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Morphological and chromosomal taxonomic assessment of *Sylvilagus brasiliensis gabbi* (Leporidae)

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Abstract

The cottontail rabbit species, *Sylvilagus brasiliensis*, is currently understood to be constituted by 18 subspecies ranging from east central Mexico to northern Argentina, and from sea level to at least 4800 m in altitude. This hypothesis of a single widespread polytypic species remains to be critically tested. In other species groups of *Sylvilagus* from other geographic areas, the use of chromosomal information has been important in delineating taxonomic boundaries. To date, however, no chromosomal data are available for *Sylvilagus* south of Mexico. Here we report the chromosomal complement of two individuals (a male and a female) putatively ascribed to *Sylvilagus brasiliensis* on the basis of morphological characters and collected from southern Península del Azuero in Panama. The diploid number (2n) of these two individuals was 38 and the fundamental number (autosomal arms, aFN) was 72. Karyotypes of *S. brasiliensis* from southern Mexico have reported two chromosomal forms: 2n=36, FN=68 and 2n=40, FN=76. We complement the chromosomal data with a morphological examination of the Panama specimens and of holotype materials pertinent to the taxonomic identity of Mesoamerican taxa of *Sylvilagus*. These findings, in association with others regarding the phylogenetic relationships of *Sylvilagus* from the Neotropics, reinforce the idea that the current taxonomic treatment of the species merits critical scrutiny. In particular, we excise *Sylvilagus gabbi* from subspecific synonymy with *S. brasiliensis* and remove the subspecies *truei* from *brasiliensis* to *gabbi*.

Keywords: Central America; cytogenetics; Panama; *Sylvilagus*; *Sylvilagus brasiliensis*; *Sylvilagus gabbi*; systematics; taxonomy.

Introduction

In the last major revision of South American cottontail rabbits, *Sylvilagus*, Hershkovitz (1950) summarized the taxonomy of the genus recognizing only two valid species in South America: *S. floridanus* and *S. brasiliensis*. In the latter, he recognized 29 subspecies distinguishable by variation in morphology and pelage. Currently, 18 subspecies are recognized (Hoffmann and Smith 2005). *Sylvilagus brasiliensis* as thus construed is distributed from east central Mexico to northern Argentina at elevations from sea level to 4800 m, inhabiting biomes ranging from dry Chaco, through mesic forest, to highland Páramo (Figure 1).

Most of the junior synonyms of *S. brasiliensis* currently represent South American taxa, with Mesoamerican forms grouped into only two recognized subspecies: *S. b. gabbi* and *S. b. truei* (Hoffmann and Smith 2005). Based on specimens from Costa Rica and Panama, Allen (1877) described *Lepus brasiliensis* var. *gabbi*, which subsequently was raised to species status (*Lepus gabbi*) by Alston (1882) based on “differences in lengths of ear and tail between Central American and Brazilian (cottontails)”. Lyon (1904), with no further comment, included *S. gabbi* as a valid species in *Sylvilagus*, together with numerous other Central and South American taxa currently considered conspecific with *S. brasiliensis*. Nelson (1909) also recognized *S. gabbi* as a distinct species, designated a lectotype, and restricted the type locality to Talamanca, Costa Rica. Hershkovitz (1950), without apparent justification, restricted the type locality further to Talamanca, Sipurio, Río Sixaola, near the Caribbean coast, Costa Rica. Gureev (1964) also recognized *S. gabbi* as a valid species in his revision.

Few investigators have tackled the taxonomic morass of South and Mesoamerican *Sylvilagus*. The Central American Páramo *S. b. dicei* was excised from *S. brasiliensis* by Diersing (1981) based on a unique combination of ecological habitus and range of body sizes. A new species from lowland Venezuela, putatively with affinities to *S. floridanus*, was recently described by Durant and Guevara (2001). With respect to the taxonomy of Central American *brasiliensis*, Diersing (1981) made great progress using morphometric data, synonymizing the multiple nominal taxa described from Panama (*L. incitatus* Bangs 1901; *S. g. messorius* Goldman 1912; *S. g. consobrinus* Anthony 1917) and Nicaragua (*L. g. tumacus* Allen 1908) with *S. b. gabbi*. Of additional interest is the fact that the two subspecies of *S. brasiliensis* that he recognized in Mesoamerica (*S. b. truei* and *S. b. gabbi*) are diagnosable based on morphometric characters. In fact, McCarthy (2000) used the discriminant factors identified by Diersing (1981) to define the geographic distributions of the two taxa in a very narrow band between Guatemala and Belize. These studies relied on morphometric variation or generalized patterns of coloration; so far, chromosomal, molecular, or qualitative morphological characters have not been used to address species limits – let alone phylogenetic hypotheses – within this group of Neotropical rabbits. The foregoing all point to a recurrent biological conclusion: the taxonomic history of Central American *Sylvilagus* is one of uncertain, unstable, and untested species limits. Robust boundaries are

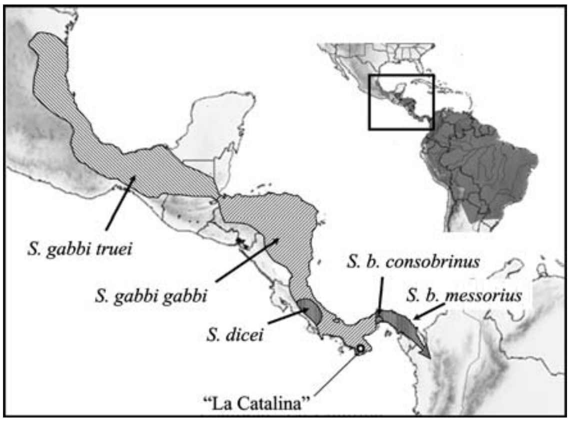

Figure 1 Distribution in Central America of *Sylvilagus brasiliensis sensu* Hoffmann and Smith (2005) (inset) and distribution of *Sylvilagus gabbi* (adapted from Diersing 1981) and Mesoamerican taxa associated with *S. brasiliensis*. Also shown is the collection locality for NK 116979 and NK 116980 (Estancia “La Catalina”, Provincia Los Santos, Panama, 5.7 miles east of Tonosí, 34 m a.s.l., 7°26.99′ N, 80°22.19′ W, GPS datum 84).

needed among these taxa to arrive at effectual hypotheses of historical biogeography, ecology, evolutionary relationships, and management and conservation strategies.

In particular, incorporating the types of data previously used with success in other geographic areas and groups of rabbit species should provide further insight into these questions in Mesoamerica. Two sources of data have proven especially useful in addressing systematic and taxonomic questions in cottontails: crown enamel patterns of the third lower premolar, p_3 (Hibbard 1963, Dalquest 1979, White 1987, 1991, Dalquest et al. 1989, White and Morgan 1995, Ruedas 1998), and the study of chromosomal information (Robinson et al. 1983, 1984, Ruedas et al. 1989, Ruedas and Elder 1994). The latter suggested that chromosomes in *Sylvilagus* are good predictors of reproductive isolation and representative of individuals in distinct species. The only chromosomal information available for taxa in the *brasiliensis* group are two reports purportedly of *S. b. truei* from Mexico: one individual from Puebla (Guereña-Gándara et al. 1983) and one from Chiapas (Lorenzo and Cervantes 1995).

Our purpose in this contribution is to combine the use of qualitative morphological characters (crown enamel patterns of p_3) with chromosomal information to address the systematic and taxonomic affinities of *S. b. gabbi*.

Materials and methods

Information obtained from newly collected material (chromosomal data and qualitative dental characters) complemented that of Diersing (1981) in addressing the specific status of *S. b. gabbi*. An attempt was made to compare the morphology of specimens trapped in Panama with type specimens and representative series of the following taxa, either formally associated with *S. brasiliensis* at the specific level (*aquaticus*, *insonus* and *palustris* within the subgenus *Tapeti*), or geographically proximate subpecific taxa within *brasiliensis* (*consobrinus*, *gabbi*, *messorius*, *incitatus*, and *tumacus*).

Specimens used in these analyses were either collected fresh in the field (catalogued at the Natural Sciences Research Laboratory, Texas Tech University), or examined in the following institutions: US National Museum (USNM), Museu Nacional (Rio de Janeiro, MN), and Museum of Vertebrate Biology (MVB), Portland State University. Cell suspensions and test slides for fresh specimens collected in the field are housed at the Natural Sciences Research Laboratory, Texas Tech University.

Chromosomes and karyology

Chromosome preparations were obtained from bone marrow following procedures outlined by Patton (1967). Standard karyotypes were constructed for one male (NK 116979) and one female (NK 116980) from Panama (Estancia “La Catalina”, Provincia Los Santos, 5.7 miles east of Tonosí, 34 m a.s.l., 7°26.99′ N, 80°22.19′ W, datum WGS84). Diploid number (2n) was determined based on a minimum of 20 equal-numbered metaphase spreads per animal. The fundamental number (FN) was calculated according to Patton (1967) and was based on the autosomal count (aFN) of 15 photographed spreads.

Morphological analyses

The dentition of holotypes of *S. b. gabbi* (USNM 37794), *S. b. messorius* (USNM 179569), and of a topotype (MN 3445) and probable topotypes (MN 24034, 24035, and 24041) of *S. brasiliensis* (from Pernambuco) was examined and illustrated using a *camera lucida* microscope. The types of *S. gabbi* (USNM 37794 [skin 11371], lectotype, and 37793, syntype) were also illustrated using a *camera lucida* microscope; syntype USNM 11372 is a skin in very poor condition with the skull not removed; this specimen was observed but was not critically examined. Dentition of a topotype of *S. palustris* (MVB 4001) and of the Panama *Sylvilagus* specimens was photographed using a Leica DFC 320 digital camera (Wetzlar, Germany) mounted on a Leica MZ12.5 microscope; the images were captured and preprocessed using Leica IM50 Image Manager and enhanced using Photoshop® (Adobe Systems Inc., San Jose, California, USA). Crown enamel patterns were traced using Canvas™ 8.0 (ACD Systems of America, Inc., Victoria, British Columbia, Canada). Dental characters of p_3 were assessed as described by Ruedas (1998).

Results

Chromosomal analysis

Analysis of cell spreads of the individuals from Estancia La Catalina, Panama, showed a chromosomal complement of entirely metacentric and submetacentric chromosomes, resulting in a diploid number of 38 and an autosomal fundamental number of 72. The complement includes eight pairs of large autosomes and 10 medium to small pairs of autosomes gradually decreasing in size. The X chromosome is medium sized and submetacentric

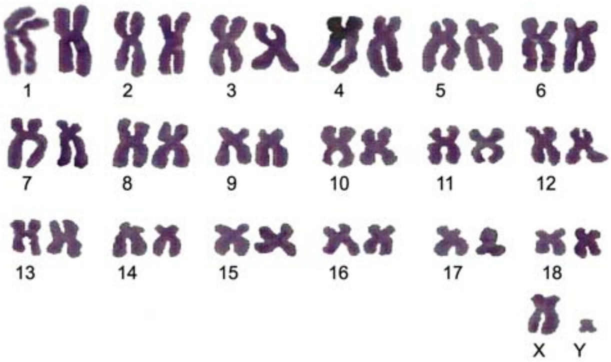

Figure 2 Standard karyotype of *Sylvilagus brasiliensis gabbi* (NK 116979) from Estancia "La Catalina", Panama. 2n=38, FN=72.

and the Y chromosome is minute and biarmed, and is likely also submetacentric (Figure 2). No secondary constrictions or satellite chromosomes were evident.

Morphology of the third lower premolar, p_3

The third lower premolars, p_3, of the specimens examined, all of which are putatively identified as *S. brasiliensis*, were in fact characterized by distinct, species-level differences allowing discrimination of at least two species (Figure 3). The series of nominal *S. brasiliensis* from the MN displays a more derived enamel pattern, as determined from characters employed by Ruedas (1998). In particular, the anterior surface shows weak to almost no anterior reentrant and the caudal surface of the posteroexternal reentrant is smooth, without crenulations. Only one of the MN series displays an anterointernal reentrant, and it is weak and shallow. The central angle on the anterior surface of the posteroexternal reentrant is weak to non-existent. The variability in the disposition of thick enamel on the posterior lamina, particularly on the external surface fold, is sufficient to warrant further population-level examination: five specimens of *S. floridanus* (holotype, *S. f. floridanus*, and *S. f. mallurus*), and three topotypes of *S. a. audubonii* examined by Ruedas (1998) showed no variation in this character, but *S. robustus* displayed some variation (absent in 1/5). In contrast to the foregoing condition, the Panama specimens display multiple, strong anterior reentrants, multiple, strong anterointernal reentrants, and a central angle in the anterior surface of the posteroexternal reentrant crenulation (weak in NK 116979, strong in NK 116980).

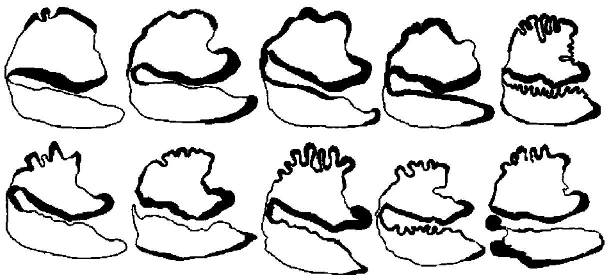

Figure 3 Enamel pattern on lower premolar three (p_3) of selected individuals in some of the taxa under consideration. All teeth not to scale to emphasize shape differences. Orientation: occlusal view, anterior at top, labial to right. Top row, left to right: *Sylvilagus brasiliensis*, Museu Nacional, Universidade Federal do Rio de Janeiro (MN 3445), topotype; MN 24034, MN 24035, MN 24041; *S. palustris*, MVB 4001, topotype. Bottom row, L–R: *S. gabbi messorius*, USNM 179569, holotype; *S. gabbi*, USNM 37794, lectotype, Talamanca, Costa Rica; NK 116979 and NK 116980, from Panama; *S. gabbi*, USNM 37793, syntype, also from Panama.

These characters are sufficient to discriminate among *S. audubonii*, *S. floridanus*, *S. robustus*, and *S. nuttallii*. In addition, since *S. brasiliensis* has been associated in the subgenus *Tapeti* (Gray 1867, *sensu* Gureev 1964) by Hershkovitz (1950) with *S. aquaticus* and *S. palustris* (as well as *S. varynaensis*, and possibly *S. insonus* and *S. dicei*), we show a comparison of one topotype of *S. palustris* (MVB 4001) with the Panamanian specimens, as well as with *S. brasiliensis*, and the holotypes of *S. gabbi*, and *S. g. messorius* (Figure 3). As in the Panamanian *Sylvilagus*, this specimen shows strong, multiple anterior reentrants and strong, multiple anterointernal reentrants. The crenulation in the caudal surface of the posteroexternal fold is stronger than that of the Panama specimens, but a second topotype (MVB 4002, not illustrated) is similar in this character to NK 116980. Unlike *S. brasiliensis*, there is a strong anteroexternal reentrant, multiple in MVB 4001, singular in MVB 4002; this is the same condition as found in the Panama specimens. In contrast, the anteroexternal reentrant of *S. brasiliensis* is weak to barely perceptible, or, when visible, extremely shallow (e.g., MN 3445).

Discussion

Comparison of our chromosomal data with those already published for *S. brasiliensis* and other *Sylvilagus* species shows a high level of variation within this group (Table 1). The karyotype presented by Guereña-Gándara et al. (1983) of an individual of *S. b. truei* from Puebla consisted of 22 metacentric autosomes, six submetacentric autosomes, and six subtelocentric autosomes (2n=36, FN=68). The X chromosome of their specimen was metacentric and the Y chromosome was subtelocentric (although their figure of the same is equivocal in this respect and could be interpreted as submetacentric). The karyotype presented for the same nominal taxon by Lorenzo and Cervantes (1995) of a specimen from Chiapas had a diploid number of 40 constituted by eight metacentric, 12 submetacentric, and 18 subtelocentric autosomes, resulting in FN=76. The X chromosome was metacentric and the Y chromosome was acrocentric. Our specimens from Panama displayed a karyotype of 2n=38, aFN=72.

The argument could be made in the present instance that the difference between the three karyotypic forms of *S. brasiliensis* are trivial, being due to simple Robertsonian events leading to an additional pair of autosomes in the Panama specimen (putatively *S. b. gabbi*) and two additional pairs in the Chiapas specimen. However, even in the absence of banding data, the presence of a fully biarmed complement in the Panamanian and Chiapas specimens rules out Robertsonian events as the sole dis-

Table 1 Diploid and fundamental numbers for chromosomally characterized taxa of *Sylvilagus*.

Species	2n	FN	Locality	Source
S. audubonii	42	72	California, USA	Worthington and Sutton 1966
S. aquaticus	38	72	Cameron Parish, LA, USA	Robinson et al. 1983, Ruedas and Elder 1994
S. bachmani	48	80	Benton County, OR, USA	Worthington 1970
S. brasiliensis	36	68	Cuetzalan, Puebla, Mexico	Guereña-Gándara et al. 1983
S. brasiliensis	38	72	Peninsula del Azuero, Panama	This report
S. brasiliensis	40	76	Chiapas, Mexico	Lorenzo and Cervantes 1995
S. cunicularius	42	72–74	Parres, D.F., Mexico	Lorenzo et al. 1993
S. floridanus	42	74–80	Connecticut, USA; D.F, Mexico	Holden and Eabry 1970, Lorenzo et al. 1993
S. graysoni	42	78	Tres Marías Islands, Mexico	Diersing and Wilson 1980
S. nuttallii	42	72	California, USA	Worthington and Sutton 1966
S. palustris	38	68	Halifax County, NC, USA	Robinson et al. 1984
S. obscurus	46	84	Garret County, MD, USA	Robinson et al. 1983, Ruedas et al. 1989
S. mansuetus	48	80	San Jose Island, Mexico	Cervantes et al. 1996
S. transitionalis	52	94	Mansfield County, CT, USA	Holden and Eabry 1970, Ruedas et al. 1989

tinction between the karyotypes of these specimens. According to the criteria of any of the numerous contemporary species concepts, the chromosomal data therefore provide strong *prima facie* evidence that the two taxa constitute distinct species, given that the differences would preclude sister chromatid pairing in prophase leading to genetic isolation from the inability to produce fertile offspring.

The question remains as to the taxonomic identity of the taxon from Panama chromosomally characterized in the present study. We lack complete data sets on all taxa under consideration, but we can begin an assessment of the question. The most pressing and basic question undoubtedly must be: "What is *S. brasiliensis*?" This remains a difficult question. When described by Linnaeus in the order Glires, family Lepus, diagnosis of the species was *cauda nulla* (no tail) and the range was noted as *America meridionalis*, i.e., South America. All *Sylvilagus* species known have a tail, albeit short – the only lagomorph without an external tail is *Ochotona* – and the distribution of *S. brasiliensis* extends from Mexico to Argentina. It might therefore be argued that, given the diagnosis and distribution specified by Linnaeus, there is no such species as *S. brasiliensis*.

Oldfield Thomas (1911) was the first to explicitly deal with the species problem in *S. brasiliensis* by restricting the type locality to Pernambuco, Brazil (Tate 1933). However, Allen (1877), in his description of *L. brasiliensis* var. *gabbi*, had already noted that "the differences [between Costa Rican and Paraná, Brazil, specimens] are so striking that at first I was inclined to regard the Costa Rican specimens as specifically distinct from the South American *L*[*epus*] [sic] *brasiliensis*…" It was only after further consideration (Allen 1877) that he decided to treat the Costa Rican specimens as merely subspecifically distinct, to wit: *S. b. gabbi*.

Examination of the enamel pattern on lower premolars of specimens of *S. brasiliensis* from Pernambuco and the study specimens from Panama (see results; Figure 3), as well as holotypes of nominal taxa from near where the Panama specimens were obtained, supports Allen's initial observation that *Sylvilagus* from the area near Panama represent a species-level taxon clearly distinct from *S. brasiliensis* both from Pernambuco and any of those potentially examined by Allen. In addition to the dental characters described above, cranial features unite the Panama specimens with *S. gabbi* and allied taxa. These include a strongly rounded lacrimal aspect of the orbital fossa (vs. angular), a dorsoventrally flattened jugo-squamosal aspect to the zygomatic arch (vs. angled), a relatively shallow rostrum (dorsoventrally) vs. relatively deeper, a smaller vs. larger auditory bullae, and relatively narrow infraorbital foramina vs. larger caudad and coming to a point craniad. This suite of characters distinctly sets apart *S. floridanus* from Mesoamerican *Sylvilagus* formerly in the *S. brasiliensis* species group (Figure 4). In addition, with specific reference to the distinction between *S. gabbi* and *S. brasiliensis*, examination of the cranium of the holotype of *S. gabbi* and comparison with topotypes of *S. brasiliensis* (Figure 4) suggests that cranial differences likewise support a species-level distinction. In particular, the frontonasal suture, sloping and shallow in *S. gabbi* vs. sharp and deep in *S. brasiliensis*, the shape and relative breadth of the rostrum, the conformation of the palatine foramina (parallel in *S. gabbi* and ending at a line drawn across the skull at the anterior surfaces of the upper premolar 2 [P^2], but largely broadening in a posterior direction and ending at a line drawn across the skull between the posterior margins of P^2 and anterior margins of P^3 in *S. brasiliensis*), and the relative anteroposterior breadth of the palatine bridge are all sharply distinct between the specimens of the two species we examined.

Based on the foregoing suites of characters, we recommend excision of *S. gabbi* Allen 1877 from *S. brasiliensis*, and assign our Panama specimens to *S. gabbi*. Although numerous nominal taxa have been described within the geographic range of what we understand as that of *S. gabbi*, Diersing (1981) found no support for subspecific recognition between forms from Costa Rica, Nicaragua, Panama, and Honduras. However, the subspecies formerly recognized in *S. gabbi*, including *S. g. tumacus* Allen 1908 from Nicaragua, *S. g. consobrinus* Anthony 1917 from Panama, *S. g. dicei* Harris 1932 from Costa Rica, and *S. g. messorius* Goldman 1912 from eastern Panama, will require further examination using morphological, chromosomal, and molecular data to definitively assess their taxonomic status with any degree of confidence.

Although there are still relatively few specimens of *S. gabbi* – a situation that must be remedied to critically test our hypotheses – an assessment of the morphology of

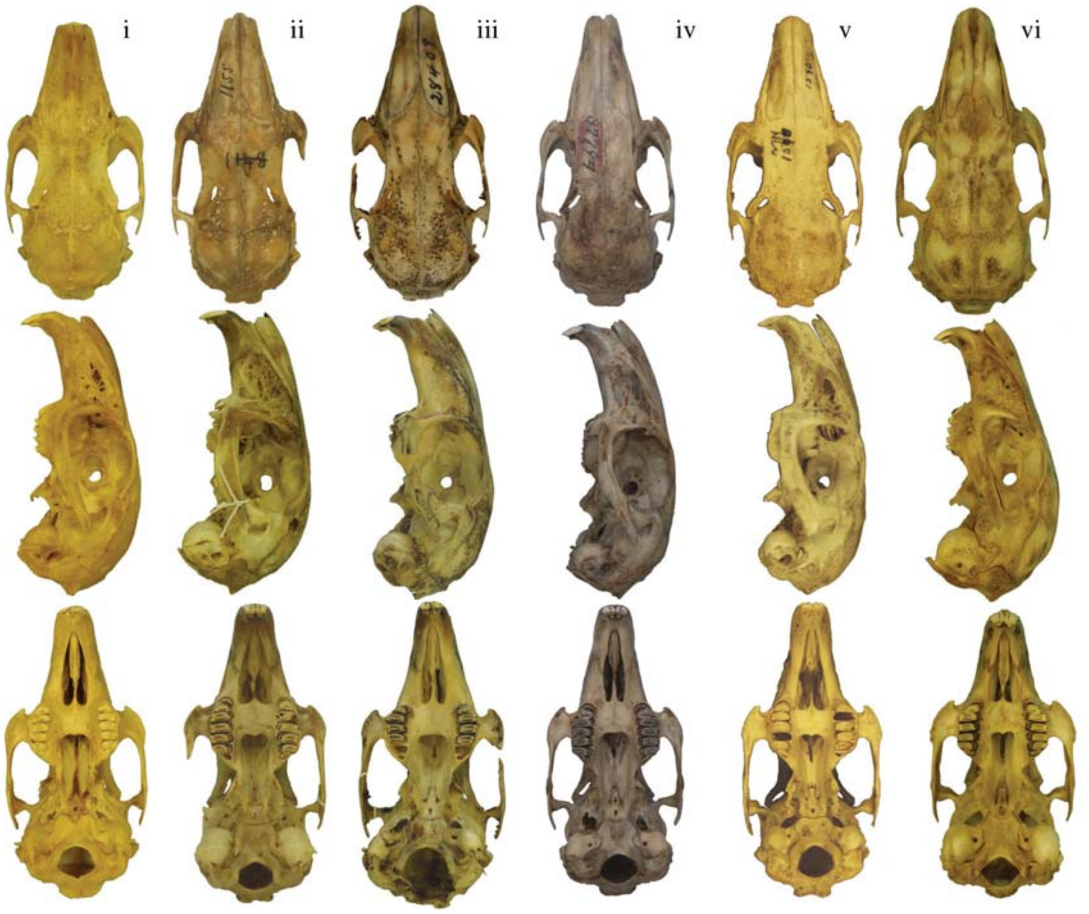

Figure 4 Dorsal (top row), lateral (center row), and ventral (bottom row) aspects of crania of *Sylvilagus* taxa pertinent to the present study. Skull are not to scale to emphasize shape differences. (i) NK 116980, *S. gabbi* from Panama, greatest length of skull (GLS) 65.9 mm; (ii) *S. floridanus* AMNH 1890/1155, holotype, GLS 66.7 mm; (iii) *S. gabbi tumacus*, AMNH 28409, holotype, GLS 62.9 mm; (iv) *S. gabbi*, USNM 37794, lectotype, GLS: 70.4 mm; (v) *S. brasiliensis*, MN 1540, near topotype (Pernambuco), GLS 73.5 mm; (vi) *S. palustris* MVB 4001, topotype, GLS 71.1 mm.

p_3 in this taxon is possible: the lectotype (37794) is, in a number of dental characters, qualitatively different from syntype USNM 37793, as well as from our own specimens from the Azuero Peninsula of Panama. Additional specimens are still required to fully explore this question from the point of view of morphology: over 100 years later, we echo the still valid comments of Lyon (1904): “These differences may be purely individual, or may indicate that the Panama specimens represent a recognizable form. This can be determined only when a series from Costa Rica [and Panama] is available for comparison.”

In view of the incorrect diagnosis of the putative species *S. brasiliensis* by Linnaeus (1758), and based on the disposition of characters displayed by the *Sylvilagus* taxa examined for this study, as well as by Ruedas (1998), we restrict *S. brasiliensis*, pending examination of additional specimens, to lowlands in the area circumscribed by the Amazon River to the North, the Andes to the West, and the Paraná and Salado rivers to the South. This remains a huge geographic area constituted by numerous biotopes. We are confident that examination of further specimens from within this geographic range will eventually yield additional taxa.

The dental characters employed by Ruedas (1998) in his study of Southwestern United States *Sylvilagus* were sufficient to discriminate among species and elucidate phylogenetic trends among the species examined in that study. In the present case, and for the taxa under consideration, the characters used in regard to p_3 remain sufficient for taxonomic purposes (i.e., identification), but are clearly insufficient for phylogenetic inferences, especially in view of the large number of nominal subspecies synonymized under *S. brasiliensis*. In the same study, Ruedas (1998) showed that the plesiomorphic character state of p_3 was the presence of a very complex enamel pattern. This character state is present in *S. gabbi* and supports a Mesoamerican origin for *Sylvilagus*, *contra* Hershkovitz (1972), who hypothesized a boreal origin for the genus. More derived species lose the complexity of the enamel pattern of p_3, a condition evident in both *S. floridanus* and *S. brasiliensis*.

Nevertheless, our data do not necessarily preclude a boreal origin for *S. brasiliensis*: data in the present work are based on characters for crown enamel alone. These data alone do not show similarities between *S. brasiliensis* and *S. aquaticus*, similarities that would be required to accept the broader conception of the subgenus *Tapeti* of Gureev (1964). A critical assessment using additional – and alternative – data is nevertheless required to test the relationships we have identified, as well as potential alternatives, given that the biogeographic consequences are important: no *Tapeti* is definitively known from Mesoamerica, although *S. dicei* has been hypothesized to be a member of this subgenus. In the absence of intermediates, two biogeographic hypotheses ensue: (1) *Tapeti* were widespread from southern North America to South America, but became extinct in the intervening regions; or (2) *S. brasiliensis* and the North American *S. palustris* and *S. aquaticus*, contrary to our dental data, really do represent reciprocally monophyletic sister taxon groups, and their current distribution is the product of rafting from South America (origin of *S. palustris* and *S. aquaticus* in *S. brasiliensis*) or from North America (origin of *S. brasiliensis* in *S. palustris* or *S. aquaticus*). Alternatively, the morphological conception of *Tapeti* is erroneous. Molecular data will be key in confirming the most likely of these hypotheses.

We further hypothesize that South America will be found to contain at least as many species of *Sylvilagus* as there are in North America. Only a much larger craniodental data set or, more robustly, sequence data from mitochondrial or nuclear genes, will yield a clear picture of the evolutionary trends and biogeography of the morphologically orthodox – but equally cryptic – leporid genus *Sylvilagus*.

Taxonomy

Sylvilagus gabbi (J.A. Allen)

Lepus brasiliensis var. *gabbi* Allen 1877; type locality, Talamanca, Costa Rica and Chiriquí, Panama. Restricted to Talamanca, Costa Rica by Nelson (1909); amended to Talamanca, Sipurio, Río Sixaola, near the Caribbean coast, Costa Rica by Hershkovitz (1950). Sipurio, Limón Province: 9°31′60″ N, 82°55′0″ W, 195 m a.s.l.

Lepus gabbi Alston 1882.

Lepus truei J.A. Allen 1890; type from “Mirador,” Veracruz (exact site unknown).

Lepus (Tapeti) incitatus Bangs 1901; type locality, San Miguel Island, Bay of Panama, Panama (8°27′26″ N, 78°56′13″ W, sea level).

Lepus gabbi tumacus J.A. Allen 1908: 649; type locality Tuma, Nicaragua (Departamento Matagalpa, 13°4′0 N, 85°45′0 W, 341 m).

Sylvilagus gabbi Lyon 1904.

Sylvilagus gabbi messorius Goldman 1912; type locality, Cana, 1800 ft (549 m) a.s.l., mountains of eastern Panama.

Sylvilagus gabbi consobrinus Anthony 1917; type locality, Old Panama (near city of Panama), Panama.

Lectotype: USNM 11371/37794, adult male, skin and skull from Talamanca, Costa Rica.

Distribution: Eastern Guatemala and Honduras, south through eastern Nicaragua, northeastern Costa Rica, and throughout Panama (Diersing 1981, McCarthy 2000).

Diagnosis: smallest species of Central American *Sylvilagus*; small body size, short ears, short hind feet, and short tail. Color is variable, ranging from near blackish to blackish-brown dorsally, sides and tail only slightly paler than dorsum; tail uniformly brown, not bicolored; venter whitish except for a dark brownish throat patch; cranium small, narrow braincase; small auditory bullae; short nasals; proportionally large mandibular toothrows.

Comments: inclusion of *truei* in *gabbi* is not warranted without explanation. We have not examined the holotype of *S. truei* (USNM 6357/34878). However, conspecificity of *truei* with *brasiliensis* would require hypothesizing an allopatric distribution for populations of *brasiliensis*: allopatry interrupted by *gabbi*. It is more parsimonious to hypothesize *pro tempore* that *truei* and *gabbi* are conspecific, at least until such time as a careful examination of the holotype of *truei* is undertaken. In the interim, since the name *gabbi* (1877) has precedence over *truei* (1890), the taxon would be construed as *Sylvilagus gabbi truei*. It should be clear from the present study, however, that this is a taxonomic hypothesis requiring rigorous testing.

Specimens examined

S. gabbi, NK 116979, NK 116980; Estancia “La Catalina”, Provincia Los Santos, Panama, 5.7 miles east of Tonosí, 34 m a.s.l. (7°26.99′ N, 80°22.19′ W).

S. brasiliensis, MN 1540, topotype, Pocao, Pernambuco, Brazil, -8.1833333° (latitude), -36.7° (longitude), 3480 ft. (1061 m) a.s.l., skull only; MN 3445, topotype, Pernambuco; MN 24034, 24035, 24041.

S. b. gabbi, USNM 37794 (lectotype), Talamanca, Costa Rica; USNM 37793 (syntype), Chiriquí, Panama.

S. b. messorius, USNM 179569, holotype, Cana, Panama, 1800 ft. (549 m) a.s.l., mountains of eastern Panama.

S. palustris, MVB 4001, topotype, eastern South Carolina, less “than forty miles from the sea coast”.

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