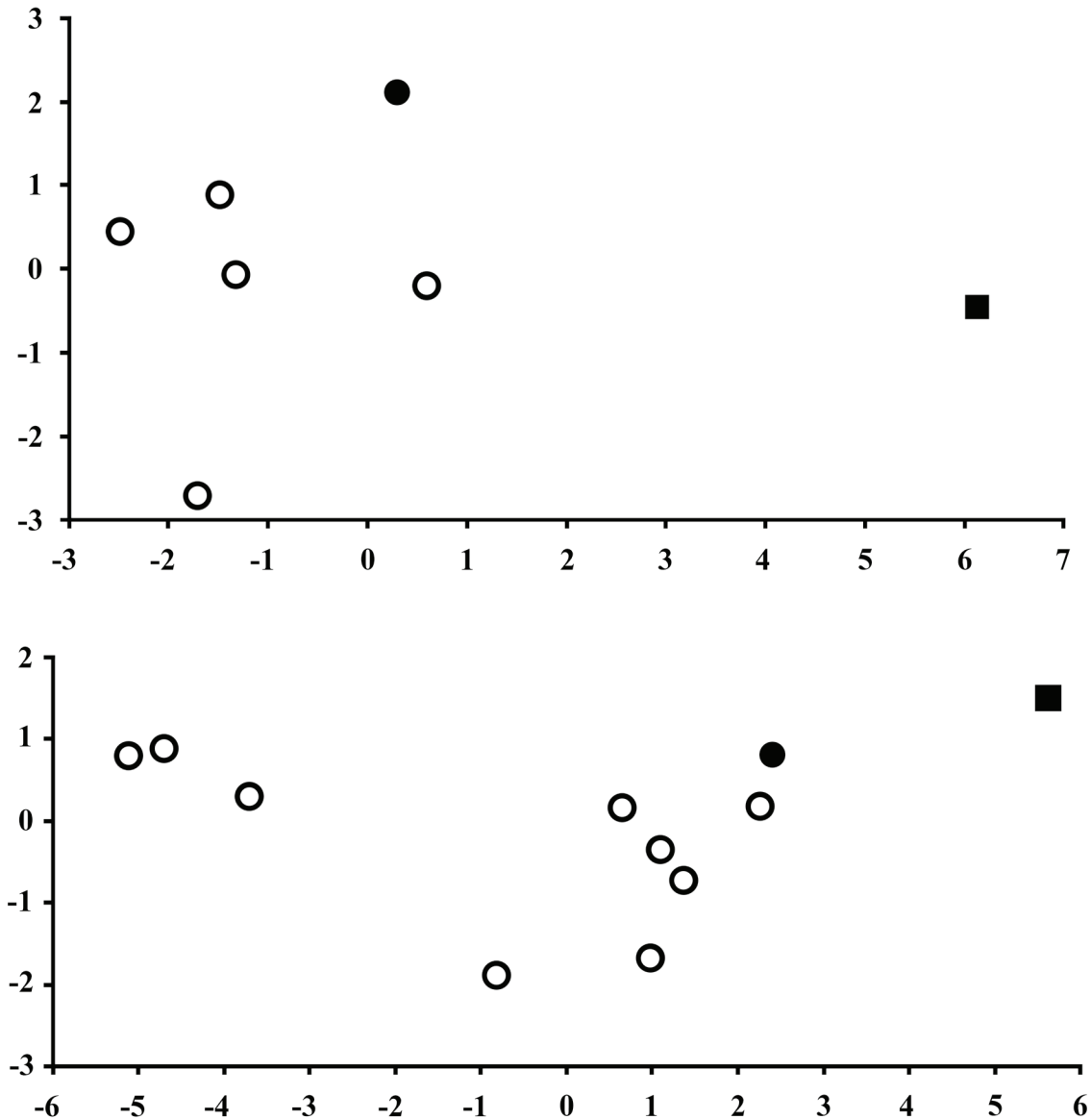


FIGURE 22— Graphical results of the Principal Components Analysis. Horizontal axis: principal component 1; vertical axis: principal component 2. Symbols are: open circles, *Sylvilagus andinus* collected by P. Hershkovitz in April and May 1935 near Cangagua, Pichincha Province, Ecuador (ca. 0°04'33.88"S, 78°05'37.32"W, 3500 m). Closed circle: holotype of *S. andinus*, NHMUK, London, no. 1897.11.7.54. Closed square, neotype of *S. brasiliensis*, Universidade Federal de Pernambuco, Recife, no. 1740. Top, all specimens included in the analysis. The cluster of three in the leftmost area of the graph are specimens aged by us as subadults and a young adult. The individual at approximate coordinates  $-1, -2$  was aged by us as a young adult. Bottom, results derived only from analysis of specimens aged as adults.

angled, and directed from posteroventrally to anterodorsally rather than flat. In the two specimens of *S. brasiliensis*, this opening is smaller, circular, and located closer to the suture between the basisphenoid and the tympanic process of the basioccipital, in the caudal third of the basisphenoid. It is, furthermore, highly angled and thus clearly identifiable as the craniopharyngeal canal. In all specimens we examined of *S. andinus*, the craniopharyngeal canal is more elongate and less angled than in *S. brasiliensis*, and located approximately

equidistant from rostral and caudal apices of the basisphenoid, distinctly framed by the two pterygoid bones.

#### Statistical analyses (Fig. 22, Tables 2–3)

Mensural data of selected cranial dimensions of the key specimens examined for this work are shown in Table 2. In general terms, the holotype of *S. andinus*, NHMUK 1897.11.7.54, has a long skull and wide zygomatic breadth,

TABLE 2— Mensural data of selected cranial dimensions of the key specimens examined for this work; a dash indicate that the measurement could not be carried out because of damage to the skull or mandible. UMMZ refers to the University of Michigan Museum of Zoology, series collected by P. Hershkovitz in April and May 1935 near Cangagua, Pichincha Province, Ecuador (ca. 0°04'33.88"S, 78°05'37.32"W, 3500 m). 1897.11.7.54 is the holotype of *Sylvilagus andinus*, NHMUK, London. UFPE 1740 is the neotype of *S. brasiliensis* described herein, specimen from Universidade Federal de Pernambuco, Recife, Brazil. 1892.11.2.43 is the holotype of *S. tapetillus*, NHMUK, London. Age categories are: A, adult; SA, subadult; YA, young adult. Adult  $\bar{X}$  is the mean of the dimension for adults examined. Adult  $\sigma$  is the standard deviation of the dimension for adults examined. Character abbreviations are as follows: **GLS**, greatest length of skull; **Nasals**, greatest rostrocaudal length of nasal bone; **BZS**, zygomatic breadth measured at zygomatic spine; **ZB**, zygomatic breadth; **ZL**, zygomatic length; **DepZ**, dorsoventral depth of zygomatic arch; **BoB**, breadth of braincase; **WXocc**, width of cranium at exoccipital bones; **LBull**, length of auditory bulla; **WBull**, width of auditory bulla; **IOB**, interorbital breadth; **HtRos**, height of rostrum; **WRost**, width of rostrum; **LInFor**, rostrocaudal length of incisive foramina; **WInFor**, width of incisive foramina; **PaIL**, rostrocaudal length of palatal bridge; **Choana**, width of choana at first upper molar; **BrACon**, breadth of alisphenoid constriction; **AlvMxTr**, alveolar length of maxillary toothrow; **Diastema**, alveolar length of upper diastema, I2–PM2; **DntTR**, dentary toothrow length; **HtDnt1**, greatest height of mandible from anterior inflection of masseteric line (just caudal to its insertion into the mandibular body) to the dorsalmost point of the condylar process; **HtDnt2**, length from anterior inflection of masseteric line to most distal point on pterygoid tuberosity.

Number	Age	Sex	GLS	Nasals	BZS	ZB	ZL	DepZ	BoB	WXocc	LBull	WBull	IOB	HtRos
UMMZ 77072	A	F	67.3	27.3	32.4	32.0	28.4	4.3	24.4	-	9.2	5.8	10.0	14.0
UMMZ 77075	A	M	64.9	27.1	31.8	32.3	27.5	4.1	24.0	21.5	8.1	5.4	11.6	12.7
UMMZ 77076	A	F	67.7	27.3	31.7	32.3	27.3	4.6	25.2	-	8.4	5.4	11.4	13.3
UMMZ 77080	A	M	70.5	28.1	32.4	32.8	30.0	4.7	24.5	22.4	-	-	12.0	13.3
UMMZ 77082	A	F	-	26.0	33.8	32.4	28.7	4.8	24.9	21.1	9.6	6.3	10.9	13.1
UMMZ 77073	SA	M	-	20.8	29.3	29.5	25.0	3.6	23.8	-	-	-	11.4	11.1
UMMZ 77077	SA	F	-	20.2	29.8	30.1	23.7	3.9	23.8	-	7.8	5.6	10.7	11.5
UMMZ 77078	YA	M	-	27.1	30.8	30.2	29.2	4.1	-	-	8.7	5.8	10.3	13.3
UMMZ 77079	YA	M	-	21.0	29.4	29.4	24.9	4.2	23.8	-	-	-	11.5	11.3
Adult $\bar{X}$			67.99	25.18	31.36	31.46	27.6	4.25	24.36	21.91	8.65	5.58	11.2	12.59
Adult $\sigma$			2.19	3.16	1.50	1.48	2.40	0.34	0.52	0.73	0.60	0.44	0.70	1.00
97.11.7.54	A	F	69.7	26.9	32.2	33.4	31.4	4.3	24.8	22.7	8.7	4.9	12.1	12.2
UFPE 1740	A	M	71.4	31.4	33.8	34.6	31.4	-	26.3	24.0	9.5	6.3	12.9	14.6
92.11.2.43	A	-	-	25.3	30.1	32.2	26.9	3.9	23.9	19.2	7.5	5.2	13.0	12.5

Number	WRost	LInFor	WInFor	PaIL	Choana	BrACon	AlvMxTr	Diastema	DntTR	HtDnt1	HtDnt2
UMMZ 77072	15.9	15.1	5.2	6.3	5.6	7.7	13.2	18.1	14.0	31.2	22.5
UMMZ 77075	16.4	14.7	4.8	7.1	4.9	7.8	13.0	18.0	13.5	31.2	21.9
UMMZ 77076	16.4	16.2	-	7.2	4.7	8.1	12.7	19.3	13.2	31.9	21.7
UMMZ 77080	16.0	16.5	5.3	6.5	5.0	8.6	13.5	19.1	14.4	32.7	22.1
UMMZ 77082	16.2	16.1	5.9	6.9	5.0	8.5	12.6	18.5	13.4	33.3	24.0
UMMZ 77073	13.9	12.3	4.8	5.6	4.1	6.9	11.0	14.6	12.0	25.9	16.9
UMMZ 77077	15.6	12.6	4.5	5.8	4.2	7.2	12.0	14.6	12.8	27.6	18.0
UMMZ 77078	15.4	15.6	4.5	6.1	4.0	7.4	12.2	18.8	13.0	30.5	20.4
UMMZ 77079	12.4	12.1	4.6	5.6	4.0	6.8	10.9	14.6	11.8	25.9	17.0
Adult $\bar{X}$	15.52	14.70	4.91	6.42	4.68	7.76	12.40	17.46	13.28	30.01	20.49
Adult $\sigma$	1.36	1.74	0.47	0.64	0.57	0.69	0.89	2.01	0.93	2.84	2.59
97.11.7.54	12.2	15.9	4.6	7.1	5.3	8.7	12.8	18.9	14.6	-	-
UFPE 1740	14.6	17.5	6.4	6.7	6.7	9.8	14.6	19.9	14.0	35.1	24.0
92.11.2.43	15.5	14.7	4.5	6.4	5.4	4.6	13.0	16.4	14.0	29.9	-



TABLE 3—Values for the first through third eigenvectors from the principal component analysis carried out on the correlation matrix of the cranial data of all specimens (left three columns right of “characters”) and adults only (right three columns) of *Sylvilagus andinus* and *S. brasiliensis*. Among all specimens examined, the first three principal components together account for 91.1% of the variation (78.45%, 8.22%, and 4.43%, respectively). Among specimens of adults, the first three principal components together account for 87.5% of the variation (61.85%, 14.61%, and 11.23%, respectively); the 4th PC accounts for 6.32%, for a cumulative total of 94.00%. Breadth of braincase was not included in the analysis of all specimens due to a missing value in a young adult specimen (UM77078). Results of the principal component analysis are graphically summarized in Fig. 23. Character abbreviations as in Table 1.

Character	All specimens			Adults only		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
	78.45%	8.22%	4.43%	61.85%	14.61%	11.23%
Nasals	0.28656	-0.14123	-0.02829	0.29760	-0.13477	-0.06741
ZBS	0.27952	-0.10561	-0.01941	0.19484	-0.17367	-0.12506
ZB	0.29269	0.17161	0.06468	0.31267	0.15959	0.10443
ZL	0.27018	-0.04844	0.16359	0.25074	0.11502	0.44980
BoB	—	—	—	0.28890	0.07490	-0.27892
IOB	0.13137	0.79967	0.14114	0.24924	0.35482	0.05914
HRos	0.25907	-0.31383	-0.39486	0.20073	-0.47380	-0.26501
WRos	0.27488	0.08566	-0.12551	0.30195	0.09956	-0.10142
LIncFor	0.28860	-0.14877	0.12944	0.28600	0.10278	-0.12427
PalLong	0.24251	-0.04149	0.62154	-0.05928	0.61359	-0.23450
Choana	0.25949	0.23387	-0.47011	0.28612	-0.22929	0.04381
WAliCon	0.28640	0.22171	-0.04404	0.31498	0.13054	-0.00161
AlvMxTR	0.28661	0.01869	-0.28734	0.28385	-0.23813	0.05810
Diastema	0.28019	-0.23255	0.22424	0.27667	0.18312	-0.13533
DentTR	0.26279	-0.09832	0.13203	0.11084	-0.01292	0.71466

and based on degree of fusion of the occiput, the holotype is an older adult. The adults from near Cangagua at the University of Michigan Museum of Zoology appear somewhat younger. In addition, there well may be sexual dimorphism in size: Orr (1940) extensively documented this phenomenon in *Sylvilagus* species in California (*S. audubonii*, *S. bachmani*, and *S. nuttallii*), as well as in *Brachylagus idahoensis* and three species of *Lepus*. In the *Sylvilagus* species, females were invariably larger on average than males. Unfortunately, the reduced sample size available for all species of South American *Sylvilagus* precludes a meaningful analysis of this phenomenon. The neotype of *S. brasiliensis* described herein tends to be larger in all linear dimensions than any of the *S. andinus*, including the holotype of *S. andinus*, although that is not the case for all dimensions.

The principal component analysis (Fig. 22; Table 3) used in our comparison between *S. andinus* and *S. brasiliensis* reinforces the overall size differences noted above. With the exception of interorbital breadth, the eigenvalues of principal component 1 are all relatively homogeneous, suggesting that PC 1 is size based. Blackith and Reyment (1971) suggested

that PC 1 often is a size vector, particularly so when all the PC 1 coefficients are of the same sign, contrasting with those of other components being of mixed signs; in the present analysis, that is the case (Table 3). The only lower eigenvector value among variables in PC1 is interorbital breadth. Among all specimens of *S. andinus*, interorbital breadth varied within narrow confines:  $\bar{X}$ : 11.19±0.70mm, range 10.02–12.06mm, 95% confidence interval, 0.43; notwithstanding, this character was the major contributor to PC 2 and accounted overall for almost 3.0% of the variation in cranial morphology. Interestingly, both smallest and largest interorbital breadth measurements were taken on adult specimens. Among adult specimens of *S. andinus*, PC 1 also was size based. Palatal length was the one character with a small contribution to PC1. In contrast, it was the principal contributor to PC2 and overall accounted for almost 2.9% of the variation in cranial morphology of adults. Palatal length varied somewhat broadly among specimens examined:  $\bar{X}$ : 6.42±0.64mm, range 5.58–7.15mm, 95% confidence interval, 0.39. Among adults, the corresponding values were: 6.86±0.34mm, 6.32–7.15mm, 0.28. The greater heterogeneity among eigenvalues of principal components 2

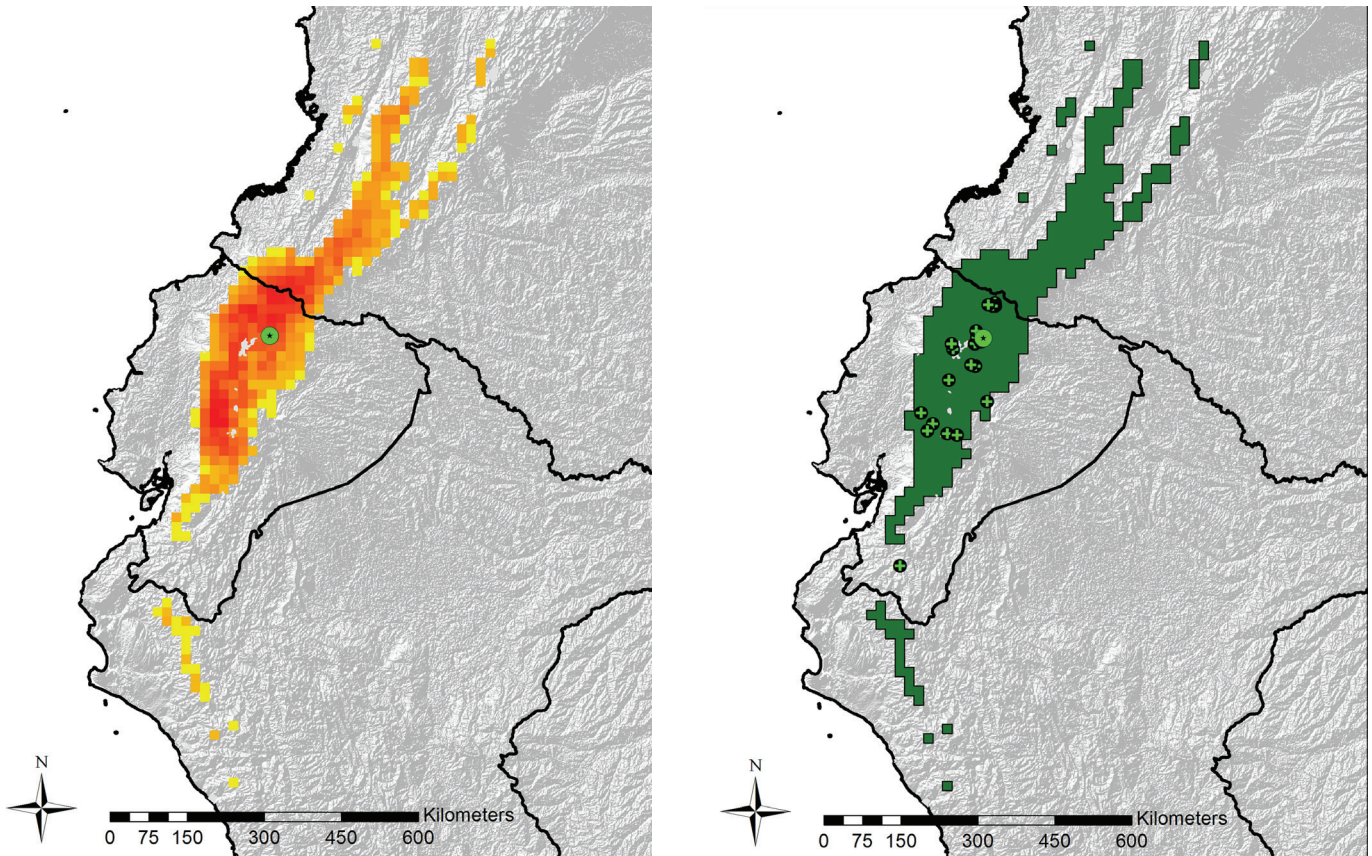


FIGURE 23— MaxEnt niche model (left) showing areas suitable for a probable distribution of *Sylvilagus andinus* based on an ecological niche modeling analysis of locality data from specimens in museum databases; urban areas removed. Average probability of occurrence derived from the model is 41%; darkest shade of red indicates a probability of occurrence of 88%; lightest shade set at 10% probability of occurrence. The bull's eye circle represents the type locality. Total area covered by *S. andinus* projected by the model is approximately 108,380 Km<sup>2</sup>. Actual locality data whence model is derived are shown represented by crosses in circles in the right panel, superimposed on the modeled distribution, solid green. The point in southern Ecuador outside the modeled distribution is from an area within a modeled probability of occurrence <10%; record corresponds to USNM 513525 from Ecuador: Loja; 1 Km WSW Las Chinchas, 2237m.

and 3 both overall and among adults only suggest that these too, in contrast to PC1, are shape based.

#### Distribution (Figs. 23–24)

The current area suitable for the presence of *S. andinus*, based on ecological niche modeling analysis, is shown in Fig. 23, with projections using hypothesized climate change into the near future in Fig. 24. Existing specimens appear to be generally restricted to the Páramo ecosystem, within the Tropical Andes biodiversity hotspot of Myers *et al.* (2000). Myers *et al.* (2000) suggested that there has been a 75% loss in area of remaining primary vegetation for this hotspot. Notwithstanding this loss, the Tropical Andes hotspot still represents *ca.* 15% of primary vegetation for all biodiversity hotspots, and holds 16% of global endemic vertebrate biodiversity. The Páramo is generally considered to be distributed in the Andes at elevations ranging between 2800 – 4700 m (Luteyn 1999).

Cuatrecasas (1958, 1968) suggested a lower limit of Páramo *sensu stricto* between 3200 – 3800 m, consistent with more recent data of Wille *et al.* (2002). Harling (1979), for Ecuador, Cuatrecasas (1979), for Venezuela, Colombia, and Ecuador, and Jørgensen & Ulloa Ulloa (1994), for the High Andes of Ecuador, proposed that the Páramo actually consists of three distinct zones: grass páramo, or pajonal (3400–4000 m), shrub and cushion páramo (4000–4500 m), and desert páramo (4500 m to snow line, 4800–4900 m) [see also Sklenář & Jørgensen 1999]. Below these is the subpáramo, a vegetation transition zone dominated by shrubs that lie between forests below and grass páramo above, and generally located from 2800 to 3400 m (Luteyn 1999), with patches of forest diminishing in density with elevation (Wille *et al.* 2002); van der Hammen & Hooghiemstra (2000) called this zone (in part: 2100–2300 m to 3500 m) the Andean forest zone. The distinction between the lower elevational limits for the Páramo of Luteyn (1999) and Cuatrecasas (1958, 1968) therefore appears definitional



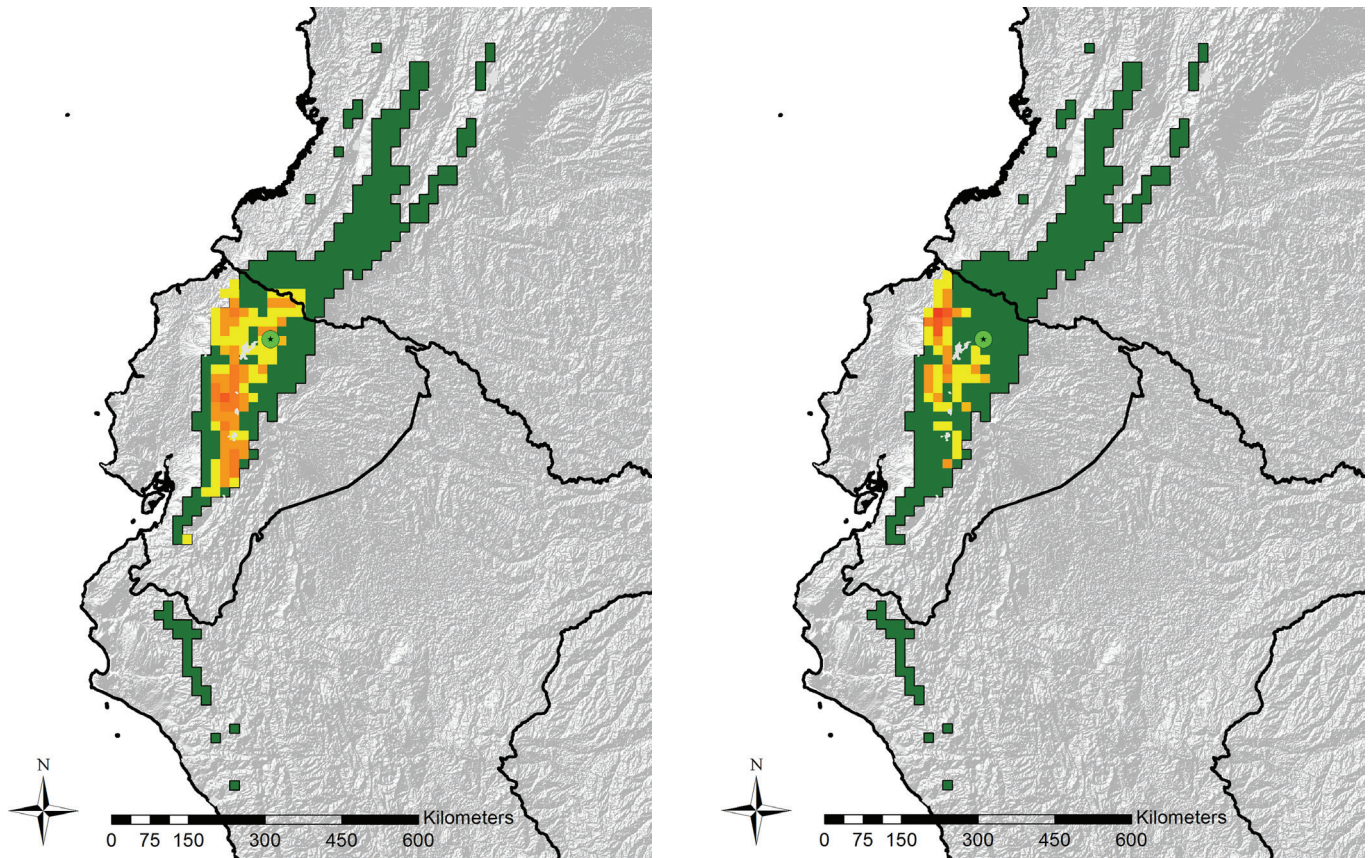


FIGURE 24— MaxEnt niche models showing the current probable distribution excluding major urban zones (green area; see Fig. 24) overlain with projected distribution by the year 2100 under Special Report on Emissions scenarios A1B (left) and A2 (right). The bull's eye circle represents the type locality. Scenario A1B predicts a best estimate increase in temperature by 2090–2099 of 2.8°C (range 1.7–4.4); scenario A2 predicts an increase of 3.4°C (2.0–5.4). Under these scenarios, the predicted ranges shrink to *ca.* 32,270 Km<sup>2</sup> (70% range reduction) with mean and maximum probability of occurrence shown as 30% and 55% (A1B), and *ca.* 14,900 Km<sup>2</sup> (86% range reduction), 30%, and 62%, respectively (A2).

rather than anything else. Because the current elevation of the Andes (Central and Northern) were only reached *ca.* 2.7 MYA (Gregory–Wodzicki 2000, Ehlers & Poulsen 2009), the altitude of the current treeline, hence lower limit of Páramo ecosystem, was hypothesized to have been reached orographically only near the end of the Pliocene, *ca.* 2.6 MYA (Madriñan *et al.* 2013). These studies serve to circumscribe an earliest age for the Páramo ecosystem and biome type, hence its earliest potential invasion by *S. andinus* (e.g., Madriñan *et al.* 2013, and Luebert & Weigend 2014, for Andean montane plant diversification). It is unclear to what extent *S. andinus* is distributed into the highest, or desert Páramo, zone, although the *S. nivicola*, which in the past has been (likely correctly) synonymized with *S. andinus*, was reported by Cabrera (1913) to be from 4800 m, on the slopes of the Antisana Volcano, Ecuador, some 60 Km airline distance from Volcán Cayambe summit. NHMUK 54.625, also from Antisana, states 18,000 ft (5586 m) on the specimen tag, although the other specimens in that series state elevations of 13,000 ft (3962 m) for 54.628,

and 12,500 ft (3810 m) for 54.626 and 54.627. We consider the elevation data for 54.625 as somewhat unlikely, given that Antisana is 5704 m in elevation and is covered in snow and ice to well below 5586 m.

From an avifaunal perspective (Stattersfield *et al.* 1998), the type locality, on Volcán Cayambe, is considered to be situated in the Central Andean Páramo endemic bird area (EBA), a region covering some 32,000 Km<sup>2</sup>, and extend into the Northern Central Andes (36,000 Km<sup>2</sup>), higher elevation portions of the Chocó, South Central Andes (10,000 Km<sup>2</sup>), and the Ecuador–Peru East Andes (28,000 Km<sup>2</sup>) EBAs. Our niche distribution model based on existing museum records of *S. andinus* conservatively predicts an approximate distributional area for *S. andinus* in the highlands of southern Colombia, Ecuador, and Peru, of *ca.* 109,167 Km<sup>2</sup>. A more restrictive model using a polygon circumscribing the points derived from physical museum specimens results in an area of *ca.* 20,245 Km<sup>2</sup>; the disparity ensues from the fact that the ecological model predicts an ample distribution throughout



the Páramo of southern Colombia. However, there exist no reliable records known to us of *S. andinus* from Colombia. A single point from Colombia is represented in the GBIF data set of *S. andinus*: five specimens from Royal Ontario Museum: 40383, 40385, 40390, 41504, and 41505, are identified as *S. andinus*. However, their locality data is “Colombia: Putumayo, Mocoa.” Mocoa is at an elevation of 590 m, well below the lowest extent of the Páramo, and indeed, solidly ensconced in the lowland rain forest zone, which extends to 700–800 m in Ecuador (Harling 1979), and to 1000 m in Colombia and Venezuela (Cuatrecasas 1979). Absent firsthand examination by us of those specimens, we are forced to discard them as *S. andinus* on the basis of their locality data, the elevation of which is in lowland rainforest, which suggests they represent the forest form of South American *Sylvilagus*, hypothesized to be more closely allied with *S. brasiliensis*, and an ecological competitor of *S. andinus* (Hershkovitz 1938). Furthermore, digital photographs of ventral aspects of the crania kindly provided to us by Dr. Burton Lim (Royal Ontario Museum—Mammalogy) clearly show the absence of the foramen premolare in the Colombian specimens, as well as a postorbital process fused to the frontal bone. These characters identify the ROM Colombian specimens as more closely allied with *S. brasiliensis* as described above, rather than with *S. andinus*, hence excludable from our niche modeling analysis. The foregoing therefore suggests either of two alternative hypotheses: 1. There has been insufficient collecting to adequately assess, describe, or otherwise estimate any ecological, population, or taxonomic characteristics for *S. andinus* in the Páramo region of Colombia, or 2. The distribution of *S. andinus* as shown, based on museum records absent from southern Colombia, is real and represents a realized niche; the species is restricted from its fundamental niche as depicted by our MaxEnt model developed from existing museum records’ locations by ecological factors unknown to us at this time.

The severely threatened nature (Stattersfield *et al.* 1998) of the habitats inhabited by *S. andinus* is underscored by climate modelling projections. Ramírez-Villegas *et al.* (2014) used 11,012 species (1,555 birds and 9,457 vascular plants) and found conservatively that by 2050, over 50% of Tropical Andean species would experience  $\geq 45\%$  loss in climatic niche, with 10% of the species potentially going extinct. Grassland communities (Páramos and Punas) were particularly singled out by Ramírez-Villegas *et al.* (2014) as being projected to experience negative changes in species richness and high rates of species turnover. Our own ecological niche models projected out to the decade 2090–2099 suggest that the current distributional model derived from ecological niche modeling and resulting in a current distribution of ca. 108,380 Km<sup>2</sup> will be reduced under IPCC scenario A1B (mean, 2.8°C, range 1.7 – 4.4) to ca. 32,270 Km<sup>2</sup>, a reduction in range of ca. 70%. Under scenario A2 (3.4°C, 2.0 – 5.4), the range reduction increases: only ca. 14,900 Km<sup>2</sup> remain habitable to *S. andinus*,

ca. 86% of the original range has been rendered unusable. The conservation implications of our hypothesized projected range reductions imply that urgent action must be taken to protect Páramo areas, particularly as these diminish in area with climate change and human population pressures.

#### Restoration of *Sylvilagus tapetillus* Thomas, 1913

*Taxonomic history.*—*Sylvilagus tapetillus* was described as a novel species of *Sylvilagus* by Thomas (1913:210). Thomas had previously identified it as unusual in suggesting that *Sylvilagus* from Rio de Janeiro could be construed to comprise three distinct species: *Sylvilagus minensis* Thomas, 1901a, *Sylvilagus paraguensis* Thomas, 1901b, and *S. tapetillus*, which—absent a definitive type locality for *S. brasiliensis*—he at the time refrained from describing as new. Indeed, in his 1901 publications, Thomas suggested that even since Marcgraff’s time, Rio de Janeiro would have been the principal settlement in that region of Brazil; the most likely origin for Marcgraff’s specimens would have been by logical extension Rio de Janeiro. He therefore considered the smaller Rio specimen as representing true *S. brasiliensis* (Thomas 1901a). Thomas’ eventual determination of “Pernambuco” as the type locality (Thomas 1911:146, see also discussion above), as well as having a putatively adequate comparative series of what he subsequently deemed “true *L. brasiliensis*,” that is, the series collected by Alphonse Robert near Lamarão, Bahia (Thomas 1901a), apparently led him to the ineluctable conclusion that “the little hare of Rio de Janeiro, hitherto taken for *brasiliensis*, is certainly an entirely different species” primarily based on its “exceedingly small” size (Thomas 1913:210).

In contrast, Hershkovitz (1950:368) synonymized *S. tapetillus* with *S. brasiliensis*. The apparent rationale for this action was that the characters of *tapetillus* were not markedly different from those of typical *S. brasiliensis* and the suggestion that the type specimen of *S. tapetillus* was—Thomas’ affirmations to the contrary notwithstanding—not representative of an adult. Subsequent authors have followed Hershkovitz’ determination that the holotype of *S. tapetillus* is merely an immature, and thus represents nothing more than age variation in otherwise “true” *S. brasiliensis*. One anonymous reviewer of this work noted for example that the following characters, among others, argued for the holotype representing a juvenile: the fissure and lack of ossification in the mandible’s condyloid process, the smooth surface at the lower part of the facial tubercle, the lack of lateral extensions at the anterior part of the nasals, and the weakness of the posterior part of the supraorbital processes. However, some of these characters may or may not be definitive: numerous individuals have fissures in various parts of the condyloid process, and the posterior part of the supraorbital processes are precisely the parts that are “ankylosed” (in Thomas’ words) to the skull at the frontoparietal suture.

We have examined the holotype of *Sylvilagus tapetillus* Thomas, 1913, NHMUK 1892.11.24.3, and find that, based on ossification of cranial sutures, as well as on wear of cranial and dental features, it represents a specimen of an adult cottontail. In addition, novel molecular data support this conclusion (Bonvicino *et al.* 2015). Those authors noted that “Although the genetic distance between *tapetillus* and *brasiliensis* was lower than between any pair of *Sylvilagus* species, Cytochrome-*b* data and karyotypic attributes supported their species status.” (Bonvicino *et al.* 2015:170). Bonvicino *et al.* (2015) found a mean genetic distance at the mitochondrial Cytochrome-*b* locus (Kimura 2-parameter) between their *S. brasiliensis* and *S. tapetillus* of 0.028, contrasting with mean intraspecific distances of 0.017 (*S. brasiliensis*) and 0.005 (*S. tapetillus*). Their specimen of *S. brasiliensis* originated from Paraiba: Cruz de Espírito Santo, 7°08'S 35°05'W, some 80 Km straight line distance from Thomas' type locality as georeferenced by us. However, genetic distance alone may not distinguish between sister species of *Sylvilagus*, whereas chromosomes will (e.g., *S. obscurus* and *S. transitionalis*, Litvaitis & Litvaitis, 1996, Litvaitis *et al.* 1997, Ruedas *et al.* 1989, this paper; *S. floridanus* and *S. robustus*, Lee *et al.* 2010, Nalls *et al.* 2012). In the case of *S. brasiliensis* and *S. tapetillus*, both species have 2n = 40, but three pericentric inversions result in an autosomal Fundamental Number (FNa) of 74 in *S. tapetillus*, and 68 in *S. “brasiliensis minensis.”* Bonvicino *et al.* (2015:168) noted that “differences between *S. b. tapetillus* and *S. b. minensis* were strongly indicative of two evolutionary lineages.” As a consequence of the foregoing, including morphological, molecular, and chromosomal data, we suggest that Thomas' hypothesis that *Sylvilagus tapetillus* in fact constitutes a species distinct from *S. brasiliensis* is not currently falsifiable and should stand.

#### Statistical analyses (Fig. 25, Tables 2, 4)

The main distinguishing feature is, as Thomas (1913) noted, size. The principal component analysis including the holotype—and only known specimen—of *S. tapetillus* and comparing it with the specimens of *S. andinus* and *S. brasiliensis* (Fig. 25; Table 4) support this important distinction. As in the previous principal component analyses, PC 1 is size based (Blackith & Reyment 1971); the large neotype of *S. brasiliensis* and small juveniles of the *S. andinus* series at either end of the distribution in multivariate space of PC1 (Fig. 25) support this hypothesis.

The distinction in principal components between *S. andinus*, for which a somewhat larger sample is available, and *S. brasiliensis* on the one hand, and *S. tapetillus* on the other is on the basis of the shape-based principal component 2. That component is loaded heavily on interorbital breadth (positive, 17% of PC2), and width of alisphenoid constriction and incisive foramina (negative, 15% and 14%, respectively); dentary tooththrow to some extent also contributes to this PC

TABLE 4— Values for the first through fourth eigenvectors from the principal component analysis carried out on the correlation matrix of the cranial data of specimens of *Sylvilagus* examined for this work: *S. andinus*, *S. brasiliensis*, and the holotype of *S. tapetillus*, NHMUK 1892.11.24.3. Among the specimens examined, the first three principal components together account for 90.8% of the variation (78.42%, 9.12%, and 6.31%, respectively). Results of this principal component analysis are graphically summarized in Fig. 26. Character abbreviations as in Table 1.

	PC 1	PC 2	PC 3	PC 4
Character	75.42%	9.12%	6.31%	3.97%
Nasals	0.27906	0.07261	-0.00678	-0.09289
ZBS	0.26538	-0.24557	-0.16947	0.02939
ZB	0.28183	0.15456	-0.01910	0.06957
ZL	0.26812	0.05230	-0.07147	0.28398
BoB	0.24974	-0.19598	0.37510	0.13390
IOB	0.09816	0.54475	0.59008	0.36060
HRos	0.25879	-0.10183	0.03179	-0.49254
WRost	0.26100	0.04725	0.01159	-0.04356
LIncFor	0.28276	0.04262	-0.04232	0.03929
WIncFor	0.21444	-0.42675	0.34013	-0.06622
PalLong	0.23260	0.15320	-0.38811	0.33277
Choana	0.26038	0.09678	0.23918	-0.31754
WAlCon	0.19950	-0.47178	-0.01199	0.41379
AlvMxTR	0.26825	0.15271	0.02525	-0.31683
Diastema	0.27972	-0.01705	-0.16659	0.10516
DentTR	0.23547	0.31158	-0.34910	-0.11142

(positive, 10%). The measurements of these characters in *S. tapetillus* (Table 2) can be confirmed to be somewhat divergent from those of *S. andinus* and *S. brasiliensis*: *S. tapetillus*, despite its small overall size, has the broadest interorbital breadth among the specimens examined for this work. The alisphenoid constriction of *S. tapetillus* is, in contrast, the smallest among the specimens measured. Similarly, the width of the incisive foramina of *S. tapetillus* is equal to those of *S. andinus* UMMZ 77077 and UMMZ 77078, which we consider subadult and young adult based on fusion of cranial sutures, and only 70% that of the adult neotype of *S. brasiliensis*. We further note that all the *S. andinus* specimens have much narrower incisive foramina than the neotype of *S. brasiliensis*, adults averaging 4.91±0.47 mm, in contrast to 6.4 mm in *S. brasiliensis*. Hershkovitz (1950) suggested that the holotype of *S. tapetillus* also was not an adult and explicitly compared it to Field Museum of Natural History (FMNH) no. 26877, a young female from Teresópolis, Rio de Janeiro (listed verbatim by Hershkovitz as “Rio Terezópolis,” we estimate the locality as ca. 22°26'S, 42°59'W, 950 m), noting that there were strong overall similarities in size. While we caution that we have not

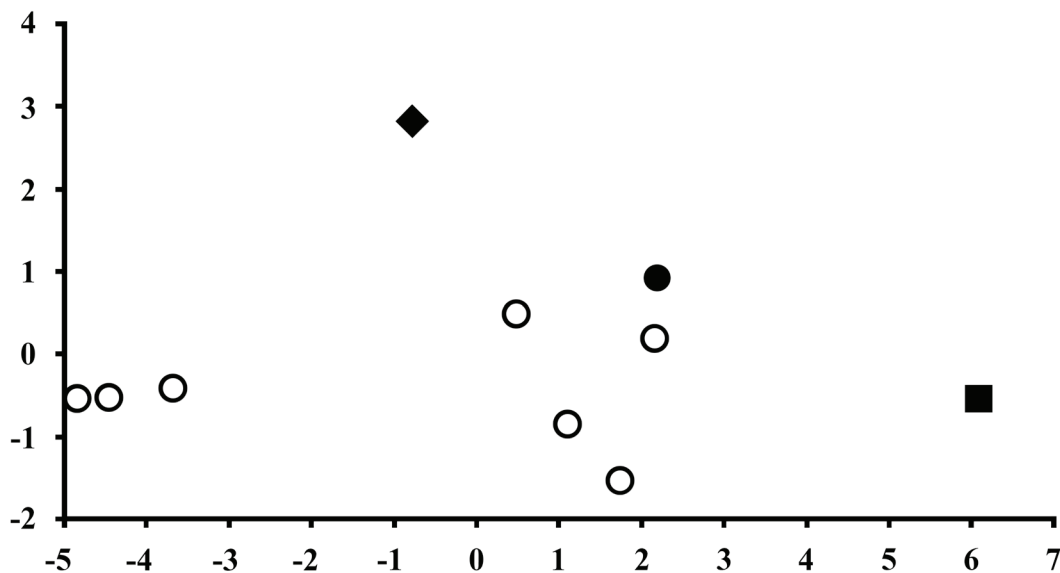


FIGURE 25— Graphical results of the Principal Components Analysis including all the focal taxa under consideration in this work: *Sylvilagus andinus*, *S. brasiliensis*, and *S. tapetillus*, with crania sufficiently complete to be included a multivariate analysis. Values for the first through fourth eigenvectors from this analysis are presented in Table 4. Horizontal axis: principal component 1; vertical axis: principal component 2. Symbols are: open circles, *Sylvilagus andinus* collected by P. Hershkovitz in 1935. Closed circle: holotype of *S. andinus*, NHMUK, London, no. 1897.11.7.54. Closed square, neotype of *S. brasiliensis*, Universidade Federal de Pernambuco, Recife, no. 1740. Closed diamond, holotype of *S. tapetillus*, NHMUK 1892.11.24.3. Data are reduced to include as many specimens as possible in the analysis. As in Fig. 23, the clusters of three *S. andinus* in the leftmost area of the graph are specimens aged by us as immature. Note the divergent position of *S. tapetillus* along principal component axis 2 relative to remaining *Sylvilagus* taxa examined. That axis is shape based and mostly determined on the dimensions of interorbital breadth (positive), width of incisive foramina, and width of alisphenoid constriction (both negative).

examined the FMNH specimen firsthand, there are mensural discrepancies between the measurements provided by Hershkovitz (1950:368) and those we took from the holotype of *S. tapetillus*. In particular, the length of the nasals for FMNH 26877 was listed as 21.5 mm, to 25.3 mm for the holotype of *S. tapetillus*, the mean of adult *S. andinus* for this dimension is  $25.18 \pm 3.16$  mm, contrasting with 31.4 mm in the neotype of *S. brasiliensis*. Similarly, alveolar length of maxillary toothrow was reported by Hershkovitz for FMNH 26877 as 11.1 mm; we recorded this dimension as 13.0 mm in the holotype of *S. tapetillus*. The mean of this dimension in adult *S. andinus* was  $12.40 \pm 0.89$  mm, the same measurement in the neotype of *S. brasiliensis* was 14.6 mm. Thus, the proportional differences in mensural characters between the holotype of *S. tapetillus* and the specimen identified by Hershkovitz as a young adult, FMNH 26877, as revealed by the principal component analysis and direct comparison of mensural data, all support Thomas' hypothesis that the holotype of *S. tapetillus* is an adult, and therefore represents a species distinct from *S. brasiliensis*.

#### Cranial morphology (Figs. 26–27)

*Sylvilagus tapetillus*: diagnosis. *Sylvilagus tapetillus* is distinguished from other species of *Sylvilagus* by the following combination of characters: cranium extensively pitted with

minute, shallow pits; pitting extending through frontal bones rostrally well into interorbital region and along frontal suture almost to antorbital region; antorbital process present only as an emargination rather than a process; narrow, relatively long postorbital process ending bluntly, tightly fused to the frontal throughout caudal half, on the tuberculum frontoparietale; masseteric spine projecting strongly rostrally from anteroventral aspect of zygomatic arch; strongly interdigitated frontoparietal suture, strongly U-shaped, between each frontal and parietal bone; frontonasal suture intermediate between V- and U-shape; short but evident process between posterodorsal process of premaxillae and nasal bones; and premolar foramen absent. Mandible relatively robust dorsoventrally; large, labially located mental foramen, with extensive ventrocaudally oriented trail of minute foramina originating from mental foramen. Crown enamel pattern of third lower premolar relatively simple, with single marked anteroflexid invagination near rostralingual aspect of anterior lobe; protoflexid marked, with uniformly slightly thick enamel throughout; deep paraflexus with some complexity at terminus and on rostral margin; shallow but distinct hypoflexus with clearly marked mesial and distal hypercones.

*Sylvilagus tapetillus*: general aspects of cranial morphology.—As noted in the diagnosis, aspects of some cranial characters further support maintaining *S. tapetillus* as distinct. The





FIGURE 26— Views of the cranium of the holotype of *Sylvilagus tapetillus* (NHMUK 1892.11.24.3): dorsal (left), lateral (center), and ventral (right). Greatest length of skull was not recorded by us due to the fact that the cranium is broken at the occiput, hence that linear dimension is unreliable; however, it was recorded by Thomas (1913) as 61 mm; zygomatic breadth, 32.2 mm.

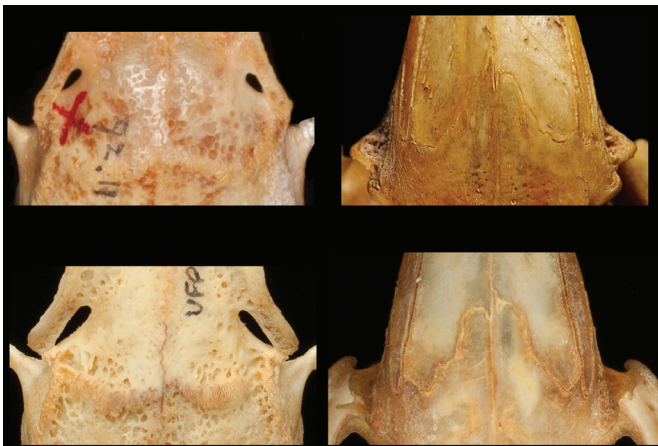


FIGURE 27— Dorsal perspectives of the crania of the holotype of *Sylvilagus tapetillus*, NHMUK 1892.11.24.3 (top) and the neotype of *S. brasiliensis*, UFPE 1740 (bottom). Left: comparison of the postorbital processes; right: comparison of the frontonasal sutures.

skull of the holotype is shown in Fig. 26. Thomas (1913:210) noted in the description of *S. tapetillus* that the slender postorbital processes were “anchylosed terminally to the skull in the type, and merely leaving a narrow foramen about 2 mm. in length.” This character is shown in the complete perspective of the cranium of *S. tapetillus* (Fig. 26) and in detail, in comparison with the neotype of *S. brasiliensis* in Fig. 27. The neotype of *S. brasiliensis* has a postorbital process that is fused to the frontal bone at the tuberculum frontoparietale, near the angulus sphenoidale of the parietal bones. The width of the postorbital process is *ca.* 2.2 mm and the length of the suture between the postorbital process and the frontal bone is *ca.* 1.7 mm in straight line distance (although the suture itself is slightly curved), the length of the resulting foramen is *ca.* 4.2 mm. In the holotype of *S. tapetillus*, as noted by Thomas, the postorbital process is more slender: *ca.* 1.5 mm, and is in fact tightly fused to the frontal bone. The length of the fusion is *ca.* 3.2 mm on either side. However, it is not a simple rostro-caudal fusion, as in *S. brasiliensis*: the caudal terminus of the postorbital process ends on the tuberculum frontoparietale, in

a laterally oriented fusion *ca.* 0.7 mm in length. Thus, the postorbital to frontal fusion is in effect L-shaped (right) and inverse L-shaped (left) when viewed dorsally, such that the frontal bone cups the terminus of the postorbital process. The resulting foramina are, as Thomas noted, *ca.* 2 mm in length. If this degree of fusion between postorbital process and frontal bone results from ontogenetic variation, then the impression of the holotype of *S. tapetillus* as an adult is reinforced, *contra* Hershkovitz' suggestion that it is immature. The adult nature of the holotype of *S. tapetillus* also is reinforced by the fact that the pitting present in the dorsal surface of the skull, as it is in the neotype of *S. brasiliensis*, is more worn than in the also adult neotype. With respect to the frontonasal suture, this character is more equivocal and subject to population variation. In spite of that reservation, the frontonasal suture of the holotype of *S. tapetillus* (Figs. 27–28) appears to be more V-shaped than the frontonasal suture of the neotype of *S. brasiliensis*, which we characterized above as having a broadly rounded rostral terminus.

#### Mandibular morphology (Fig. 28)

The mandibles of the pertinent specimens examined for this work are shown in Fig. 28. In the neotype and referred specimen of *S. brasiliensis*, there is variation in the size of the mental foramen; the neotype has a relatively inconspicuous mental foramen, the referred specimen, UFPE 470, has a more evident, somewhat longer and slender mental foramen. The mental foramen is small and inconspicuous in the holotype of *S. andinus*. The holotype of *S. tapetillus* has a relatively larger, more substantial, mental foramen in both vertical and horizontal dimensions. In addition, the mandibular body of *S. tapetillus* bears some fenestration, or the presence of numerous

pinhole size openings, leading ventrocaudally from the mental foramen toward the ventral margin of the mandibular body. This fenestration is completely absent from the neotype of *S. brasiliensis*. The referred specimen of *S. brasiliensis* has some rugosity present in this portion of the mandibular ramus. The holotype of *S. andinus* has even less rugosity than the referred specimen of *S. brasiliensis* but is not as featureless in this character as the neotype of *S. brasiliensis*. Additional pitting is visible in the holotype of *S. tapetillus* at the rostral edge of the mandibular ramus where it meets the mandibular body. This pitting is absent from any of the key reference specimens examined herein.

The relative location of the coronoid process in the holotype of *S. tapetillus* differs from that of *S. brasiliensis* in that it is located on the rostral aspect of the mandibular ramus approximately midway between the articular head of the condylar process and the sulcus ascenden; in the *S. brasiliensis* specimens, the coronoid process is located about a third of the distance down the rostral aspect of the mandibular ramus. The holotype of *S. andinus* is more similar to *S. tapetillus* in this character. The anteroposterior dimension of the mandibular ramus relative to its height also appears to differ among the specimens examined: the ratio of width to height of mandibular ramus (width measured from anteriormost inflection point of posterior mandibular incisures [terminology of Bensley 1910] to anteriormost point of coronoid process) is 0.34 in *S. tapetillus*, 0.30 in *S. andinus*, and 0.29 and 0.28 in the neotype and referred specimen of *S. brasiliensis*, respectively. Indeed, although the holotype of *S. tapetillus* has the shortest dorsoventral dimension among adults of the comparative series examined (Table 2), it has the broadest anteroposterior mandibular ramus: *S. tapetillus*: 10.3 mm; *S. brasiliensis* neotype and referred specimen: 10.2 mm

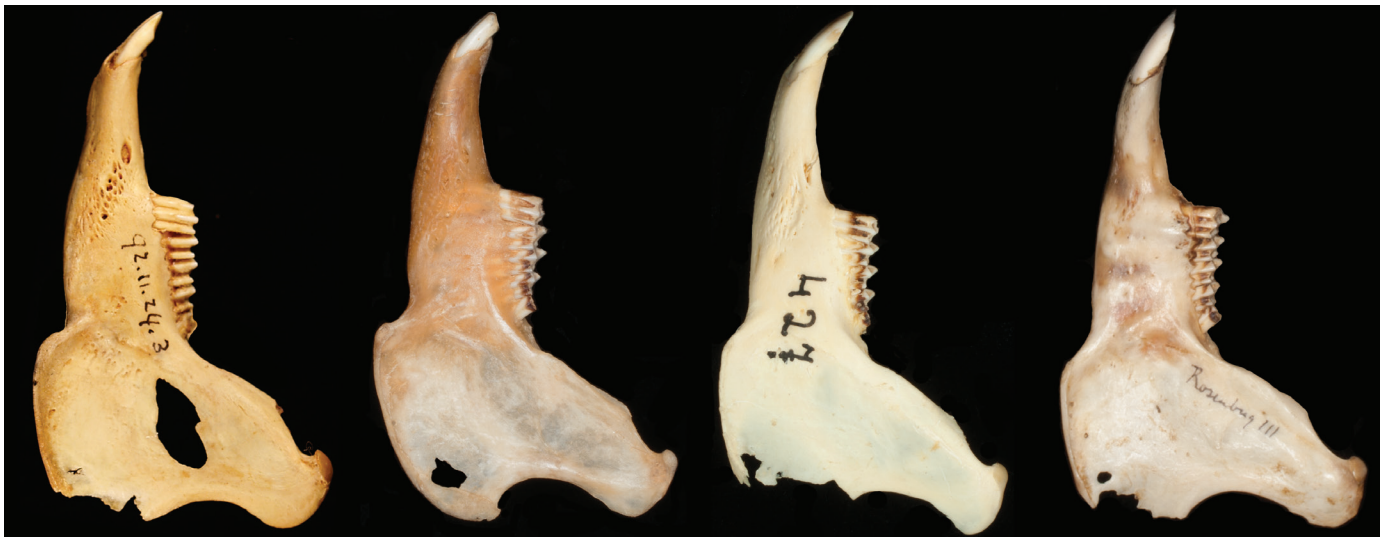


FIGURE 28— Comparison of the right dentary bones of (left to right): holotype of *Sylvilagus tapetillus* (NHMUK 1892.11.24.3); neotype of *S. brasiliensis* (UFPE 1740); referred specimen of *S. brasiliensis* (UFPE 427); holotype of *S. andinus* (NHMUK 1897.11.7.54). Images not to scale.



and 9.4 mm, respectively; holotype of *S. andinus*, 10.2 mm. The masseteric line, wherein inserts the superficial masseter muscle, on the ventral edge of the angle of the mandibular ramus, also differs somewhat among the specimens examined. However, it may represent to some extent ontogenetic variation (Bang & Enlow 1967): the neotype of *S. brasiliensis* has a prominent masseteric line ending rostrally in an ovoid process and caudally in the masseteric and pterygoid tuberosities; the masseteric line and ovoid process are not as prominent in the referred specimen of *S. brasiliensis*. The caudal aspects of the mandibular ramus are not available for inspection in any of the critical comparative material examined herein. Notwithstanding, the masseteric line is thin but evident in *S. tapetillus*; in *S. andinus*, the masseteric line is reduced in size but still evident, but the anterior ovoid process is extremely reduced. The ovoid process in *S. tapetillus* is manifested as a large, diffuse region in the anteroventral portion of the mandibular ramus, rather than as a discrete process, as in the neotype of *S. brasiliensis* (Fig. 28).

A final distinction between *S. tapetillus* and remaining specimens examined is the prominent vacuity present in the mandibular ramus. A vacuity often is present in the ramus of *Sylvilagus* specimens. Habitually, it is located in the ventrocaudal region of the angle, however, in the holotype of *S. tapetillus*, it is large and located in the center of the masseteric fossa. Wible (2007) pointed out that there is a small ridge in *Ochotona* in the same region of the angle as these vacuities are present in *S. brasiliensis* and *S. andinus*. One may speculate that in the absence of this ridge, the edges of the vacuity may provide insertion points for a subdivision of the masseter muscle. In *S. tapetillus*, the vacuity is located at the insertion point of the posterior deep masseter, whereas the vacuities in the ventrocaudal region of the angle are at the insertion of a branch of the superficial masseter (Schumacher and Rehmer 1959). The location and size of the vacuity in the ramus therefore strongly suggests a functional distinction in the masticatory apparatus between *S. tapetillus* and remaining species examined, and as such may also be phylogenetically informative; a broader population sample will be required to assess more fully the extent and significance of this character.

#### Dental morphology (Fig. 29)

The dentition of *S. tapetillus* (Fig. 29) is similar to that of *S. brasiliensis*, but somewhat simpler. In particular, the third lower premolar has a single anteroflexid, to a double in *S. brasiliensis*. Specimens of *S. andinus* show a great deal of variation in this character, thus it is possible that the number of anteroflexida will vary. Both specimens have a slight depression in the area corresponding by homology to the paraflexid, but the paraflexid is absent in both. The thickness of the enamel in this region of the rostral loph differs between the holotype of *S. tapetillus* (thin) and the neotype of



FIGURE 29— Third lower premolar (top row) and second upper premolar (bottom row) of the holotype of *Sylvilagus tapetillus* (NHMUK 1892.11.24.3; left column) and the neotype of *S. brasiliensis* (UFPE 1740; right column). Images not to scale.

*S. brasiliensis* (thick). The protoflexid of the holotype of *S. tapetillus* is shallow, and shaped as a somewhat open, shallow V. Above, we characterized the protoflexid of the neotype also as broadly U-shaped. The holotype of *S. tapetillus* in addition displays enamel of homogeneous thickness throughout the protoflexid, in contrast to the neotype of *S. brasiliensis*, which tapers from extremely thick on the labial margin of the protoconid, to extremely thin on the labial wall of the protoflexid. The hypoflexid is similar in both specimens, with the rostral margin showing a single central angle and thick enamel, and the caudal margin being constituted by thin enamel and almost devoid of crenellations. The second upper premolar differs between the two specimens in that the mesoflexus of *S. tapetillus* is shallow and surrounded by thick enamel, contrasting with deeper mesoflexus and thick enamel lingually transitioning to thin labially in *S. brasiliensis*. The hypoflexus is absent in the neotype of *S. brasiliensis* but present and shallow in the holotype of *S. tapetillus*, distinctly isolating a mesial hypercone, which is absent in the neotype of *S. brasiliensis*. In terms of size of the teeth, the anterior loph of lower premolar 3 of the holotype of *S. tapetillus* is 2.2 mm in greatest width to 3.1 mm in the neotype of *S. brasiliensis*, and 1.7 mm in anteroposterior length (from the central angle to the rostral inflection point between the labial anteroconid and the anteroflexid), to 1.9 mm in the neotype of *S. brasiliensis*. Both specimens are subequal in greatest anteroposterior length of pm3, 2.6 mm in the holotype of *S. tapetillus* to 2.7 mm in the neotype of *S. brasiliensis*. The second upper premolar of the neotype of *S. brasiliensis* is 3.1 mm in width, the corresponding measurement in *S. tapetillus* is 2.9 mm. It remains to be ascertained how these characters will stand up to the scrutiny of a larger population sample, however, in the absence of such a sample; they reinforce the distinct nature of the two species.



Cladistic analysis of morphological characters  
(Table 5; Figs. S1–S2)

As outlined in the materials and methods, an initial analysis of the morphological characters was undertaken by combining the taxa from the analysis of Ruedas (1998) with those examined in the present manuscript. Because that analysis resulted in an unresolved polytomy among *Sylvilagus* species, we then reduced the taxa to include the taxa focal to this research, namely: *S. andinus*, *S. brasiliensis*, *S. tapetillus*, and *S. dicei*, as well as *S. floridanus*, rooted by *L. californicus* (Table 5). Two equally most parsimonious trees resulted from that analysis (Fig. S1). Including in the analysis only the aforementioned taxa recovered *S. brasiliensis* as basal, and a con-

sistent sister taxon relationship between *S. floridanus* and *S. tapetillus*. The relationships of *S. andinus* and *S. dicei* in the analysis were not consistent, and bootstrap and jackknife analyses (Fig. S1C) yielded an unresolved polytomy at the base of an ingroup *Sylvilagus* exclusive of *S. brasiliensis*.

Ancestral state reconstruction carried out in Mesquite (v. 3.03, build 702) indicated that, for this limited analysis, basal nodes a and f, discriminating between *Lepus* and *Sylvilagus* are defined by character xvi of Ruedas (1998), and character xxiv, defined above. The former refers to p3, central angle angled such that an [almost closed] lacuna is formed in the medial portion of the hypoflexid (0 in *Lepus*), vs. no lacuna formed by CA in hypoflexid (1 in *Sylvilagus*). Nodes d and j, uniting *S. floridanus* and *S. tapetillus*, are defined by characters x and

TABLE 5— Distribution of character states used in the morphologically based phylogenetic analyses (Supplementary Figs. 1-2).

	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii
<i>L. californicus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. brasiliensis</i>	1	0	1	0	0	0	0	0	1	0	1	0
<i>S. andinus</i>	1	1	1	1	0	1	1	1	1	0	?	1
<i>S. tapetillus</i>	1	0	1	1	1	1	1	1	0	1	0	0
<i>S. dicei</i>	1	1	0	0	1	1	0	1	1	0	1	1
<i>S. nuttallii</i>	1	0	0	0	0	0	0	0	0	0	0	0
<i>S. cunicularius</i>	1	0	0	0	0	0	1	1	0	0	0	1
<i>S. palustris</i>	1	0	1	1	0	1	0	0	1	0	?	1

	xiii	xiv	xv	xvi	xvii	xviii	xix	xx	xxi	xxii	xxiii	xxiv
<i>L. californicus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. brasiliensis</i>	0	0	1	1	0	1	?	?	?	?	?	1
<i>S. andinus</i>	0	0	0	1	0	0	?	?	?	?	?	1
<i>S. tapetillus</i>	1	0	0	1	0	1	?	?	?	?	?	1
<i>S. dicei</i>	0	0	0	1	0	0	?	?	?	?	?	1
<i>S. nuttallii</i>	0	0	0	0	0	1	?	?	?	?	?	1
<i>S. cunicularius</i>	0	0	0	1	0	1	?	?	?	?	?	1
<i>S. palustris</i>	0	0	1	1	0	0	?	?	?	?	?	1

	xxv	xxvi	xxvii	xxviii	xxix	xxx	xxxi	xxxii	xxxiii	xxxiv
<i>L. californicus</i>	0	0	0	0	0	0	0	0	0	0
<i>S. brasiliensis</i>	1	0	0	0	0	0	1	1	1	0
<i>S. andinus</i>	0	0	1	1	1	0	0	1	1	1
<i>S. tapetillus</i>	1	1	0	0	1	0	0	1	?	1
<i>S. dicei</i>	1	1	0	1	1	0	0	0	0	1
<i>S. nuttallii</i>	0	0	1	1	0	0	1	1	1	0
<i>S. cunicularius</i>	1	0	0	0	0	1	0	1	0	0
<i>S. palustris</i>	1	1	0	0	0	0	1	0	1	1

Figure 30— Maximum Likelihood phylogeny derived from the analysis of the expanded 12S rRNA dataset, as implemented in RAxML (HPC-2 v. 8.2.4, Stamatakis 2014). Numbers above the branches indicate bootstrap support based on 1000 bootstrap replicates. Numbers below the branches indicate the percent of 5X10<sup>7</sup> trees supporting the topology in the Bayesian analysis (initial 2.8X10<sup>7</sup> trees discarded as burnin) implemented in MrBayes 3.2.5 (Ronquist *et al.* 2012). The neotype of *S. brasiliensis* is denoted by an asterisk. A more detailed version of this figure is available as Supplementary Figure 6.

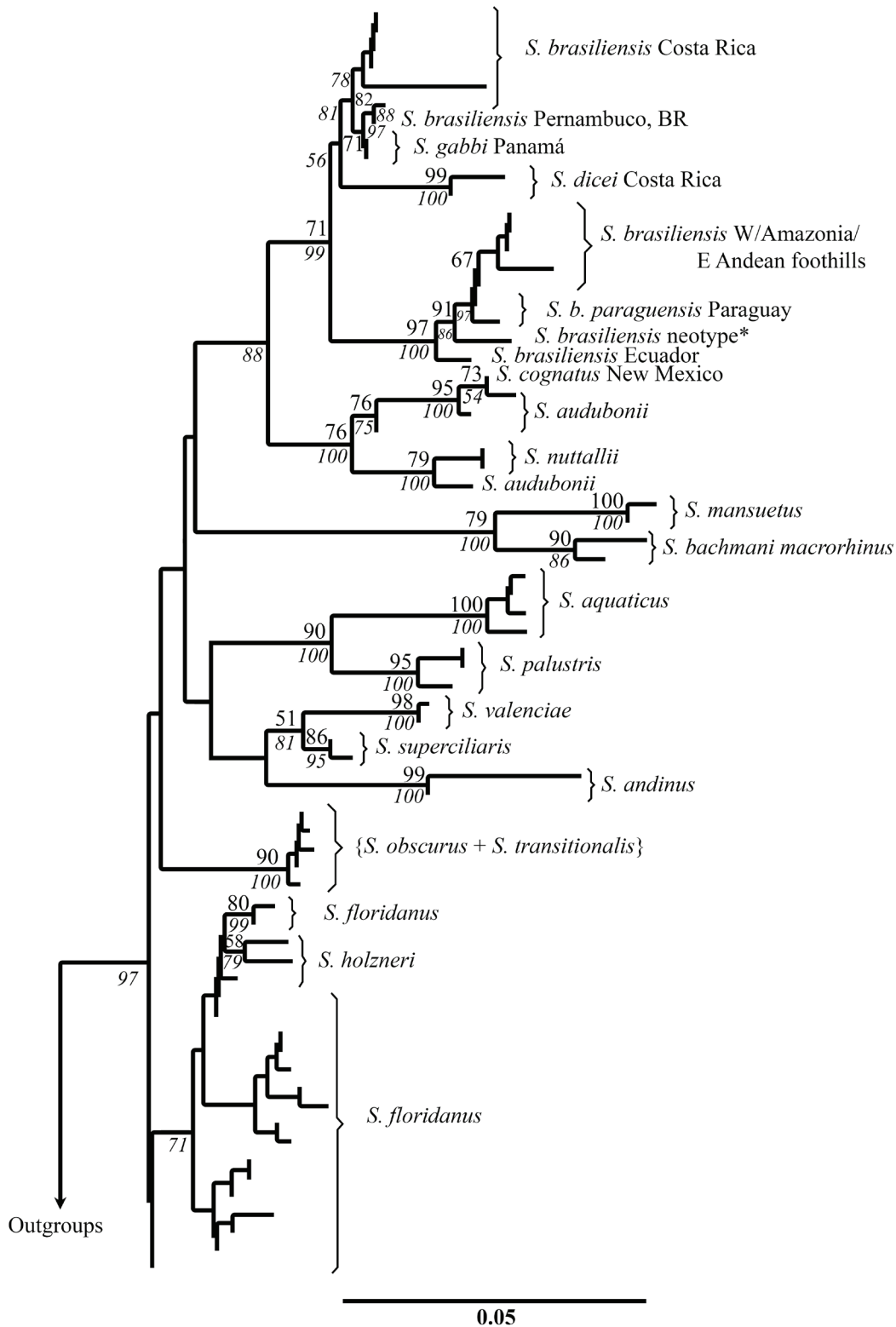
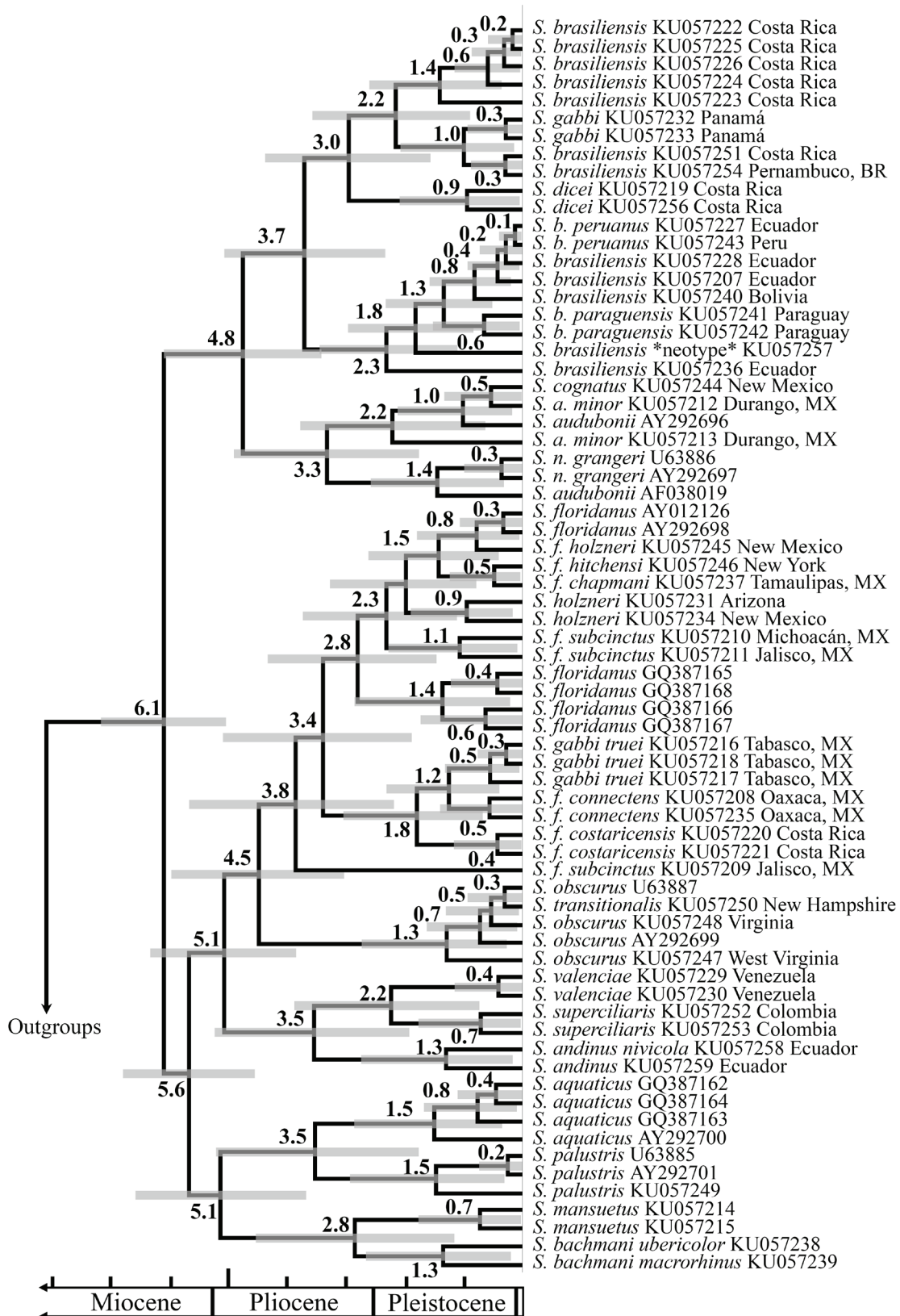


Figure 31— Divergence dates and 95% credibility intervals (grey bars) resulting from the analysis of the expanded 12S rRNA dataset using the uncorrelated lognormal relaxed clock method implemented in BEAST (v. 1.8.2, Drummond *et al.* 2012). The neotype of *S. brasiliensis* is denoted by an asterisk.





xiii of Ruedas (1998): x, thick enamel present in anteroflexid (*S. floridanus* and *S. tapetillus*) or absent (remaining taxa); and xiii, protoflexid enamel thick (*S. floridanus* and *S. tapetillus*) or thin (remaining taxa). Node e, uniting *S. andinus* and *S. dicei*, is supported by characters xii and xviii of Ruedas (1998): xii, p3 protoflexid constituted by multiple reentrants (*S. andinus* and *S. dicei*) or single reentrant (remaining taxa); and xviii, caudal wall of hypoflexid crenelated (*S. andinus* and *S. dicei*) or smooth (remaining taxa). Node c represents a shift in characters vi and viii from plesiomorphic to derived: vi, P2 paraflexus lingual aspect enamel smooth (*S. brasiliensis*) versus crenellated (remaining *Sylvilagus*); and viii, p3 protoflexid enamel thin (*S. brasiliensis*) versus thick (remaining *Sylvilagus*). Node h represents a transition in characters ii, vi, and viii: vi and viii were explicated above; character ii is P2 mesoflexus enamel thin (*S. brasiliensis*) versus thick (remaining *Sylvilagus*). Finally, node i is supported by character v: P2 paraflexus lingual aspect enamel thin (*S. andinus* and *S. brasiliensis*) or thick (*S. dicei*, *S. floridanus*, and *S. tapetillus*).

We expanded the analysis by including additional taxa (*S. cunicularius*, *S. nuttallii*, and *S. palustris*) and in addition, the cranial morphological characters used in the diagnoses of *S. andinus*, *S. brasiliensis*, and *S. tapetillus*. The expanded analysis yielded six equally most parsimonious trees, 56 steps in length, with a consistency index of 0.518 and a retention index of 0.449 (Fig. S2). Twenty-four of the characters were parsimony informative. A number of clades were recovered more consistently in this analysis. Dental characters defining clades were covered above. With respect to the additional cranial characters, none supported the generic dichotomy between *Sylvilagus* and *Lepus*. Within *Sylvilagus*, *S. nuttallii* was consistently recovered as outgroup to remaining *Sylvilagus* (five of the six equally most parsimonious trees, 100% of the bootstrap and jackknife trees). However, this localization was due to retention of primitive characters rather than the species being defined by any autapomorphy, dental or cranial.

A monophyletic clade comprising *S. brasiliensis* and *S. palustris* was recovered in all the equally most parsimonious trees, albeit of uncertain affinities. This clade received support from 56% of the bootstrap trees and 70 of the jackknife trees (Fig. S2). The group is defined only by dental character xv, reflected angle of p3 hypoflexid not highly reflected, versus reflected in remaining taxa. The cranial morphological characters we used define the clade by their combination rather than any single or multiple characters being consistently derived in this clade to the exclusion of remaining species.

All other recovered groupings were not defined by any consistent autapomorphic characters; rather, by the distribution and combination of characters. This included for example the clades comprising *S. andinus* and *S. tapetillus*, represented in three of the equally most parsimonious trees, 28% of the bootstrap trees, and 38% of the jackknife trees;  $\{S. andinus + S. tapetillus\} S. dicei$ , represented in three of the equally most parsimonious trees, 18% of the bootstrap trees, and 28% of

the jackknife trees; and  $\{S. floridanus + S. tapetillus\}$ : two of six trees, 32% of the bootstrap trees, and 36% of the jackknife trees.

While the morphological characters we employed, both dental and cranial, served in combination to diagnose the species, few were diagnostic of clades. Additional morphological characters will be required in order to indubitably define the clades based on synapomorphies unique to the constituent species pairs or groups. However, we wish to highlight two findings. First, although *S. andinus* and *S. tapetillus* appear as sister taxa in three of the morphological trees, there are no synapomorphies exclusive to this morphological clade, the clade is not supported at a level greater than 50% in either bootstrap or jackknife analyses, and the distribution of characters is such as to lead us to conclusively reject the hypothesis of conspecificity for this pair of species. Similarly, in none of the analyses did *S. andinus* obtain as sister to *S. brasiliensis*, thereby highlighting from a morphological perspective the stark taxonomic and evolutionary differences between the two taxa, whose hypothesis of conspecificity is definitively rejected by the ensemble of our data.

#### Molecular systematics of the South American *Sylvilagus* (Figs. S3-S5, 30–33)

We first undertook analyses of the molecular data on each mitochondrial gene separately. For the 12S rRNA gene, 1070 nucleotides were recovered from the neotype of *S. brasiliensis*, encompassing the complete gene sequence. The degraded nature of the DNA recovered from the *S. andinus* specimens proved more problematic, 588 nucleotides in two segments (232 and 356 nt) were recovered from UMMZ 77075. The gap between the two segments almost completely overlapped a loop feature from the proposed two-dimensional structure model of the 12S rRNA (Springer et al. 1995), which would have rendered alignment in that region difficult. As a consequence, analysis of the 12S sequences was ultimately undertaken on a 660 nucleotide segment of the gene. The model of evolution resulting from jModelTest for the more complete 12S sequence dataset was the GTR+I+ $\Gamma$  (Tavaré 1986, with proportion of invariant sites and Gamma-distributed among site rate variation). The transition:transversion (ti:tv) ratio for the data set was 5.0681, nucleotide frequencies were: A, 0.3744, C, 0.2454, G, 0.1576, and T, 0.2226. The proportion of invariable sites was 0.4240, with rates at variable sites conforming to a gamma distribution with shape parameter of 0.488. For the *cyt-b* mitochondrial gene, we recovered 1057 nucleotides from the neotype of *S. brasiliensis*, and 237 nucleotides from *S. andinus* UMMZ 77075. The model of evolution resulting from jModelTest for the *cyt-b* data was the HKY with Gamma-distributed among-site variation. The ti:tv ratio was 7.9733 for this marker, nucleotide frequencies were: A, 0.2765, C, 0.3265, G, 0.1199, T, 0.2771. The Gamma shape parameter was 0.186. We also created chimeric

species by concatenating the 12S rRNA and *cyt-b* sequences corresponding to the same species. Since these were from the same studies, it is likely that they correspond to the same individual, hence there should be no doubt as to the taxonomic identity, or about “creating” an artificial species by joining sequences from distinct genes. For the combined data set, the best model of evolution resulting from jModelTest was the GTR+I+ $\Gamma$ . Nucleotide frequencies were: A, 0.3007, C, 0.29970, G, 0.14440, T, 0.25520. The proportion of invariant sites was 0.585. The Gamma shape parameter was 0.716.

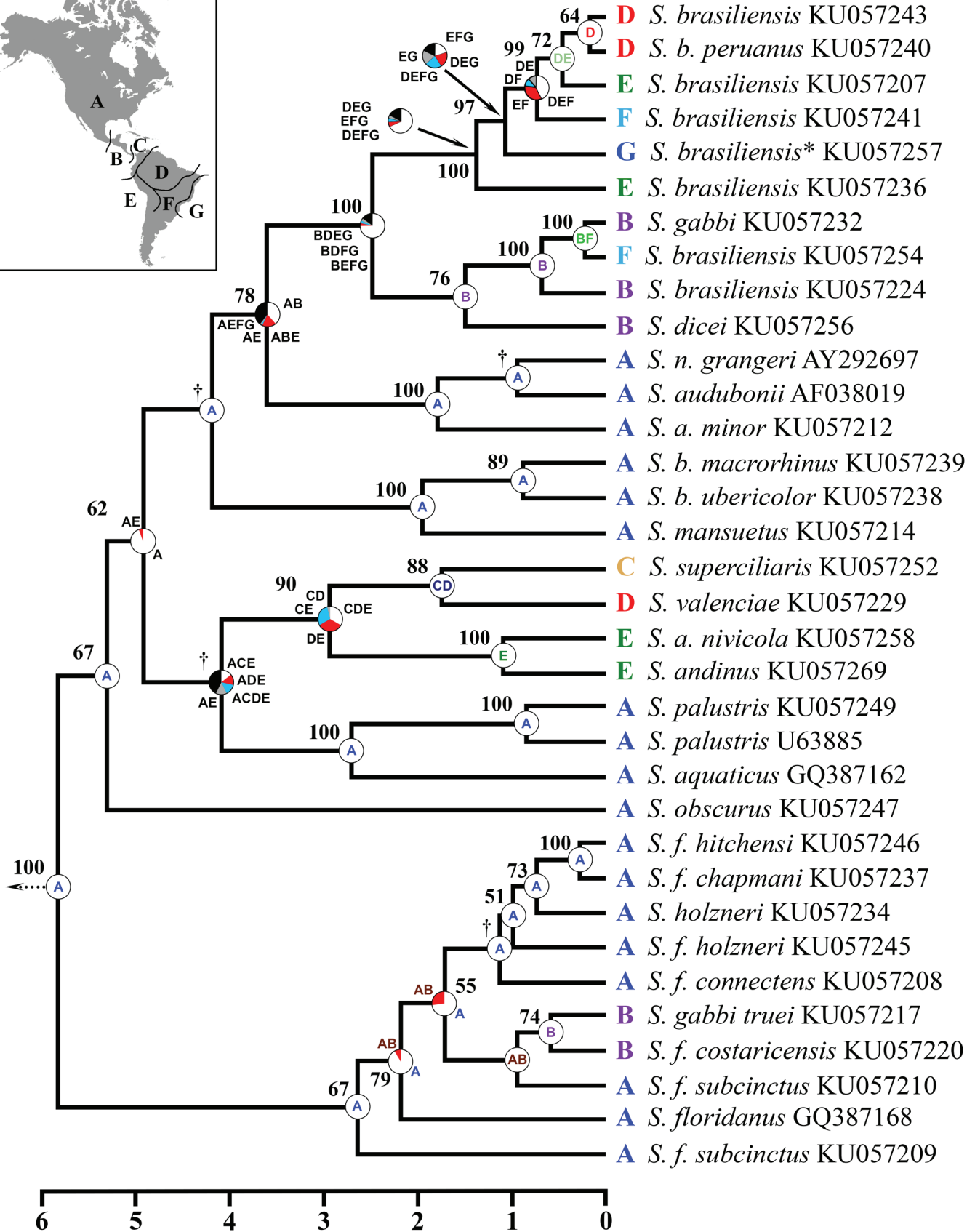
The topologies of the ML trees derived from integration of our data on South American *Sylvilagus* with existing data for the same genus are not fully concordant between the two mitochondrial markers. However, there is definitive agreement as to the fact that *S. andinus* and *S. brasiliensis* are not conspecific. In the analysis of 12S rRNA (Fig. S3, top), *S. andinus* is in a clade with *S. aquaticus* and *S. palustris*, *S. nuttallii* and *S. audubonii* are in a clade sister to that, with *S. brasiliensis* in turn sister to those five species. The relationships of *S. andinus* with *S. audubonii* and *S. nuttallii* remain consistent in the analysis based on *cyt-b* sequences (Fig. S3, bottom), but *S. brasiliensis* now obtains as the most basal member of *Sylvilagus*, albeit with no bootstrap support. In the analysis of the combined mitochondrial sequences, the ML algorithm weakly supports a sister relationship of *S. andinus* to *S. audubonii* + *S. nuttallii*, and a sister relationship of *S. brasiliensis* to *S. floridanus* + {*S. transitionalis* + *S. obscurus*} (Fig. S4, top). This topology also is supported by the Bayesian analysis implemented in BEAST (Fig. S5). In contrast, the Bayesian analysis implemented by MrBayes brings *S. andinus* as sister to all remaining *Sylvilagus* (Fig. S4, bottom). The relatively unstable topological nature of the branches of *S. andinus* and *S. brasiliensis*, an effective polytomy, may reflect speciation by peripheral isolate formation (Frey 1993, Brooks & McLennan 2002). If that is the case, then sampling intervening taxa of *Sylvilagus* in the putative *S. brasiliensis* group (for example the widespread *minensis*), would better resolve the relationships among the taxa of *Sylvilagus* sampled. Certainly, adding more sequence data also would better resolve the relationships; that is already in process. More inclusive sampling may change some of the topology (Matthee *et al.* 2004). One thing that appears relatively certain is that *S. andinus* and *S. brasiliensis* are not each other’s sister taxa, further underscoring their species status as described above based on morphological data.

The timing of the various cladogenic events was assessed using uncorrelated lognormal relaxed molecular clock techniques implemented in BEAST, with results shown in Fig. S5. Based on our calibration points, the basal radiation of *Sylvilagus*, or diversification from a common ancestor, occurred between 4.435 MYA (95% CI: 3.96–4.90, combined *cyt-b* + 12S dataset) and 6.08 MYA (5.04–7.16, expanded 12S). The lineage leading to *S. brasiliensis* would have split from that including *S. floridanus* + (*S. transitionalis* + *S. obscurus*)

3.88 MYA (3.0–4.6), making *S. brasiliensis* one of the most basal lineages in *Sylvilagus*. The lineage leading to *S. andinus* is hypothesized to have separated from that leading to *S. audubonii* + *S. nuttallii* 3.09 MYA (2.29–4.35). We hypothesize, based on molecular data, that the cladogenesis between *S. transitionalis* and *S. obscurus* occurred 11,750 years ago (3,024 – 21,910), an estimate in agreement with Ruedas *et al.* (1989) who suggested 12,500 years, based on chromosomal and ecological data. Cladogenesis between *Brachylagus* and *Sylvilagus* lineages is hypothesized to have occurred 6.79 MYA (5.29–8.39), between *Oryctolagus* and (*Brachylagus* + *Sylvilagus*), 7.95 MYA (6.21–9.72), and between *Lepus* and (*Oryctolagus* + (*Brachylagus* + *Sylvilagus*)), 8.46 MYA (6.59–10.24). Our data are robust relative to the criteria of Zheng & Wiens (2015), however, the accuracy of the dates reported herein relies on the accuracy of the calibration points, many of which remain nebulous at best, as described above (Materials and Methods). Furthermore, our focus was in estimating the cladogenic events within *Sylvilagus* and more specifically as applied to *S. brasiliensis* and *S. andinus*. The fossil data and dating are more reliable in *Sylvilagus* than they appear to be in *Lepus*, thus we feel some confidence in these results.

Because we had a more comprehensive data set of lagomorphs for the 12S mitochondrial locus, we undertook a separate analysis to assess the timing of the radiation of *Sylvilagus* using this locus only, using the same techniques as described above (Figs. 30–31). The taxonomic and geographic coverage of the dataset enabled us to propose some hypotheses that may ultimately be tested using a broader sampling of genes and taxa.

Analyses of genetic distances further corroborate the species level distinction between *S. andinus* and *S. brasiliensis*. We used the approach of Bradley & Baker (2001) and Baker & Bradley (2006) to the Genetic Species Concept, extending from *cyt-b* to our 12S rRNA data, using published sequences as well as our own. Among lagomorphs, four species of *Ochotona* displayed genetic distances in 12S rRNA sequences (GTR, matrix provided as Appendix 2) of 0.074±0.026, 0.040–0.010 (average ± standard deviation, range). For eight species of *Lepus*, comparable data were 0.034±0.007, 0.011–0.048. For the individuals of *Sylvilagus* examined herein, the same data were: 0.037±0.017, 0.000–0.114. Sister taxa of *Sylvilagus* sampled herein vary in their interspecific distances: *S. obscurus* is indistinguishable from *S. transitionalis* using this marker, underscoring their recent speciation (Ruedas *et al.* 1989). Other pairs range from 0.012±0.002, 0.017–0.022 (*S. mansuetus* v. *S. bachmani*), 0.02±0.004, 0.017–0.024 (*S. dicei* v. *S. gabbi*), 0.019±0.002, 0.017–0.021 (*S. cf. valenciae* v. *S. cf. superciliaris*), 0.024±0.005, 0.018–0.033 (*S. dicei* v. *S. cf. brasiliensis* from Costa Rica), to 0.047±0.008, 0.033–0.055 (*S. aquaticus* v. *S. palustris*). The mean genetic distance between *S. brasiliensis* (neotype only) and the two specimens identified as *S. andinus* on the basis of morphology and molecules (KU057258 and KU057259) in the 12s





rRNA mitochondrial gene is 0.046, 0.5 standard deviation above the mean interindividual distance in *Sylvilagus*, and approximately the same as that between *S. aquaticus* and *S. palustris*; that between the neotype and specimens identified as *S. b. paraguensis* (mean: 0.011, range: 0.010–0.013) matches that between *S. mansuetus* and *S. bachmani*, another hypothesized pair of sister taxa. At the *cyt-b* locus, for which more extensive taxonomic data are available (Bradley & Baker 2001, Baker & Bradley 2006), results were as follows: *Ochotona*, 0.114±0.021, 0.087–0.135, *Lepus*, 0.098±0.017, 0.039–0.127, *Sylvilagus*, 0.114±0.016, 0.062–0.153. The genetic distance between *S. andinus* and *S. brasiliensis* is 0.153, the largest genetic distance for *cyt-b* in *Sylvilagus*, and 2.3 standard deviations from the mean interspecific distance in *Sylvilagus*.

One additional item of interest concerns the Mesoamerican taxa sometimes considered *S. brasiliensis*. Diersing (1981) divided these based on morphology into two allopatric groups: *S. b. truei* and *S. b. gabbi*. Based on morphological and chromosomal data, Tate (1933) and Ruedas & Salazar-Bravo (2007) placed these taxa into *S. gabbi*, as *S. g. gabbi* and *S. g. truei*. The molecular data presented above suggests that there is at least one additional taxon allied to *S. gabbi* in Costa Rica, and distinct from Panamanian *S. g. gabbi*.

We ran two separate analyses on the 12S rRNA dataset in BEAST in order to arrive at Bayesian estimates for times of diversification: the first comprised the complete dataset, the second was trimmed to include only putatively distinct taxa based on the topological results of the Maximum Likelihood analysis, as well as genetic distances, the latter in order to remove the effect of oversampling terminal taxa as individuals rather than species in a subsequent examination of lineages through time (Van Valen 1973). These analyses suggest a

basal diversification of *Sylvilagus* between 4.56 MYA (3.68–5.44, posterior estimate, 95% credibility interval) and 6.08 MYA (5.04–7.16). For the combined 12S+ *cyt-b* dataset, the estimate is 4.43 MYA (3.97–4.91). That initial division of *Sylvilagus* into two major clades is reflected in both 12S and *cyt-b*+12S datasets, and marks the depth between *S. andinus* and *S. brasiliensis*. Indeed, we could denominate the two clades a “Southern” clade (with a small northern sister clade constituted by *S. cognatus*, *S. audubonii* and *S. nuttallii*), and a “Northern” clade containing a smaller southern clade comprised by *S. andinus*, and taxa that absent physical examination of specimens, we are considering *S. superciliaris*, and *S. valenciae* because of their origin (Colombia and Venezuela, respectively).

We examined potential areas of origin using the Bayesian dispersal–vicariance analysis module (S–DIVA, Yu *et al.* 2010) in RASP (Yu *et al.* 2015). S–DIVA runs DIVA 1.2 (Ronquist 1997, 2001) in a shell to enable statistical dispersal–vicariance analyses by implementing the methods of Nylander *et al.* (2008) and Harris and Xiang (2009) which in particular account for the uncertainty in phylogenetic inference when ancestral ranges are reconstructed onto a fixed tree topology assumed to be without error (Nylander *et al.* 2008). We used a tree based on the 12S rRNA sequence data, with the terminal taxa reduced to a single representative per hypothesized species level taxon within *Sylvilagus* based on the topology of the comprehensive ML analysis, and the magnitude of the genetic distances among the taxa. The reduction was carried out in order to remove the effect of oversampling terminal taxa as individuals rather than species (Van Valen 1973). We first ran a Bayesian Markov chain Monte Carlo (MCMC) analysis using BEAST v. 1.8.2 (Drummond *et al.* 2012) in order to generate a chronogram for *Sylvilagus* based on a 50% majority–rule consensus of the best 100 resulting trees based on  $-\ln$  likelihood. The resulting tree file was then used as the input file for S–DIVA in RASP, in order to generate an ancestral biogeographic reconstruction. We recognize that the areas used in the biogeographic reconstruction represent an oversimplification of the environmental heterogeneity of the region (e.g., Haffer 2008, Řičan *et al.* 2013), however, the results (Fig. 32) mirror (with the exception of “North” and “Central” America) those of R. N. Leite *et al.* (2014). Notwithstanding, we chose this representation because firstly, our focus was on elucidating patterns and relationships among South American taxa, and in the second instance, because although the present work moves forward towards a basic understanding of taxonomy of *Sylvilagus*, we recognize that much of the diversity of the genus remains unknown, and this is true of Mesoamerica no less than South America. As a consequence of the foregoing, our hypotheses must remain tentative.

In combination, the perspectives derived from the various analyses support a Nearctic origin for *Sylvilagus*. An initial divergence resulted in a primarily Nearctic clade constituted principally by *S. floridanus* and allies that produced a

Figure 32— Results of the Bayesian dispersal–vicariance analysis (S–DIVA, Yu *et al.* 2010) implemented in RASP (Yu *et al.* 2015). The tree is based on the 12S rRNA sequence data, reduced to hypothesized species level taxa within *Sylvilagus* based on the topology of the comprehensive ML analysis as well as the magnitude of the genetic distances among the taxa. Pie charts at internal nodes represent the marginal probabilities for each alternative ancestral area, derived by using S–DIVA. In the pie charts, the first four areas with highest probability are colored according to relative probability in the following order: white > red > blue > gray; remaining areas are collectively assigned black. The geographic region of each putative taxon, color coded, is shown in front of each taxon name. Inset: Key to areas of origin of the terminal taxa. A: North America to the Isthmus of Tehuantepec; B: Central America, from the Isthmus of Tehuantepec to Isthmus of Panamá; C: Cis–Andean South America, from the Isthmus of Panamá to the North Andean Cordilleras; D: Trans–Andean Guyana and Amazonia; E: Andes and east Andean foothills and highlands; F: lowland grasslands; G: Atlantic Forests. The specimen denoted with a \* is the neotype of *S. brasiliensis*. A dagger symbol (†) indicates nodes with less than 50% support.

single incursion into Mesoamerica, constituted by what we hypothesize might constitute *S. gabbi truei* and *S. "floridanus" costaricensis* (likely a species in its own right: Yates *et al.* [1979] determined that *S. f. costaricensis* was distinct enough in Nicaragua and Costa Rica to at least warrant subspecific rank). The node uniting these two taxa dates to between 0.58 MYA (0.10–1.22) and 1.79 MYA (0.67–3.07), depending on the algorithm and data set employed. The S-DIVA analysis suggests that even as far back as 2.63 MYA (1.05–4.90) and 3.40 MYA (1.88–5.09), there would have been a 9% probability of an ancestral taxon occupying the southern extent of the Nearctic region as we define it: our *S. f. subcinctus* samples originate from Jalisco and Michoacán, México. Our limited dataset ably defines recently diverged taxa, but is not as conclusive with respect to deeper divergences within *Sylvilagus*. Thus, another South American clade is defined by the 12S data set constituted by the Cisandean *S. valenciae* and the northern Transandean *S. superciliaris*. These two sister taxa are in turn joined to the Andean *S. andinus*. Divergence estimates for the lowland taxa range from 1.74 MYA (0.53–3.16) to 2.23 MYA (0.71–3.90), and for the common ancestor of the two lowland taxa and *S. andinus* from 2.94 MYA (1.57–4.35) to 3.54 MYA (1.92–5.24). That South American clade has uncertain relationships depending on the dataset and algorithm. The sister taxon to *S. andinus* in the combined cyt-*b* + 12S dataset is the Southeastern North American *S. aquaticus* + *S. palustris*: that clade joins with the *S. andinus* group at 3.88 MYA (3.05–4.61). In the 12S dataset, the South American taxa join with a larger *S. floridanus sensu lato* clade at 5.06 MYA (3.85–6.33), while in the reduced taxon analysis we examined for S-DIVA, the South American taxa plus *S. aquaticus* + *S. palustris* is ensconced in a broader southern Nearctic clade at 4.09 MYA (2.80–6.01). In either case, that South American lineage is relatively independent of the larger South American clade wherein resides the neotype of *S. brasiliensis*. Interestingly, the most likely (69%) ancestral area for the neotype, putatively restricted to the Atlantic Rainforest, is in the eastern foothills of the Andes, although other—composite—areas also include Amazonia (as well as the Andean foothills). In this respect, we wish to stress that elevation alone may not “make” *S. andinus*: four of our specimens (KU057207, KU057227, KU057228, and KU057258) were from the Andean highlands (2995 to 4300 m) and variously identified as *S. brasiliensis*, *S. b. andinus*, or *S. b. nivicola*, yet all but one (KU057258, from 4332 m) fell phylogenetically within the largely lowland South America clade. The latter specimen, *S. a. nivicola*, formed a clade with the historical specimens of *S. andinus* collected by P. Hershkovitz whose identity was ascertained by comparison with the holotype of *S. andinus*. Those two specimens had a common ancestor between 1.09 MYA (0.27–2.11) to 1.29 MYA (0.17–2.74). The largely lowland South American *Sylvilagus* clade appears to have had a southern Nearctic origin between 4.75 MYA (3.41–6.13) and 4.91 MYA (3.76–6.06) with an initial diversification in Mesoamerica

between 2.48 MYA (1.40–3.71, reduced data set) and 3.71 MYA (2.34–5.08) before radiating into most of South America. Our molecular data support a recent and explosive radiation in the genus *Sylvilagus*. Interestingly, the dates and biogeographic patterns appear to be largely concordant with those proposed for Sigmodontini by R. N. Leite *et al.* (2014) and the cladogenesis of *Sylvilagus* is concordant with the dates suggested for Sigmodontini by Vilela *et al.* (2013). The internal diversification of South American *Sylvilagus* species is further concordant with dates proposed for New World siskins and goldfinches in the Central Andes proposed by Beckman and Witt (2015). The temporal coincidence in diversification with other—distinct—groups, suggests perhaps not a common mechanism but at least a common trigger.

This explosive radiation also is supported by an analysis of lineages through time undertaken on the molecular data, which estimates the speciation and extinction rates in the groups under consideration (Fig. 33). We examined these using ultrametric trees derived from the complete 12S dataset including outgroups, as well as with that dataset reduced to hypothesized species level taxa within *Sylvilagus* based on the topology of the comprehensive ML analysis, and the magnitude of the genetic distances among the taxa. The reduction was carried out in order to remove the effect of oversampling terminal taxa as individuals rather than species (Van Valen 1973). Calculations of  $\lambda$  (speciation rate) and  $\mu$  (extinction rate) were undertaken using the Diverse Package (Midford & Maddison 2007) and Diversification (Char. Indep.), both implemented in Mesquite 3.04 (Maddison & Maddison 2015, see also Maddison *et al.* 2007). For the comprehensive data set,  $\lambda$  was 0.583, and  $\mu$  0.516, with a  $\lambda/\mu$   $-\ln$  likelihood of 188.238. For the dataset reduced to *Sylvilagus* only,  $\lambda$  was 0.505, but  $\mu$  dropped to  $1.75 \times 10^{-6}$  ( $\lambda/\mu$   $-\ln$  likelihood 55.782). Both values for  $\lambda$  are higher than those reported for example for Sigmodontinae as a whole (0.469, 90% HPD 0.416 – 0.536) by Parada *et al.* (2015). Thus, with the caveat that our taxonomic sample size is less than acknowledged as optimal for this type of analysis (Davis *et al.* 2013), although net diversification appears relatively stable within Lagomorpha as a whole, *Sylvilagus* in contrast is diversifying rapidly based on its age, apparently by eschewing extinction. A number of slowdowns can be observed in the LTT for Lagomorpha, however, *Sylvilagus* in isolation show no slowdown over time in numbers of lineages. Interestingly, our data show the same phenomenon in speciation and extinction as demonstrated by Rolland *et al.* (2014) for other groups of mammals: faster speciation and reduced extinction rates in the Tropics. However, Rolland *et al.* (2014) singled out lagomorphs as the exception to that rule because of their “inverse diversity gradient” relative to other mammals’ global latitudinal species gradient. We propose instead that Tropical species diversity in Lagomorpha, here demonstrated in *Sylvilagus*, but likely also in African *Lepus*, has been to date overlooked. We hypothesize that when a more complete taxonomic understanding of Lepo-

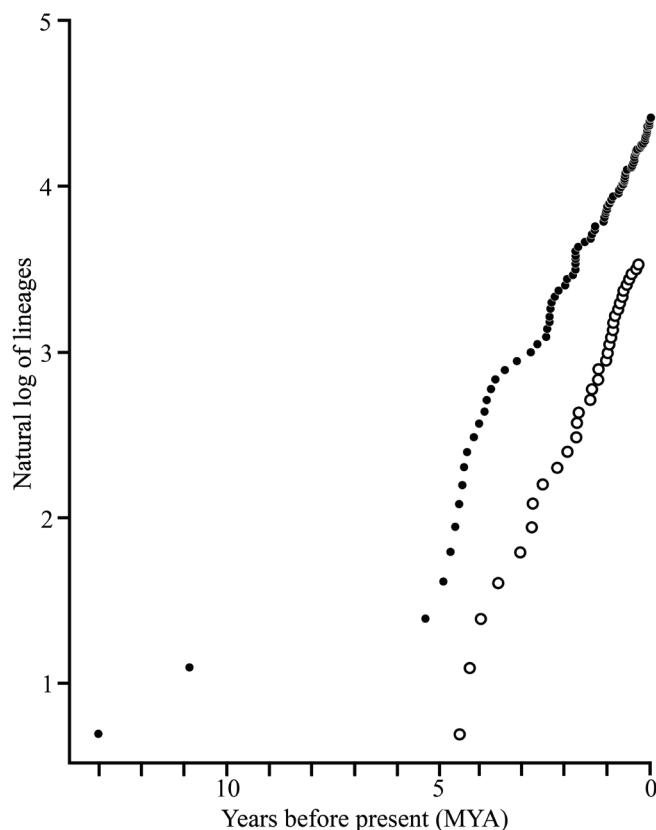


Figure 33— Lineage through time (LTT) plot resulting from the analysis of the expanded 12S rRNA dataset. The likelihoods were calculated using a speciation extinction model reduced from the binary-state speciation and extinction (BiSSE) model of Maddison *et al.* (2007) implemented in Mesquite (Maddison and Maddison 2015). Solid circles: complete dataset. Speciation rate,  $\lambda$ , 0.583; extinction rate,  $\mu$ , 0.516;  $\lambda/\mu$   $-\ln$  likelihood of 188.238. Open circles: *Sylvilagus* species only;  $\lambda$  = 0.505;  $\mu$  =  $1.75 \times 10^{-6}$ ;  $\lambda/\mu$   $-\ln$  likelihood 55.782s.

ridae has been achieved, a much more vast Tropical diversity will be revealed. Indeed, we hypothesize that numerous taxa remain to be described from these Tropical areas, something that will fill in biogeographic gaps that currently remain. With particular reference to *Sylvilagus*, it may become possible to test the hypothesis proposed by Buffon (1799a) of a Tropical origin for the group. In his discussion of varieties of hares and rabbits, Buffon (1799a:109) stated that "...in the Isthmus of Panama, one finds also animals that travelers have taken for hares but that are rather species of rabbits, because the rabbit is native to warm countries, and one does not find it in northern climates, instead of the hare which is stronger and larger and inhabits colder climates."

The various algorithms, analyses, and datasets, in combination suggest that *Sylvilagus* underwent an initial deep cladogenesis into two major groups approximately coeval with the Late Miocene to Early Pliocene transition. Deep

scale climate records (J. Zachos *et al.* 2001) suggest a general cooling trend starting at the Mid-Miocene and progressing to the Holocene, further complicated by orbital eccentricity on 100 KY and 400 KY cycles, axial obliquity on a 41 KY cycle, and axial precession on a 23 KA cycle (Milanković 1941, Haffer 2008, Zachos *et al.* 2001). However, more detailed records suggest that the Miocene-Pliocene transition would have seen a change from a colder, drier climate in the Miocene to a warmer, wetter interval during the Pliocene (Salzmann *et al.* 2011, 2013), with in particular, a weaker El Niño Southern Oscillation and weakened temperature changes along the Equator during the early Pliocene (Brierley 2015), a Piacenzan warm period 2.58–3.6 MYA with temperatures 2–3°C warmer than today (Dowsett *et al.* 2009, 2010), greater seasonality (Valentine *et al.* 2011), and greater temperature differentiation between higher and equatorial latitudes driven primarily by the orbital and axial cycles (Salzmann *et al.* 2011, 2013). Cooler climates therefore appear to favor speciation and diversification in *Sylvilagus*. The initial diversification of *Sylvilagus* is associated with the colder, drier Miocene, followed by a slight slowdown in accumulation of lineages during the Piacenzan warm period, followed by an increased number of lineages coinciding with a cooling trend with significant glaciation starting *ca.* 2.75 MYA (Ravelo *et al.* 2004) and a cooler, increasingly glaciated Late Pliocene and Pleistocene (Joannin *et al.* 2007).

## DISCUSSION

"Among the various Genera of Quadrupeds of which descriptions have been given, there are few that have presented greater difficulties than the Hares. [...] the difficulty of procuring specimens is so great, and 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." (Bachman 1837:282). The Reverend John Bachman would have known about how morphologically similar are species in Leporidae: in his work on the North American species, he listed eight species for North America, noting that "In addition to the eight species enumerated in this article it is very probable that one or two may yet be added to our Fauna." (Bachman 1837:361). In that work, although Bachman described three species that remain valid today (*S. aquaticus*, *S. palustris*, and *S. nuttallii*), two of the species are now considered synonymous (*Lepus americanus* and *L. virginianus* [= *L. americanus virginianus*]) and two sunk into synonymy with previously existing species (*L. glacialis* = *L. a. arcticus*, *L. campestris* = *L. townsendii campanius*). In addition, one of the species Bachman treated was *L. princeps* (= *Ochotona princeps*, Ochotonidae), of which he noted that "This diminutive animal, [...] bears so little resemblance to the hares, that it will probably not long remain even as a sub-genus to *Lepus*..." (Bachman 1837:354). Thus, the morphological conservatism evident among Leporidae,



and indeed, lagomorphs in general, has been an issue and to this day remains an issue in resolving not just the taxonomy but consequently also the systematics of the group.

Scheffers *et al.* (2012) identified the problem of synonymy, together with discriminating species by morphology, as one of the major challenges in our ability to describe the Earth's biota. These authors considered the problem of synonymy as the application of distinct names to a single taxon. However, the "problem of synonymy" also may refer to the converse: the application of a single name to distinct taxa. In that respect, for example, recent work on Bovidae (Groves and Grubb 2011) resulted in the recognition of 279 species of Bovidae, from 143, a move heavily criticized as an example of "splitting frenzy" (F.E. Zachos 2012) and "taxonomic inflation" (Heller *et al.* 2013). More broadly, F.E. Zachos *et al.* (2013a) and Heller *et al.* (2013) took issue with precisely what we are doing in this paper: raising subspecies to species, noting that "the increase in species numbers, or taxonomic inflation, is due mainly to subspecies being raised to full species, rather than to new discoveries" (F.E. Zachos *et al.* 2013a:1), and suggesting that such actions place conservation at risk (F.E. Zachos *et al.* 2013a, 2013b). However, as Cotterill *et al.* (2014) argued in response to these criticisms, we are in fact redressing a taxonomic wrong: cryptic species have been overlooked and misclassified, subsumed into taxonomic oblivion or at best recognized as subspecies. Furthermore, the suggestion that finely elucidating taxonomy and systematics of a group is counterproductive to conservation strikes us as a spurious argument: to be effective, adequate conservation policies require taxonomies that are resolved.

In the present instance, we have laid the groundwork for a more finely resolved framework for the taxonomy and phylogenetic relationships of *Sylvilagus* in South America. Our molecular analyses may suffer from Brooks' dictum: "If analyses using different types of data and/or different methods of phylogeny reconstruction do not produce the same results, more data are needed." (Brooks *et al.* 2007). Notwithstanding, the necessity of this basic taxonomic work is underscored by the prediction of Pimm *et al.* (2010) that (at that time), no more than 38 species of mammal remained to be described from Brazil. A cursory perusal suggests that since 2010 (inclusive), and as of this writing, at least 43 species of mammals have been described (or noted absent formal description) from Brazil. That includes species in such putatively well known and large animals such as tapirs (*Tapirus*, Cozzuol *et al.* 2013), river dolphins (*Inia*, Hrbek *et al.* 2014), and Saki Monkeys (five species of *Pithecia*, Marsh 2014). It also includes three new genera of mammals, including bats (Nogueira *et al.* 2012) and rodents (Percequillo *et al.* 2011, Pardiñas *et al.* 2014). Were we to have gone back to 2006, a remarkable ten new genera of oryzomyine rodents were described in a single paper (Weksler *et al.* 2006). Increasingly detailed morphological data, integrated with molecular data, have been crucial as much in these discoveries as in elucidating the taxonomy of

South American *Sylvilagus* species. The enhanced visibility of ecological data likewise has played a role. The importance of mountains not only as geographic barriers, but also inasmuch as their climatic properties are concerned—hence their ability to act as evolutionary drivers—has long been acknowledged (von Humboldt 1805, Janzen 1967). In the Tropics, these higher montane areas are separated from lowlands by the mid–montane belt of higher species richness (McCain 2004). The increasing reliability and sophistication of niche modeling methods provides a tool to apply these ecological hypotheses (Rissler & Apodaca 2007, Tocchio *et al.* 2015), particularly in light of the documentation of accelerated rates of evolution at high elevations (Madriñan *et al.* 2013). Indeed, among Lagomorpha, ecological divergence is implicated as a driver in higher level taxonomy, let alone in species level cladogenesis (Humphreys & Barraclough 2014). All these independent data sets can be brought together to enhance conservation and management strategies, a critical need in the Brazilian Atlantic Forest (Brito 2004). In South American *Sylvilagus*, the confluence of morphological, molecular, and ecological data leads to the ineluctable conclusion that more species are present than previously have been appreciated.

#### TAXONOMIC SUMMARY

The morphological and molecular analyses presented herein, together with the chromosomal and molecular data of Bonvicino *et al.* (2015) support the restoration of two species–level taxa within *Sylvilagus* that until recently had been considered synonyms of *S. brasiliensis*: *S. andinus* and *S. tapetillus*.

##### *Sylvilagus brasiliensis* (Linnaeus, 1758)

*Lepus brasiliensis* Linnaeus, 1758:58. Type locality "America meridionali" [=South America]. Based on "Tapeti Brasiliensibus" of Marcgraff 1648:223 (Fig. p. 224).

*Lepus Tapeti* Pallas, 1778:30. Also based on Marcgraff, unavailable name combination.

*Lepus Tapeti* Schreber, 1792:902. Unavailable name combination.

Le tapeti Buffon 1799b:342. Vernacular, unavailable name. Locality: "on le trouve au Brésil et dans plusieurs autres endroits de l'Amérique" [one finds it in Brazil and several other places in America]

tapitý Azara, 1809:313. Vernacular, unavailable name. Locality: South America north of 30° degrees latitude South.

*Lepus Brasilianus* Lesson, 1842:99. Incorrect subsequent spelling, following Brisson (1756:141, unavailable on the basis of date), who in turn cited type locality as "Brésil" [=Brazil].

Le Tapéti Lesson, 1842:99. Alternate subsequent spelling of unavailable vernacular names of Buffon (1799b:342) and Azara (1809:313)

*Lepus nigricaudatus* Lesson, 1842:100. Locality “Brésil” [=Brazil] Part. Not Mexico or California.

*Tapeti brasiliensis* Gray, 1867:224. Name combination. First use of genus *Tapeti*. Locality “Para and Bolivia.” Presumably Pará, Brazil. Neither location refers to our concept of *S. brasiliensis*.

*Lepus brasiliensis* Thomas, 1901a:535. Type locality “From Porto Real, near Rezende, Rio.” Thomas referred to *S. tapetillus* (see below).

*Lepus brasiliensis* Thomas, 1911:146. Restricted Linnaeus’ type locality to “Pernambuco.”

*L[epus] brasiliensis* Thomas, 1913:209. Type locality reiterated as “Pernambuco” but added that a series of specimens collected by Alphonse Robert from “Lamarão, Bahia” [...] “not so very far from Pernambuco [...] may be treated as true *L. brasiliensis*.” Lamarão restricted by Coimbra-Filho *et al.* (2006) to: “on the railway line midway between the towns of Água Fria (south) and Serrinha (north), 11°45’S, 38°53’W, northwest of Salvador, about 140 km as the crow flies.”

*S[yvilagus] brasiliensis* Thomas, 1913:211. First use of current name combination.

*Sylvilagus brasiliensis brasiliensis* Hershkovitz, 1950:366. Name combination.

We have detailed in the preceding pages a rather restrictive concept of what is *Sylvilagus brasiliensis*. On the basis of the above discussion, it is of interest to ask not just what is *Sylvilagus brasiliensis*, which we believe we have answered, but also: what are the species called that were formerly included in *Sylvilagus brasiliensis*? Taxa with distributions as disparate as the Guyanas (Hoogmoed 1983) to vast tracts of Amazonia (de Sousa e Silva Júnior *et al.* 2005) have been given the same name. The issue of names was broached by Tate (1933) who provided a list of named forms with their type localities. However, for those taxa in his “South Amazonian Region,” he listed *S. b. paraguensis* Thomas, 1901, first followed by *S. b. minensis* Thomas, 1901. Both taxa were described in separate articles by Thomas in “The Annals and Magazine of Natural History” in 7<sup>th</sup> Series, volume 8. However, *S. b. minensis* was listed on page 534 (Thomas 1901a), whilst *S. b. paraguensis* was published in the following paper, on page 539 (Thomas 1901b). While it is unlikely that these represent the same biological species, it seems convenient *pro tempore*, while further studies are being undertaken, to use the name *Sylvilagus minensis* Thomas 1901:534 for *Sylvilagus* species south of the Amazon excluding *S. brasiliensis* as defined herein and *S. tapetillus*. To the best of our knowledge, the only name for taxa allied with *S. brasiliensis* north of the Amazon would be *S. b. sanctaemartae* Hershkovitz 1950:353. However, that taxon—our ecological modeling in Appendix notwithstanding—is

most likely restricted to the Sierra Nevada de Santa Marta. Indeed, Hershkovitz noted that, “Once the night hunter emerges from forests bordering the Cesar [–Guaimaral region] he steps abruptly into savannas, palm groves, or scrub country. Here tapitis [*S. brasiliensis*] are no longer seen, and only the eye of the cottontail [*S. floridanus*] reflects back the light of the lantern.” (Hershkovitz 1950:355). The elevation of the type locality of *S. sanctaemartae* was estimated by Hershkovitz (1950:333) to be 335 m; Caracolcito is at ca. 10°11’42.00”N, 73°58’17.78”W [datum: WGS84], elev. 155 m. The Ariguani River lies about 8 Km NNW (bearing 328°) from Caracolcito; following that river to an elevation of 335 m suggests the type locality for *S. sanctaemartae* would be at ca. 10°22’14.16”N, 73°55’26.35”W (datum: WGS84). *Sylvilagus defilippi* is from north of the Amazon, but the holotype, described by Cornalia in 1850 and at the Museo Civico di Milano, was lost in World War II; it is therefore unlikely that the taxon will ever definitively be known (there is one specimen at the Museo Nacional de Historia Natural, Madrid, identified as *S. defilippi*, it is possible that Cabrera may have had firsthand knowledge of the holotype of *S. defilippi* and based the identification on primary material). Notwithstanding, the type locality of Ecuador: Napo Province, Puerto Napo, head of navigation of the Rio Napo, (ca. 01°02’13.1”S, 77°43’4”W [datum: WGS84]), elev. ca. 417 m, suggests that this is an unlikely candidate name for the lowland *S. brasiliensis* north of the Amazon. Thus, lowland *Sylvilagus* species north of the Amazon largely do not have a name.

#### *Sylvilagus andinus* (Thomas, 1897)

The differences that we have described above in ecology, in key discrete characters, and in mensural data, support the hypothesis that the coastal lowland species from the Recife area, *Sylvilagus brasiliensis*, is specifically distinct from the taxon found in the Ecuadorean Andean Páramos and first collected in the Páramo to the west of Volcán Cayambe. This latter highland species, described by Thomas (1897:551) as *Lepus andinus*, should henceforth be known as *Sylvilagus andinus* (Thomas, 1897).

*Lepus andinus* Thomas, 1897:551, by original designation.

Type locality “W. slope of Cayambé Mountain, [Province of Pichincha, Cantón Cayambe,] Eastern Cordillera of Ecuador, altitude 4000 metres” [ca. 0°01’47.24”N, 78°01’26.89”W (datum: WGS84)].

*S. meridensis* Thomas 1904:36. Type locality: “Sierra de Merida, Venezuela.” Est. ca. 8°32’19”N, 71°5’52”W, WGS84, alt. 4000 m. Holotype, NHMUK 1904.5.14.1.

*S. fulvescens* J. A. Allen, 1912:73. Type locality Colombia: Cauca, Belén, W. Popayán, near summit of Cordillera Occidental, just N. Cerro Munchique. Est. ca. 2°31’06”N, 76°57’22”W, WGS84, alt. 3152 m. Holotype, AMNH 32360.

- S. salentus* J. A. Allen, 1913:477. Type locality Colombia, Caldas, Salento, at head of Río Quindío, W. Mt. Tolima, W. Quindío Andes, 2134 m. Est. ca. 4°38'31.6"N, 75°33'30.6"W, WGS84. Holotype, AMNH 33050.
- Sylvilagus andinus* Thomas, 1913:212. First use of current name combination.
- S. a. chimbanus* Thomas, 1913:212. Type locality Ecuador: Bolívar Province, W slope of Mt. Chimborazo, Sinche, upper Río Chimbo, just north of Guabanda. Altitude, ca. 4000 meters. Est. ca. 1°28'30.3"S, 78°54'30"W, WGS84. Holotype, NHMUK 1899.9.9.114.
- S. a. canarius* Thomas, 1913:213. Type locality "Cañar, Andes of Ecuador. Alt. 2600 m." Est. ca. 2°31'22"S, 78°58'0"W, WGS84. Holotype, NHMUK 1899.9.9.123.
- S. capsalis* Thomas, 1913:213. Type locality "San Pablo, Cajamarca, Pacific slope of N. Peru. Alt. 2000 m." W. Slope Cordillera Occidental. Est. ca. 7°6'33"S, 78°51'4"W, WGS84. Holotype, NHMUK 1900.3.15.29.
- S. nivicola* Cabrera, 1913:4. Type locality Ecuador: Pichincha Province, Mount Antisana, Cordillera Oriental, near snow line, ca. 4,800 m. Est. ca. 0°28'26.5"S, 78°7'15"W, WGS84. Holotype lost in Spanish Civil War.
- Sylvilagus andinus* Stone 1914:15. Not *Sylvilagus andinus* (Thomas, 1897). Stone acknowledged that these specimens likely represented *S. a. chimbanus*. In the transcript account from collector S.N. Rhoads (Stone 1914:15), there is evidence of ecological separation of two forms: one in the Páramo, one in the grasslands below the Páramo.
- S. kelloggi* Anthony, 1923:9. Type locality Ecuador: Provincia de Loja, Guachanamá, headwaters of the Ría Chira, 2758 m. Est. ca. 4°25'42"S, 79°13'19"W, WGS84. Holotype, AMNH 60515.
- S. chillae* Anthony, 1923:12. Type locality Ecuador: Provincia del Oro, Cordillera de Chilla, trail from Salvias to Zaraguro, 2012 m. Est. ca. 3°37'2"S, 79°30'12"W (WGS84). Holotype, AMNH 60511.
- S. apollinaris* Thomas, 1920:31. Type locality Colombia: Cundinamarca, Choachi, Cordillera Oriental, 20 Km SE Bogotá, ca. 1966 m. Est. ca. 4°31'29.5"N, 73°55'32.6"W (WGS84). Holotype, NHMUK 1919.10.15.2.
- S. nicefori* Thomas, 1921:442. Type locality Colombia: Antioquia, Cordillera Central, San Pedro, 24 Km N Medellín, ca. 2435 m. Est. ca. 6°27'50.6"N, 75°33'21.6"W (WGS84). Holotype, NHMUK 1921.7.1.26.
- Sylvilagus andinus andinus*: Hershkovitz, 1938:9. Name combination.
- S. a. carchensis* Hershkovitz, 1938:5. Type locality Ecuador: Carchi Province, Montúfar, about five miles southwest of San Gabriel, foot of the Páramos of Boliche, alt. ca. 2900 m. Est. ca. 0°33'56.8"N, 77°46'20.6"W (WGS84). Holotype, UMMZ 77062.
- S. a. chotanus* Hershkovitz, 1938:8. Type locality Ecuador: Imbabura Prov., Pimampiro, slopes of the Chota Valley, alt. ca. 1500 m. Est. ca. 0°25'13.6"N, 77°56'09.6"W (WGS84). Holotype, UMMZ 77061.

Readers interested in a more complete, but not necessarily more correct, synonymy are referred to Hershkovitz (1938, 1950). We prefer at this time to not provide a more complete synonymy on the grounds that an incorrect synonymy is worse than none at all. Establishing the species limits for *S. andinus* promises to be a long and arduous task. The taxa listed above are hypothesized by us to be in the *S. andinus* group, and nothing more. This is based on elevation and habitat only: we have not examined all the pertinent material, which should be done in order to indubitably ascertain species limits, phylogenetic relationships, and biogeography. We originally hypothesized that the named Ecuadorean highland subspecies would be found to be conspecific with *S. andinus*, as would be those from the southern Colombian Páramo. However, the molecular data presented above conclusively demonstrate that members of the "lowland" clade of *S. brasiliensis* are parapatric or perhaps even sympatric with *S. andinus* at almost the highest elevations reached by the latter in the Andes.

In his summary of the "mountain hares of the *Sylvilagus andinus* group," Thomas (1913) indicated that specimens existed in the NHMUK from Cayambe (the type locality) as well as "Guaillabamba, near Riobamba, the Paramos E. of Riobamba, and Telagua in Province Bolívar." Guaillabamba [=Guayllabamba, Pichincha Prov., Cantón de Quito, Ecuador, ca. 0°03'36.48"S, 78°20'47.09"W (datum: WGS84), 2142 m] is ca. 182 Km (straight line) distant from Riobamba [=San Pedro de Riobamba, Chimborazo Prov., Cantón de Riobamba, ca. 1°40'28.66"S, 78°38'46.1"W, (datum: WGS84), elev.: 2757 m]. These latter two localities are therefore somewhat distant from each other and both are at elevations we deem too low at this latitude for *S. andinus*. The Páramos east of Riobamba, and heights surrounding Cerro El Altar (also known as Kapak Urku, 5,319 m), may constitute more adequate habitat. More recent (1934) specimens also reside at NHMUK from Mt. Antisana (4,500 m) and Cerro de Puntas (3,950 m). Mount Antisana is the type locality of *S. a. nivicola*, and our analyses of the 12S sequences show only 1.6% sequence divergence between the two populations (Appendix 2), or ca. 1.3 MYA divergence time estimate (Fig. 35). We have yet to undertake a detailed morphological examination of these specimens.

Accordingly, the taxonomic affinities of "highland" taxa putatively associated with *S. andinus* in the past also need to be carefully evaluated in light of our findings. This would include the taxa "*canarius*," Thomas, 1913, 2600 m; "*carchensis*," Hershkovitz, 1938, 2900 m; "*chimbanus*," Thomas, 1913, 4000 m, "*ecaudatus*," Trouessart, 1910, 2930 m; "*kelloggi*," Anthony, 1923, 2758 m; and "*nivicola*," Cabrera, 1913, 4500 m. The taxa "*chillae*," Anthony, 1923, 2012 m, and "*chotanus*" Hershkovitz, 1938, are likely excluded as being described from an elevation corresponding to lower montane rain forest belt. Whether central Colombian ("*fulvescens*," Allen, 1912, 3152 m), northern Colombian ("*apollinaris*," Thomas, 1920, 1966 m, "*salentus*," Allen, 1913, 1895 m, and "*nicefori*," Thomas, 1921, 2435 m), and



Venezuelan (“*meridensis*,” 4000 m) highland taxa belong to *S. andinus* or instead are independent of *S. andinus* and *S. brasiliensis*, how far into Peru *S. andinus* extend (“*capsalis*” Thomas, 1913, 2000 m—the taxa “*inca*” Thomas, 1913, and “*peruanus*” Hershkovitz, 1950, are excluded on the basis of elevation: 890 m and 700 m, respectively), and what the altitudinal distribution of *S. andinus*, all are questions that still remain open to investigation.

*Sylvilagus tapetillus* (Thomas, 1913)

The characters that we listed above corroborate Thomas’ hypothesis that there is in fact a species level distinction between *Sylvilagus tapetillus* and *Sylvilagus brasiliensis*. Henceforth, therefore, the Rio de Janeiro dwarf cottontail should be known as *Sylvilagus tapetillus*:

*Lepus brasiliensis* Pelzeln, 1883:79. Referred to specimens from Rio de Janeiro (including Sapitiba [=Sepetiba, Rio de Janeiro, ca. 22°58’03”S, 43°42’19”W (WGS84)], Ypanema [= Ipanema, Rio de Janeiro, ca. 22°59’05”S, 43°11’53”W (WGS84)], and Caiçara, which we are unable to determine) that may constitute *S. tapetillus*. Not the specimen from Bahia.

*Sylvilagus brasiliensis* Thomas, 1901a:535. “From Porto Real, near Rezende, Rio.” Thomas clearly referred to the specimen listed as the holotype below, and suggested that during Marcgrave’s time “Rio de Janeiro was the chief settlement in this part of Brazil, it would seem best to consider the Rio animals as representing” *S. brasiliensis*. Thomas (1911) subsequently fixed Pernambuco as the type locality of *S. brasiliensis*.

*Sylvilagus tapetillus* Thomas, 1913:210, by original designation. Holotype, NHMUK 1892.11.24.3, type locality (from Thomas 1913:210): “Rio Janeiro, from Porto Real, near Rezende.” Type locality from specimen label: “Brazil: Rio de Janeiro, Porto Real, Rio Paraíba, near Rezende” Estimated coordinates, ca. 22°24’40.43”S, 44°19’14.72”W (WGS84), ca. 390 m.

*Sylvilagus brasiliensis tapetillus*: Hershkovitz, 1950:368. Name combination. Listed type locality of Thomas’ holotype as “Porto Real, Rio Parahyba, near Rezende, Rio de Janeiro, Brazil, altitude, 380 meters.”

*Sylvilagus brasiliensis tapetillus*: Vieira, 1953:130. Name combination. Cited type locality as “Porto Real, perto [*sic*] de Rezende, Estado do Rio de Janeiro.”

*Sylvilagus brasiliensis tapetillus*: de Oliveira e Silva and Dellias, 1969:524. Name combination.

*Sylvilagus brasiliensis tapetillus*: de Oliveira e Silva and Dellias, 1973:27. Name combination. Locality: São Paulo state, “imediações do km 125 da Estrada Estadual São Jose dos Campos—Campos do Jordão” [vicinity of Km marker 125 on the State Road from São Jose dos Campos to Campos do Jordão]. Estimated coordinates on SP–050, near

Monteiro Lobato, ca. 22°57’18”S, 44°50’19”W (WGS84), ca. 682 m. Possibly *S. tapetillus* or, more likely, taxon allied to that represented by FMNH 52350.

The discerning reader will have noted that our synonymy differs from that of Hershkovitz (1950:368) and Vieira (1953:130) for the same species. Both Vieira (1953) and particularly Hershkovitz (1950) listed numerous records of *Lepus brasiliensis* from Rio de Janeiro and São Paulo as synonymous with *S. tapetillus* (as *S. brasiliensis tapetillus*). However, we showed above that the young female, FMNH 26877, upon which Hershkovitz based his opinion that the holotype of *S. tapetillus* was not an adult, is in fact quite distinct, and likely represents a different species. By the same token, FMNH 20972 and 52350, which we also have not seen, differ in their markedly larger size from *S. tapetillus*, and should therefore most likely not be considered conspecific with the latter. Moreover, the locality of FMNH 52350 is over 430 Km from the coast and is isolated from the coastal plain by a steep, rugged serrania, reaching upwards of 880 m in elevation. In addition, one of us has had occasion to examine specimens from the Rio de Janeiro area in the collection of Brazil’s National Museum of Natural History, Universidade Federal de Rio de Janeiro. These will form the basis of a future work, however, there is strong morphological evidence among those specimens of the presence of multiple species in the Rio de Janeiro area, segregated by elevation within very short geographic distances. This variation merits further scrutiny, but suggests that only the lowland cottontails in Rio de Janeiro will be found to be *S. tapetillus*, and that they may have at one time coexisted with other *Sylvilagus* species (e.g., FMNH 20972, also from Rio de Janeiro). Two additional specimens likely referable to *S. tapetillus* are in the collection of the Naturalis, Leiden; neither specimen is catalogued: one is an adult collected by Hardy du Dréneuf in 1890 in Porto Real, the other is a juvenile also collected by H. du Dréneuf in Porto Real in 1892. Both appear to have the skulls contained in the skins.

Given the high human population density in the putative type locality area, and the current degraded nature of the habitat in and around Rio de Janeiro, we suggest that *S. tapetillus* may be extinct. One recent survey of the coastal mammal fauna in the state of Rio de Janeiro noted that increased immigration, urbanization, and road networks had affected coastal mammal populations, particularly medium-sized and larger species that were of greater hunting value and less able to cope with increasing urban and road densities (Pessôa *et al.* 2010). Notwithstanding, novel species of smaller mammals are still being added to the regional fauna, including species of *Cerradomys* (Pessôa *et al.* 2010) and *Trinomys* (Tavares & Pessôa 2010, Tavares *et al.* 2015). Tavares *et al.* (2015) in particular noted that the faunal peculiarities of the region dictated that it should be considered a priority for conservation. Brandão (2015) reported a similarly restricted fauna for the

state of São Paulo, with the sigmodontines *Abrawayomys ruschii*, *Phaenomys ferrugineus*, and *Rhagomys rufescens*. The Atlantic Rainforest, and in particular the southern extremity of that biome that covers the states of São Paulo and Rio de Janeiro, may contain at least 39 species of sigmodontine rodents in 23 genera that are restricted to that biome type. Thus, the potential that *S. tapetillus* still exists, as Bonvicino *et al.* (2015) have suggested, together with the rich endemic fauna of rodents alluded to above, as well as endemic species of primates and didelphids, enhances the conservation value of the Rio de Janeiro region.

#### ACKNOWLEDGEMENTS

Portions of this work were carried out under the auspices of NSF grant DEB-0616305 to LAR and JSB. SMS was funded under the auspices of a fellowship from the Programa Nacional de Pós Doutorado/Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (PNPD-CAPEs) at the Department of Zoology in the Museu Paraense Emílio Goeldi/Universidade Federal do Pará (PPGZOO/MPEG/UFPA). Laboratory work in Brazil by SMS was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), process no. 447460/2014-5. LAR thanks Diego Astúa de Moraes, the Curator of Mammals at the Laboratório de Mastozoologia, Departamento de Zoologia, Universidade Federal de Pernambuco, for kindly allowing access to the specimens under his care, and for answering the many questions that remained unanswered (sometimes even unasked) after the initial work had been undertaken in Recife. This work also greatly benefitted from examination of the *Sylvilagus* material at the National Museum of Natural History, Universidade Federal de Rio de Janeiro, under the curatorship (Departamento de Vertebrados, Mastozoologia) of João Oliveira. LAR thanks M. Campbell for kindly providing lodging for the length of that visit. Conversations in that museum with A. Feijó were particularly fruitful and stimulating. We gratefully acknowledge loan 2072421 of the Smithsonian Institution, National Museum of Natural History of (still somewhat mysterious) *Sylvilagus* material from Ecuador. Comparisons of the Brazilian material with type material at The Museum of Natural History, London, under the care of Mammal Group Curator Roberto Portela Miguez (Life Sciences—Vertebrate Division), proved invaluable. Fascinating discussions with Fernando Palacios in the course of those visits constituted an education unto themselves. J. R. Wible's magisterial monograph on lagomorph cranial morphology was of great assistance, as was J. R. Wible himself with questions regarding particular cranial characters. J. H. Wahlert (American Museum of Natural History) likewise contributed to the lively discussion on morphological characters, particularly on cranial foramina. We thank R. P. Anderson for helpful discussions on ecological niche modeling, resulting in a better final product. Reviews of previous drafts from A. L. Gardner and F. Palacios, who have extensive knowledge of

the literature and the material (and a discerning eye), greatly improved the quality of the manuscript. LAR thanks J. E. Podrabsky (Chairman), the Department of Biology, and Portland State University, for enabling the freedom to pursue this work.

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**DIGITAL MATERIALS:**

**Appendix I, II and Supplementary Materials** have uploaded to Deep Blue (<http://deepblue.lib.umich.edu/>) is an online storage service employed by the University of Michigan for archiving and accessing research materials.