ANARTIA

UNIVERSIDAD DEL ZULIA · Serbiluz Sistema de Servicios Bibliotecarios y de Información · Biblioteca Digital Repositorio Académico

Publicación del Museo de Biología de la Universidad del Zulia
ISSN 1315-642X (impresa) / ISSN 2665-0347 (digital)

https://doi.org/10.5281/zenodo.13755829 / *Anartia, 38 (junio 2024): 23-44*

http://zoobank.org/urn:lsid:zoobank.org:pub:75873A56-5383-42BE-8F68-F02E0571F35E

A new subspecies of *Conepatus semistriatus* (Boddaert, 1784) (Mammalia, Carnivora, Mephitidae) from Venezuela, and the first known case of insular dwarfism in living skunks

Una subespecie nueva de *Conepatus semistriatus* (Boddaert, 1784) (Mammalia, Carnivora, Mephitidae) de Venezuela, y el primer caso conocido de enanismo insular en mofetas vivientes

Jesús Molinari[1], María R. Abarca-Medina[2] & Belkis A. Rivas-Rodríguez[1]

[1]*Departamento de Biología, Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela*
[2]*Departmento de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas 1020, Venezuela*

Correspondencia: jmvault@gmail.com

(Received: 21-06-2024 / Accepted: 24-07-2024 / On line: 12-09-2024)

ABSTRACT

The Striped Hog-nosed Skunk, *Conepatus semistriatus* (Boddaert, 1784), is distributed from southern Mexico to northern Peru. It is one of the least studied carnivorans of the New World. Not even basic morphometric information exists for the species. This study assesses the taxonomic status of the Striped Hog-nosed Skunk occurring on Margarita Island, off the coast of eastern Venezuela. Multivariate analyses of 25 cranial measurements revealed the Margaritan skunk to be much dwarfed with respect to its nearby mainland congener, thus complying with the 'island rule', which predicts that under insular conditions large continental animals become smaller, and small continental animals become larger. The craniometric differences between the Margaritan and mainland skunks are of similar or greater magnitude to those found in interspecific comparisons within genera of several carnivoran families. Geographic variation in cranial size was not evident within the Margaritan sample, or within the mainland sample, analyzed separately. The Margaritan form is sufficiently distinct to be deemed a new subspecies, thus it is here formally described as *C. semistriatus elieceri* **ssp. nov.** This skunk becomes the seventh mammal known to be endemic to Margarita Island. Its conservation status is undetermined.

Key words: Caribbean islands, endemism, geographic variation, island rule, Margarita Island, morphometry, Striped Hog-nosed Skunk.

RESUMEN

El zorrillo rayado, *Conepatus semistriatus* (Boddaert, 1784), se distribuye desde el sur de México hasta el norte de Perú. Es uno de los carnívoros menos estudiados del Nuevo Mundo. Ni siquiera se ha publicado información morfométrica básica sobre la especie. Este trabajo evalúa el estatus taxonómico del zorrillo rayado de la Isla de Margarita, frente a la costa oriental de Venezuela. Los análisis multivariados de 25 medidas craneanas demuestran que el zorrillo margariteño es mucho más pequeño que su congénere continental más cercano, cumpliendo así con la "regla de las islas", la cual predice que bajo condiciones insulares los animales continentales grandes reducen y los animales continentales pequeños incrementan su tamaño corporal. Las diferencias craneométricas entre los zorrillos de Margarita y tierra firme son de magnitud similar o mayor a las encontradas al efectuar comparaciones interespecíficas dentro de géneros de varias familias de carnívoros. No se encontró variación geográfica evidente en el tamaño del cráneo dentro de la muestra de Margarita, ni dentro de la de tierra firme, analizadas por separado. La forma margariteña es lo suficientemente distinta para ser considerada una subespecie nueva, que aquí se describe formalmente como *C. semistriatus elieceri* **ssp. nov.** Esta mofeta se convierte en el séptimo mamífero endémico de la Isla de Margarita. Su estado de conservación es indeterminado.

Palabras clave: endemismo, Isla de Margarita, Islas del Caribe, morfometría, regla de las islas, variación geográfica, zorrillo rayado.

INTRODUCTION

The family Mephitidae accounts for 0.8% of the generic and 4.4% of the specific diversity of living carnivorans (order Carnivora); it includes two species of stink badgers (genus *Mydaus* F. G. Cuvier, 1821) occurring in insular Malaysia, Indonesia and the Philippines, and 12 species of skunks (genera *Mephitis* E. Geoffroy Saint-Hilaire & F. G. Cuvier, 1795; *Spilogale* Gray, 1865; and *Conepatus* Gray, 1837) occurring in North, Central, and South America (ASM 2024). Fossil skunks are known from the late Miocene to Pliocene (13.5–3 Mya) of Eurasia, and from the Late Miocene (9 Mya) of North America (Wang & Qiu 2004, Wang *et al.* 2005).

Skunks are charismatic mammals that are renowned for their unusual coloration, serving as a warning, and for their smelly spray, used in self-defense. They have been regarded as symbols of cuteness, confidence, pacifism, humor, and luck (Miller 2015). Descented skunks are becoming popular pets. Despite their appeal, the scientific knowledge of skunks shows substantial gaps. They have been best studied in North America, but even there major discoveries have been made in the last decades: thus, *Conepatus mesoleucus* (Lesson, 1865), long considered a separate species, was shown to be not distinct from the American Hog-nosed Skunk, *C. leuconotus* (Lichtenstein, 1832) (Dragoo *et al.* 2003); conversely, the Spotted Skunks, genus *Spilogale*, were shown to possess a greater species diversity than traditionally recognized (McDonough *et al.* 2022). In the other hemisphere, the Jaritacaca, *C. amazonicus* (Lichtenstein, 1838), long considered a subspecies of the Striped Hog-nosed Skunk, *C. semistriatus* (Boddaert, 1785) (Cabrera 1958), was shown to be more closely related to the Molina's Hog-nosed Skunk, *C. chinga* (Molina, 1782), from southern South America (Rodrigues 2013, Schiaffini *et al.* 2013); and based on morphometric and genetic analyses, *C. humboldtii* Gray, 1837 was considered a synonym of the latter (Schiaffini *et al.* 2013), though this conclusion has been disputed also based on genetic data (Rodrigues 2013). Both *C. amazonicus* and *C. humboldtii* are currently deemed conspecific with *C. chinga* (ASM 2024).

Except for *Spilogale* (McDonough *et al.* 2022) and *C. leuconotus* (Dragoo *et al.* 2003, Dragoo & Sheffield 2009), whose southern distributional limits reach Costa Rica, the skunks occurring in southern Mexico and Central America, and in South America from Venezuela and Colombia to Bolivia, have never been revised taxonomically: not even basic morphometric information exists for them. Current classifications for skunks from this ample region are largely based on the viewpoints of twentieth-century authorities (Cabrera 1958, Hall 1981), who did not use modern study methods. Such classifications remain widely used in national and regional species lists (*e.g.*, Solari *et al.* 2013, Pacheco *et al.* 2021, Boher-Bentti *et al.* 2023, Tirira *et al.* 2023), distributional analyses (Meza-Joya *et al.* 2018, Castillo & Caruso 2024), and conservation assessments (Belant *et al.* 2009, Hernández-Sánchez *et al.* 2022).

Hall (1981) assigned the populations from Veracruz and Campeche to *C. semistriatus conepatl* (Gmelin, 1788), those from Yucatan and Quintana Roo to Nicaragua to *C. s. yucatanicus* Goldman, 1943, and those from Costa Rica and western Panama to *C. s. trichurus* Thomas, 1905. Cabrera (1958) assigned the populations from Colombia and Venezuela to *C. s. semistriatus*, those from Ecuador to *C. s. quitensis* (Humboldt, 1812), those from northwestern Peru to *C. s. zorrino* Thomas, 1901, those from northeastern Peru to *C. s. taxinus* Thomas, 1924, and those from southern Peru and Bolivia to *C. rex* Thomas, 1898. Except for the reallocation of *C. rex* to *C. chinga*, this classification was maintained by Wozencraft (2005). Rodrigues (2013) departed markedly from these schemes by applying the name *C. conepatl* to the Mexican and Central American populations, and the name *C. quitensis* to Southern Colombian, Ecuadorian, and Peruvian populations. The three Central American subspecies, and three South American subspecies (*C. s. semistriatus*, *C. s. zorrino*, *C. s. taxinus*), are currently included in *C. semistriatus*; the other two (*C. s. quitensis, C. c. rex*) in *C. chinga* (ASM 2024).

Skunks are remarkable among carnivorans for their poor capacity to cross water barriers: for example, skunks do not occur to the south of the Orinoco and the north of the Amazon Rivers, and the Uruguay River has been implicated in the genetic differentiation between Argentinian and Uruguayan skunks (Rodrigues 2013); the only known insular skunks are those occurring on the Channel Islands of California (Van Gelder 1959, McDonough *et al.* 2022), and on Margarita Island of Venezuela (Bisbal 1983). The colonization of these islands by skunks likely required the formation of ecologically suitable land bridges to the mainland, which may have occurred during a glacial period (Van Gelder 1959, Molinari 2007).

As in other mammals, it is debated whether carnivorans follow the 'island rule', according to which on islands large continental animals become smaller, and small continental animals become larger (Meiri *et al.* 2004, Lyras *et al.* 2010, Molinari 2023a). The Channel Islands skunk, *Spilogale gracilis amphialus* Dickey, 1929, despite being sufficiently differentiated genetically to be deemed a full species (Floyd *et al.* 2011, McDonough *et al.* 2022), is indistinct morphometrically (Van Gelder 1959), thus it does not follow the island rule. No data exist for the Margaritan skunk, but based on this rule it could be predicted to be small because its nearby mainland relative is large.

The fauna of Margarita Island (Fig. 1) includes 16 species of bats, and 13 species of nonvolant mammals (Smith & Genoways 1974, Linares 1998). None of the bats is endemic, but specimens of the Allen's Common Moustached bat, *Pteronotus fuscus* (J. A. Allen, 1911), from the island show 'a notable reduction in overall size', and 'are somewhat paler (Sayal Brown) in color than adjacent mainland populations' (Smith 1972). Six of the nonvolant mammals are endemic, namely:

1. The Margaritan Robinson's Mouse Opossum, *Marmosa robinsoni robinsoni* Bangs, 1898, about which and other insular forms of the species it has been concluded that they are 'nothing more than large island forms with habitat-correlated coat color differences' (Rossi *et al.* 2010) [no genetic information exists for Margaritan specimens to test this hypothesis].
2. The Margaritan Cottontail Rabbit, *Sylvilagus floridanus margaritae* Miller, 1898. Unstudied taxonomically using modern methods.
3. The Margaritan Red-tailed Squirrel, *Syntheosciurus granatensis nesaeus* (G. M. Allen, 1902), which is 'easily distinguished from mainland samples' (Vivo & Carmignotto 2015).
4. The Yellow Speckled Tree-rat, *Pattonomys flavidus* (Hollister, 1914), which is 'cranially distinctive and readily diagnosable' (Emmons 2005).
5. The Margaritan Brown Capuchin monkey, *Sapajus apella margaritae* Hollister, 1914, about which based on the 800 km separation from its southern Venezuelan conspecifics, Linares (1998) and Groves (2001) suggested that it might have been introduced to the island in Pre-Columbian times. Groves also

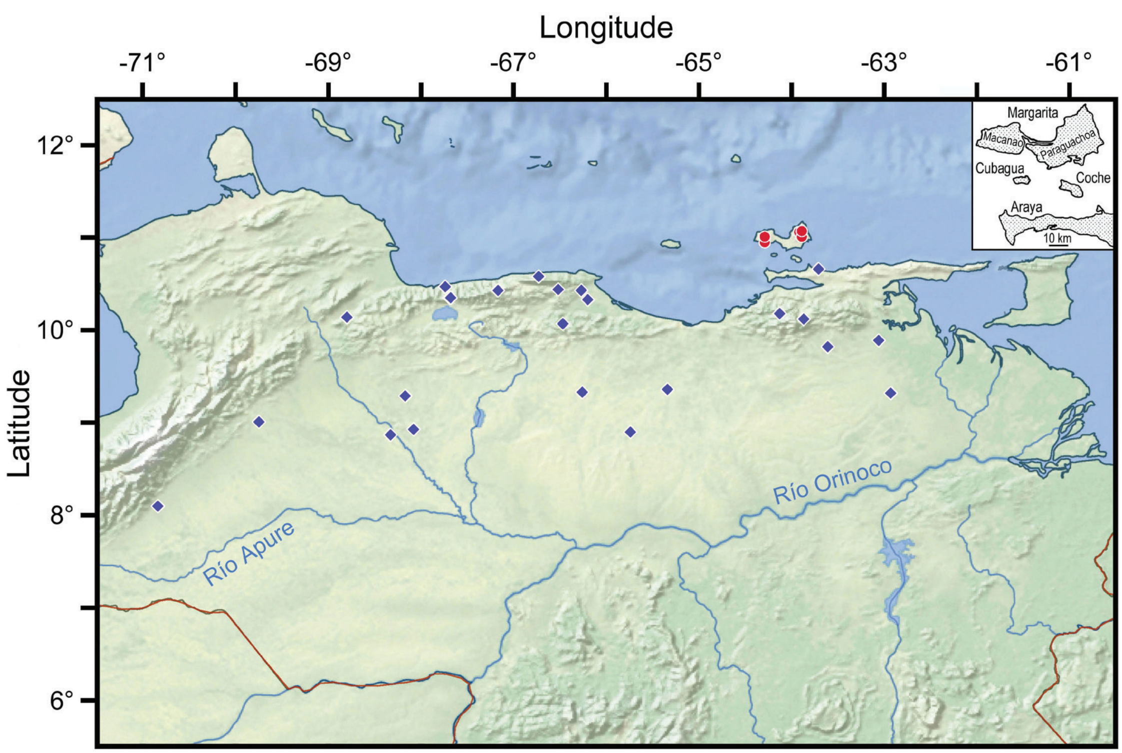

Figure 1. Map of Venezuela east of the Andes and north of the Orinoco River showing the geographic origin of the specimens of the new subspecies (red dots) and *C. s. semistriatus* (blue diamonds) included in this study. The insert in the top left shows the relative positions of Margarita Island, its two divisions (Margarita Oriental, also known as Paraguachoa; and the Macanao Peninsula), the Cubagua and Coche Islands, and the Araya Peninsula. For the geographic coordinates of localities, see Materials and methods.

thought it to be more allied to *S. a. fatuellus* (Linnaeus, 1766) from Colombia than to *S. a. apella* (Linnaeus, 1758). However, the latter subspecies is now known to occur in Guyana, and in the Orinoco Delta (Boher-Bentti & Cordero-Rodríguez 2000), thus could potentially range or have ranged more widely along the coastal forests of northeastern Venezuela, which reach the Araya Peninsula south of Margarita, making a natural colonization of the island possible through a land bridge connecting it to the mainland during a glacial period [no genetic information exists for Margaritan specimens to test these hypotheses].

6. The Margaritan White-tailed Deer, *Odocoileus margaritae* Osgood, 1910, deemed a distinct species due to its very small size and highly distinctive cranial characters (Molinari 2007). Based on D-loop sequences, the separation of this deer from its mainland congeners has been estimated to have occurred at least 118,000 years ago (Moscarella 2001).

Over the course of decades, specimens of *Conepatus* from both mainland Venezuela and Margarita Island, many of them roadkills salvaged by selfless scientific collectors, have slowly accumulated in zoological museums. The point has been reached in which the material available is satisfactory for statistical analyses. We take the opportunity that this represents to conduct the first morphological and morphometric assessment of members of the *C. semistriatus* group, with the main objective of clarifying the taxonomic status of the Margaritan populations.

MATERIALS AND METHODS

Taxonomic categories

We adhere to a version of Simpson's (1951) Evolutionary Species Concept that has been expanded to include operational criteria (Molinari 2023b), according to which a species is 'a phyletic lineage (ancestral-descendent sequence of populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies, and diagnosably distinct based on heritable morphological characters, genetic markers, or both'. We deem a subspecies to be 'a collection of populations occupying a distinct geographic range and diagnosably distinct from other such conspecific populations based on heritable morphological characters' (Patten & Unitt 2002, Molinari 2023b).

Institutions

The collection acronyms mentioned in this study are: AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; CFA, Colección de Mastozoología, Fundación de Historia Natural "Félix de Azara", Buenos Aires, Argentina; CVULA, Colección de Vertebrados de la Universidad de Los Andes, Mérida, Venezuela; EBRG, Museo de la Estación Biológica Rancho Grande, Maracay, Venezuela; FMNH, Field Museum of Natural History, Chicago, USA; IAvH, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia; ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; MACN, Colección Mastozoología, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MBUCV, Museo de Biología de la Universidad Central de Venezuela, Caracas, Venezuela; MCNG, Museo de Ciencias Naturales de Guanare, Guanare, Venezuela; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MEPN, Museo de la Escuela Politécnica Nacional, Quito, Ecuador; MHNLS, Museo de Historia Natural La Salle, Caracas, Venezuela; MHNM, Museo Nacional de Historia Natural, Montevideo, Uruguay (specimens with this acronym were obtained as an exchange and will be recatalogued in the CVULA); MNHN, Muséum national d'Histoire naturelle, Paris; MZUFV, Museu de Zoologia João Moojen, Viçosa, Brazil; QCAZ, Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador; RBMC, Centro de Visitantes de la Reserva Biológica Montecano, Paraguaná Peninsula, Venezuela; USNM, National Museum of Natural History, Washington, USA; UV, Colección de mamíferos de la Universidad del Valle, Cali, Colombia. All specimens were examined physically, except for a few from the CFA, MACN, MCZ, MZUFV, and UV collections, which were examined photographically.

Measurements

Unless otherwise indicated, cranial measurements (Fig. 2A) were taken with a digital caliper. Letter and number combinations (*e.g.*, M1–M3) refer to opposite points of the skull used as landmarks. A total of 25 skull measurements were obtained, as follows:

1. Basilar length* (M1–M3), distance from the posteriormost margin of the first upper incisors to the anteriormost margin of the foramen magnum.

* Measurements marked with an asterisk after Van Gelder (1968).

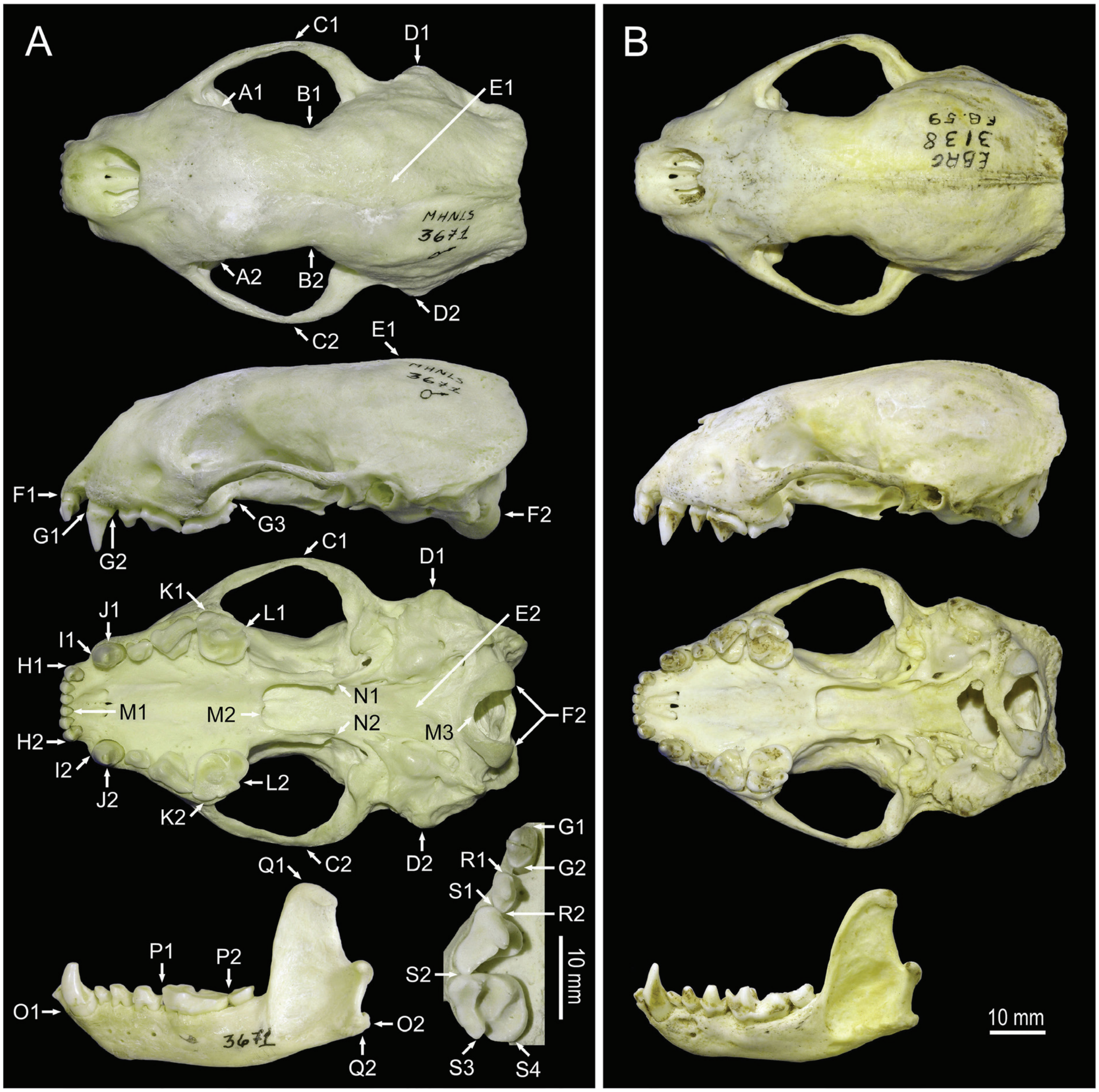

Figure 2. A) Points between which skull measurements were taken: from top to bottom, dorsal, lateral and ventral views of the cranium, and lateral view of the mandible of a specimen of *C. s. semistriatus* (MHNLS 3671), condylobasal length = 81.5 mm, and left half of the palate of a specimen of the new subspecies (CVULA 9124), condylobasal length = 73.0 mm. B) Skull of the holotype of new subspecies (EBRG 3138): from top to bottom, dorsal, lateral and ventral views of the cranium, and lateral view of the mandible. The scales are based on condylobasal lengths and zygomatic breadths (in ventral view). The horizontal scale (right) applies to MHNLS 3671 and EBRG 3138. The vertical scale (left) applies to CVULA 9124.

2. Condylobasal length* (F1–F2), distance from the anteriormost margin of the premaxillae to the posteriormost margin of both occipital condyles.
3. Zygomatic breadth* (C1–C2), maximum distance across the outer margins of the zygomatic arches.
4. Mastoid breadth* (D1–D2), maximum distance across the mastoid processes.
5. Interorbital breadth* (A1–A2), distance across the frontal bones at the level of the frontomaxillary sutures.
6. Postorbital breadth* (B1–B2), minimum distance across the frontal bones posteriorly to the frontomaxillary sutures.
7. Palatilar length* (M1–M2), minimum distance from the posteriormost margin of the first upper in-

* Measurements marked with an asterisk after Van Gelder (1968).

cisors to the posterior margin of the bony palate. If a nasal spine was present postero-centrally, this measurement was taken laterally to it.

8. Precanine length (F1 to I1–I2), minimum distance from the anteriormost margin of the premaxillae to the imaginary line connecting the anteriormost margins of the canines. This measurement is obtained digitally based on a photograph of the palate.
9. Canine to notch length (I1–I2 to L1–L2), minimum distance from the imaginary line connecting the anteriormost edges of the canines to the imaginary line connecting the vertices of the notches between the metacone and the hypocone of each molar. This measurement is obtained digitally based on a photograph of the palate.
10. Post-notch length (L1–L2 to M2), minimum distance from the imaginary line connecting the vertices of the notches between the metacone and the hypocone of each molar and the posterior margin of the bony palate. This measurement is obtained digitally based on a photograph of the palate.
11. Postpalatal length* (M2–M3), maximum distance from anteriormost posterior margin of the bony palate to the anteriormost margin of the foramen magnum.
12. 12. Heigth of the cranium* (E1–E2), distance from the basicranium at the center of the junction of the basisphenoid and basioccipital bones, and the upper surface of the parietal bones, excluding the sagittal crest.
13. Length of the maxillary toothrow* (G1–G3), distance from the anteriormost margin of the canine to the posteriormost margin of the molar at the alveolar levels.
14. Width across incisors* (H1–H2), distance across the latero-labial margins of both third upper incisors.
15. Width across canines* (J1–J2), distance across the latero-labial margins of both upper canines.
16. Width across molars* (K1–K2), distance across the latero-labial margins of both upper molars.
17. Diameter of the canine* (G1–G2), distance from the anteriormost to the posteriormost margin of one of the two upper canines at the alveolar level. On crania in which both canines were missing, this measurement was guessed based on the innermost margins of the alveolus.
18. Length of PM3 (R1–R2), distance from the antero-labial to the postero-lingual margin of the third upper premolar at the alveolar level (PM1 and PM2 are absent in *Conepatus*).
19. Length of PM4* (S1–S2), distance from the antero- to the postero-labial margin of the fourth upper premolar at the alveolar level.
20. Length of the molar (S2–S3), maximum distance from the labial junction of the fourth upper premolar (PM4) and the molar to the posteriormost margin of the molar along the parastyle-metacone axis.
21. Width of the molar (S2–S4), maximum distance from the labial junction of the fourth upper premolar (PM4) and the molar to the postero-lingual margin of the molar.
22. Width of the interpterygoid fossa* (N1–N2), maximum distance across the tips of the hamuli of the pterygoids.
23. Length of the lower carnassial (P1–P2), maximum distance from the anterior to the posterior margin of the lower carnassial.
24. Height of the coronoid* (Q1–Q2), distance from the highest point of the coronoid process to the lowest point of the angular process of the mandible.
25. Length of the mandible* (O1–O2), maximum distance from the mandibular symphysis to the posteriormost margin of the angular process.

In the case of breath measurements, when the measuring landmark was available on one side of the cranium and missing on the other, as for example in specimens with one intact and one broken zygomatic arch, the minimum distance from the available landmark to the longitudinal midline of the cranium was measured, and the resulting value was multiplied by two. This was done to minimize the proportion of missing measurements.

A posteriori, it was found that conventional linear measurements were not sufficient to reflect some visually evident shape differences, particularly with regard to the proportions of the rostrum. For this reason, an additional measurement was added, here referred to as rostral angle. Adobe Photoshop CS6 was used to measure on photographs of crania in lateral view the angle formed by two lines, both starting in the posteriormost alveolar margin of PM3, one of them crossing the antero-central margin of the nasal bones, and the other crossing the alveolar margin of the canine.

Morphometric analyses

Adult specimens of *Conepatus* have been defined as those possessing a fully erupted permanent dentition, and

* Measurements marked with an asterisk after Van Gelder (1968).

a (visibly) fused and obliterated basisphenoid-basioccipital suture (Van Gelder 1968). These simplified criteria may be insufficient. In skunks, subadult-juvenile specimens already show a permanent dentition (Van Gelder 1959), and the basisphenoid-basioccipital suture may stay unfused past and estimated age of eight months (Mead 1967, J. Molinari personal observation). Moreover, cranial sutures may appear unfused in fully adult specimens whose skeletal remains have been exposed to weather for a long time. For this reason, to judge whether specimens were adult, we added three criteria. First, as illustrated for other carnivores (García-Perea 1996), young skunks possess two ridges along the parietal surfaces that are widely apart from the dorsal midline of the cranium. During growth, these ridges migrate centrally until they converge in the sagittal line. Irrespective of whether a well-developed sagittal crest was present or not, a much reduced distance between both ridges was deemed an indicator of adulthood. Second, adult skunks score low in postorbital breadth relatively to interorbital breadth, thus a marked constriction in the postorbital region was deemed an indicator of adulthood. Third, owing to their partly hypogean diets, meaning that food often comes mixed with mineral particles; wild skunks suffer substantial dental wear along their lives. Thus the possession of markedly worn teeth, or the absence of teeth accompanied by scarring or obliteration of the alveoli, was deemed an indicator of adulthood. The morphometric analyses performed in this study include only specimens judged to be adult based on the combination of these criteria.

We divided the sample into two geographic groups: Margarita Island, and mainland (Fig. 1). In the case of the latter, we only included specimens from Venezuela east of the Andes) (note that *Conepatus* has not been recorded in cis-Andean Colombia, Venezuela south of the Orinoco, and the Guianas) under the assumption that the ancestors of the Margaritan populations came from this region. For the multivariate assessment of the data, we used Principal Component Analysis (PCA) and Linear Discriminant Analysis (LDA), which were computed using PAST, version 4.16 (Hammer 2024). For univariate tests (chi-square and correlation analysis), we used SPSS version 17.

To give equal weight to all measurements, the PCA was performed on the correlation matrix. Missing measurements were imputed through regression analysis, using known values for the same measurement as predictors. This was done separately for each geographic group. In PCA, variables often have positive loadings on Component 1 (PC1), and both positive and negative loadings in the remaining components. Thus PC1 has been interpreted as a univariate measure of multivariate size, and PC2–PC*n* as univariate measures of multivariate shape (*e.g.*, Jolicoeur & Mosimann 1960, Gutiérrez & Molinari 2008, Molinari *et al.* 2023). To quantify the relative contribution of the measurements to overall differences in shape, we calculated their communalities, which equal the sum of the squared loadings of the measurement in the components of interest (McGarigal *et al.* 2000), which in our case were PC2–PC16. We excluded PC17–PC25 because they explain a very small fraction of total variance. In PCA performed on the correlation matrix, the total communality of any variable (*i.e*., the sum of its squared loadings in PC1–PC*n*) equals unity (McGarigal *et al.,* 2000).

To determine whether the western (Macanao Peninsula) and eastern (Paraguachoa) Margaritan populations differ in skull size, and whether the mainland populations show west-to-east clinal variation in skull size, we calculated the Pearson correlation coefficients (*r*) between: 1) the Component 1 (PC1) scores of the specimens in the PCA; and 2) the geographic longitudes at which they were collected. We also carried out this procedure using condylobasal lengths instead of PC1 scores.

Material examined

We carefully georeferenced specimen localities using Google Earth Pro (https://www.google.com/earth/), and the combination of various sources of information, including collector's field notes, museum databases, zoological and botanical literature, and maps. The list of specimens used in the comparisons between the new subspecies and cis-Andean *C. s. semistriatus*, and the localities (Fig. 1) in which they were collected, is as follows:

C. semistriatus elieceri **ssp. nov.** (*n* = 22).— **VENEZUELA: Nueva Esparta,** Margarita Oriental (Paraguachoa), Cerro El Tamoco, 4 km E Santa Ana, 11.07°, -63.89°, 400 m (EBRG 3138*, MBUCV 5274*); Margarita Oriental, Parque Nacional Cerro El Copey, 3 km SW La Asunción, 11.01°, -63.89°, 500 m (MBUCV 5275*); Margarita Oriental, Río Tacarigua, 1.5 km SSE Santa Ana, 11.06°, -63.92°, 35 m (EBRG 3137*); Península de Macanao, near San Francisco, 11.01°, -64.29°, 160 m (CVULA 5770*, 5771*, CVULA 8539*, 8540*, 8541*, 9121*, 9122*, 9123, 9124*, 9125*, 9126*, 9127, 9128*, 9129*, EBRG 18978*); Península de Macanao, Quebrada la Montaña, 12 km W Boca de Río, 10.95°, -64.29°, 12 m (EBRG 18981*, 18983*, 18984*).

C. s. semistriatus (*n* = 39).— **VENEZUELA: Aragua,** 0.5 km NW Cata, 10.47°, -67.74°, 35 m (EBRG 21079*); Estación Biológica Rancho Grande, Parque Nacional Henri Pittier, 14 km NW Maracay, 10.35°, -67.68°, 1150 m (AMNH 144821, EBRG 197*, 274*, 276*, 803*). **Barinas,** Reserva Forestal Ticoporo, 15 km S Socopó, 8.10°,

-70.84°, 175 m (EBRG 15721*). **Cojedes,** Hato Los Caballos, km 68 carretera Tinaco-El Baúl, 54 km SE Tinaco, 9.29°, -68.17°, 85 m (MHNLS 6496*, 6497*); Hato Piñero, near El Baúl, 8.93°, -68.08°, 68 m (MCNG 990*); Río Portuguesa, 11 km SSW El Baúl, 8.87°, -68.33°, 70 m (MHNLS 1225). **Guárico,** Chaguaramas, 9.33°, -66.26°, 183 m (CVULA 1510); Hato Santa Bárbara, 10 km S El Socorro, 8.90°, -65.74°, 135 m (MBUCV 3775); Zaraza, 9.36°, -65.34°, 75 m (AMNH 135481*). **Miranda,** Agua Blanca, Parque Nacional Guatopo, 10.07°, -66.47°, 400 m (CVULA 761*); El Junquito–Colonia Tovar road, 10.43°, -67.17°, 2075 m (MHNLS 3412*); Estación Experimental Río Negro, 5.5 km W Río Negro, 10.33°, -66.20°, 45 m (MBUCV 3032*, 3964*, 4007*, 4025*, 4145*); Near Guarenas, 10.44°, -66.52°, 280 m (MBUCV 3968*); Toma de agua, Río Marasmita, 0.3 km NE Capaya, 10.43°, -66.27°, 95 m (MHNLS 3671*). **Monagas,** Caicara de Maturín, 9.82°, -63.61°, 190 m (USNM 296626*); Hato Mata de Bejuco, 47 Km SSE Maturín, 9.32°, -62.93°, 23 m (EBRG 3190, 3190, 3191, USNM 388241, 388242, 388243, 388244*); Río Guarapiche, Cachipo sector, 9.89°, -63.06°, 20 m (MHNLS 10772*). **Portuguesa,** Autopista José Antonio Páez, 3.8 km S Guanare, 9.01°, -69.75°, 153 m (CVULA 8371). **Sucre,** 16 km Chacopata, towards Cariaco, 10.66°, -63.71°, 10 m (CVULA 8538*); Mount Turimiquire, 10.12°, -63.87°, 2300 m (FMNH 38061*); Río Neveri, 24 km WSW Cumanacoa, 10.18°, -64.13°, 425 m (AMNH 69609). **Vargas,** Canales de Naiguatá, vertiente norte del Parque Nacional El Ávila, 10.58°, -66.73°, 800 m (EBRG 3009, MHNLS 8727*). **Yaracuy,** Puente Yaracuy, Nirgua-Chivacoa road, 10.14°, -68.80°, 210 m (EBRG 490).

The specimens whose skull measurements were used for multivariate analyses are indicated with an asterisk. The remaining specimens consist of immature skulls with or without study skin, or study skins only. Many other specimens of *Conepatus* were examined for the comparisons performed in the Taxonomy section (Appendix 1).

RESULTS

Measurements

The skull (not including imputed values) measurements of the holotype, the Margarita Island sample, and the mainland sample, are provided in table 1. Except for the width of interpterygoid fossa (Fig. 2A), the new subspecies averages smaller than its mainland relative in all measurements. No overlap was observed between both forms in six measurements (basilar length, condylobasal length, mastoid breadth, interorbital breadth, postpalatal length, and width across molars). The skull of the holotype is longer than the average for its subspecies (Fig. 2B, Table 1). Expressed as the mean ± SD (min–max) [n], the rostral angle (see Methods) for the new subspecies was 43.8° ± 3.4° (38.3°–48.7) [16], and that of *C. s. semistriatus* was 52.7° ± 1.8° (50.8°–57.0°) [21].

Morphometric analyses

The summary results of the PCA performed on the correlation matrix are shown in Appendix 2. PC1 explained 69.44% of total variance. All measurements, except for the weakly negative width of interpterygoid fossa, have positive loadings. Thus PC1 can be viewed as an axis primarily reflecting multivariate size. The remaining components show even mixtures of negative and positive loadings, indicating that they can be viewed as comparisons of shape. Based on the communality values on the second to sixteenth axes, measurements weakly associated with skull volume, such as precanine length, width of interpterygoid fossa, length of PM4, and post-notch length have the greatest influence on overall differences, whereas the opposite is true for measurements strongly associated with skull volume, such as mastoid breadth, basilar length, and condylobasal length.

Based on specimen scores (Fig. 3), the two forms segregate sharply in the first axis of the PCA, with no overlap observed between the 95% confidence intervals of their scores. On the contrary, they overlap broadly in the second axis, as they do in the remaining 23 axes (not shown). To determine whether despite this finding the PCA reflects interspecific 'shape' differences, we performed a LDA on the specimen scores in the second to twenty-fifth axes. This analysis produced a single axis (eigenvalue = 0.11) explaining 100% of the variance. The resulting discriminant function was able to classify correctly 14 of the 20 specimens of the new subspecies, and 17 of the 25 specimens of *C. s. semistriatus*. A chi-square analysis revealed these proportions to differ significantly ($p < 0.05$) from the expected proportions should there be no differences between both forms. Thus the PCA did detect a differentiation in shape, albeit an incomplete and diffuse one.

For the new subspecies, the Pearson correlation coefficient between PC1 scores and geographic longitude was $r = 0.23$ ($p = 0.34$). For *C. s. semistriatus* it was $r = -0.05$ ($p = 0.80$). The results using condylobasal length instead of PC1 were similar: $r = 0.19$ ($p = 0.43$) and $r = -0.17$ ($p = 0.41$), respectively. Hence, with respect to skull size, there is not differentiation between the populations of western (Macanao Peninsula) and eastern (Paraguachoa) Margarita, which are connected by a narrow isthmus, and there is not west to east clinal variation within the populations of mainland Venezuela east of the Andes.

Table 1. Summary statistics for the skull measurements (mm) of adult *Conepatus* specimens used in this study. The values are expressed as mean ± SD (min–max) [*n*]. Only specimens from Margarita Island (*C. semistriatus elieceri* **ssp. nov.**) and the mainland of Venezuela east of the Andes (*C. s. semistriatus*) are included (Fig. 1).

Measurement (mm)	Holotype (EBRG 3138)	*C. s. elieceri* **ssp. nov.**	*C. s. semistriatus*
Basilar length	65.7	63.8 ± 2.1 (60.0–66.4) [18]	73.8 ± 3.1 (67.7–79.2) [24]
Condylobasal length	73.0	71.9 ± 2.0 (68.3–74.7) [18]	82.4 ± 3.1 (77.9–88.8) [24]
Zygomatic breadth	50.5	47.4 ± 2.4 (43.4–50.9) [15]	54.6 ± 2.8 (50.0–59.4) [24]
Mastoid breadth	39.7	38.6 ± 1.3 (36.4–40.9) [20]	45.0 ± 1.6 (42.4–47.9) [24]
Interorbital breadth	22.8	23.4 ± 0.7 (22.3–24.5) [20]	27.0 ± 1.4 (24.9–29.9) [24]
Postorbital breadth	21.3	21.3 ± 0.7 (20.1–22.5) [20]	23.3 ± 0.9 (21.8–25.5) [24]
Palatilar length	30.4	29.5 ± 1.1 (26.7–30.7) [18]	33.5 ± 1.5 (30.4–36.8) [25]
Post-notch length	5.2	4.2 ± 0.6 (3.1–5.2) [18]	4.4 ± 0.9 (2.5–5.9) [25]
Notch to canine length	22.3	21.7 ± 0.9 (19.6–23.3) [18]	25.4 ± 1.4 (23.3–28.6) [25]
Precanine length	4.7	5.4 ± 0.4 (4.7–6.2) [20]	5.8 ± 0.4 (5.0–6.9) [25]
Postpalatal length	33.9	33.4 ± 1.0 (31.5–35.1) [18]	38.8 ± 2.2 (36.0–43.8) [24]
Heigth of cranium	27.1	26.5 ± 0.7 (25.2–27.8) [19]	29.9 ± 1.9 (25.5–35.1) [24]
Length of maxillary toothrow	23.0	22.9 ± 0.8 (21.3–25.3) [20]	26.3 ± 1.0 (24.8–27.9) [25]
Width across incisors	12.1	11.7 ± 0.6 (10.0–12.7) [20]	13.1 ± 0.7 (11.4–14.6) [25]
Width across canines	19.5	18.4 ± 0.7 (17.2–19.5) [20]	21.7 ± 1.0 (19.5–23.4) [25]
Width across molars	31.1	30.3 ± 0.6 (29.2–31.6) [20]	34.9 ± 1.1 (32.6–37.5) [24]
Diameter of canine	4.8	4.4 ± 0.3 (3.8–5.1) [20]	5.4 ± 0.4 (4.5–6.2) [25]
Length of PM3	4.3	3.9 ± 0.5 (2.2–4.5) [20]	4.7 ± 0.4 (3.9–5.7) [25]
Length of PM4	7.8	7.9 ± 0.3 (7.2–8.4) [20]	8.9 ± 0.5 (7.9–9.8) [25]
Length of molar	7.7	8.0 ± 0.4 (7.3–8.6) [19]	9.5 ± 0.7 (8.5–11.7) [25]
Width of molar	10.0	10.4 ± 0.4 (9.6–11.2) [19]	11.9 ± 0.6 (10.5–12.8) [25]
Width of interpterygoid fossa	6.4	8.6 ± 0.9 (6.4–9.7) [16]	8.0 ± 1.2 (6.1–10.5) [23]
Length of lower carnassial	10.6	10.7 ± 0.3 (10.2–11.1) [12]	11.5 ± 0.3 (11.0–12.2) [23]
Height of coronoid	22.9	24.5 ± 1.3 (22.5–27.8) [19]	26.6 ± 1.9 (23.5–29.7) [21]
Length of mandible	49.0	48.8 ± 2.2 (44.6–53.0) [19]	53.9 ± 2.6 (49.8–58.7) [21]

A LDA performed directly on the skull measurements also produced a single axis (eigenvalue = 49.96), thus the results are presented as one histogram for each subspecies on the same axis (Fig. 4). A normal curve (new subspecies, mean = 7.7, SD = 0.9; *C. s. semistriatus*, mean = 6.2, SD = 1.1) was fitted to each histogram. The means are separated by more than 12 (rightwards) and 16 (leftwards) standard deviations. Hence, the discriminant function obtained should be able to classify correctly all specimens of both subspecies even if much larger samples were available.

The discriminant function is: specimen score = 68.54 + (loading 1 × measurement 1) + (loading 2 × measurement 2) + ... + (loading 25 × measurement 25). The mean of the loadings on the single axis is 0.30. The loadings below the mean are: length of pm4, 2.10; width across incisors, 1.89; basilar length, 1.27; condylobasal length, 1.19;

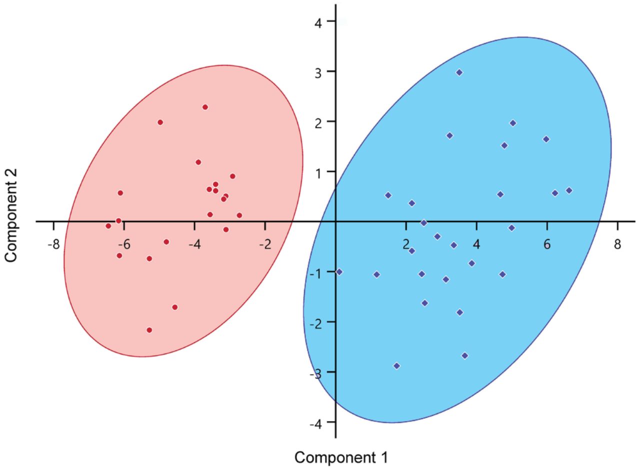

Figure 3. Specimen scores on the first two axes of the Principal Components Analysis (PCA) of the cranial measurements. New subspecies (red dots). *C. s. semistriatus* (blue diamonds). The ellipses enclosing the specimen symbols represent the 95% confidence intervals.

zygomatic breadth, 0.84; width of interpterygoid fossa, 0.75; diameter of canine, 0.51; height of coronoid, 0.47; height of cranium, 0.44; postorbital breadth, 0.36; length of lower carnassial, 0.28; length of molar, 0.24; and length of mandible, 0.28. The loadings above the mean are: notch to canine length, 0.32; width across molars, 0.54; post-notch length, 0.72; palatilar length, 1.02; length of pm3, 1.30; mastoid breadth, 1.43; width across canines, 1.59; length of maxillary toothrow, 1.69; interorbital breadth, 1.70; precanine length, 2.07; postpalatal length, 2.12; and width of molar, 2.60.

TAXONOMY

Conepatus semistriatus elieceri ssp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:3363DEF5-5EAA-4BF7-ADA4-5BF710E457B7

Margaritan Hog-nosed Skunk
Zorrillo rayado margariteño

Holotype (Figs. 2B and 5A)

An adult female (EBRG 3138), consisting of cranium, mandibles, and study skin.

Type locality

Venezuela, Estado Nueva Esparta, Margarita Island, Cerro El Tamoco, 4 km E Santa Ana, 11.07° N, 63.89° W, 400 m.

Paratypes

We designate as paratypes three specimens of unknown sex: MBUCV 5274, from the type locality; EBRG 18983, from Quebrada la Montaña, 12 km W Boca de Río, 10.946° N, 64.287° W, 12 m; and CVULA 9121, from near San Francisco, 11.01° N, 64.29° W, 160 m.

Measurements of the type material

The measurements of the holotype are provided in Table 1. The skull measurements (mm) of the paratypes (MBUCV 5274, EBRG 18983, CVULA 9121) are: basilar length, 63.4, 65.0, 62.3; condylobasal length, 71.8, 73.0, 70.6; zygomatic breadth, 46.6, 50.1, 44.0; mastoid breadth, 39.7, 40.0, 36.6; interorbital breadth, 23.5, 24.3,

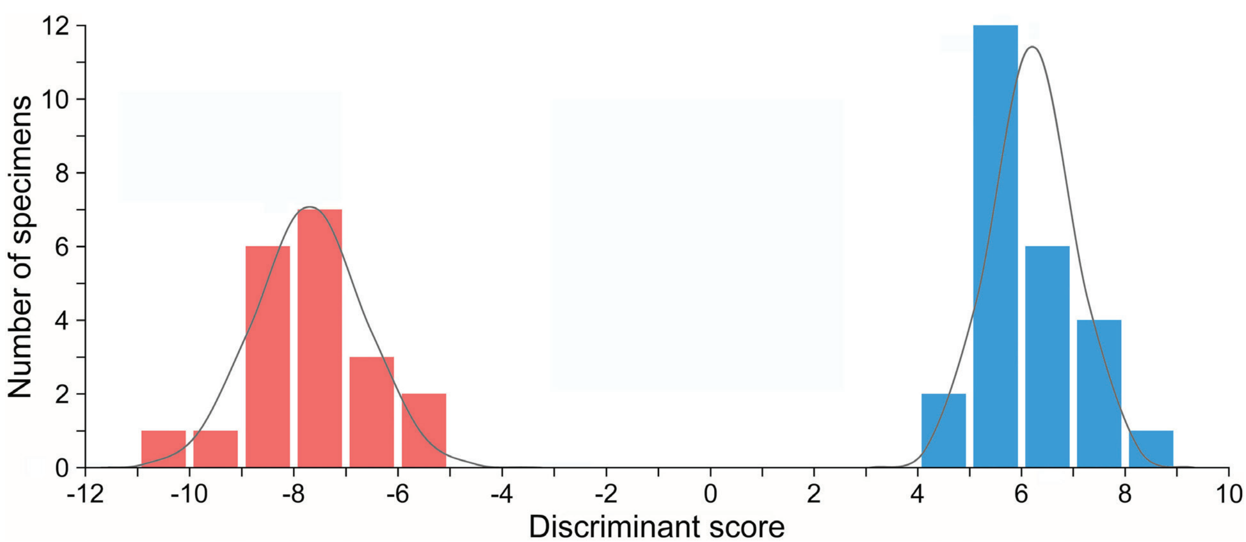

Figure 4. Results of the Linear Discriminant Analysis of the cranial measurements. A single axis explaining 100% of variance was obtained. The scores of the specimens of the new subspecies (left, red) and *C. s. semistriatus* (right, blue) are represented as two histograms along the axis.

23.0; postorbital breadth, 20.7, 22.5, 20.5; palatilar length, 29.3, 30.3, 28.7; post-notch length, 5.0, 3.9, 4.0; notch to canine length, 22.6, 23.3, 20.7; precanine length, 5.6, 5.1, 5.2; postpalatal length, 32.9, 33.5, 32.9; height of cranium, 25.6, 27.8, 25.2; length of maxillary toothrow, 22.1, 23.7, 22.4; width across incisors, 11.3, 12.1, 11.6; width across canines, 17.2, 19.3, 18.1; width across molars, 29.9, 30.8, 29.8; diameter of canine, 4.2, 5.1, 4.0; length of PM3, 3.6, 4.5, 3.2; length of PM4, 7.2, 8.0, 7.8; length of molar, 7.3, 7.8, 8.0; width of molar, 9.7, 10.2, 10.6; width of interpterygoid fossa, 8.2, 8.9, 9.7; length of lower carnassial, —, 10.6, 10.5; height of coronoid, 27.8, 25.0, 22.5; length of mandible, 49.1, 48.6, 44.6.

Diagnosis

Small for a South American member of the *C. semistriatus* group. The rostrum is relatively low (rostral angle less than 50°, see Methods) in lateral view (Fig. 2B). On dorsal view of the cranium, the anteriormost margins of the nasal bones do not project fully over the palatal plane, leaving the anterior region of the premaxillae and the incisive and interincisive foramina fully exposed. In most specimens, the anterior opening of the infraorbital foramen is single (not divided) in at least one side of the cranium. The nasal spine is short or absent, and the nasal septum (part of the vomer bone) does not extend rearwards, thus does not form a keel, past the postpalatal shelf. The hypoglossal (condyloid) foramen is well separated from the posterior lacerate foramen.

Description

As other Venezuelan, Colombian, and Central American members of the *C. semistriatus* group, the holotype possesses two white dorsal stripes, joined only on the head, each of them broader anteriorly and narrower posteriorly, and with little separation between them (Fig. 5A). The type specimen is unusual in possessing numerous dark spots on the dorsal stripes, and a fully dark tail with short hairs all along (Fig. 5A). The hairs of the dorsal stripes are longer than those of the back. The pelage is brown and the skin is yellowish. As characteristic of *Conepatus*, the area around the nose is bare, the ears are much reduced, and the claws on the forefeet are long.

The cranial size (Table 1) is medium for the genus: condylobasal length is more than 70 mm, and less than 77 mm. The skull is much higher in the temporal than in the frontal region. The rostrum is narrow and short in dorsal view (Fig. 2B). In older adults, a low (usually 1–2 mm) sagittal crest is present. The zygomatic arches vary from moderately to strongly bowed upwards. The tympanic bullae are small, and not inflated. The dental formula is: incisors 3/3, canines 1/1, premolars 2/3, and molars 1/2 on each side, for a total of 32 teeth. The single upper molar is much enlarged; P1 is absent, as in all skunks; P2 is absent, as in most *Conepatus*. There is a distinct notch between the metacone and the hypocone of the upper molars. The lower edges of the mandibles are bowed downwards. Most specimens have a single mental foramen (few have one or two small accessory foramina near the mental foramen) on each mandible. The coronoid process has a narrow tip, and is bowed forward both anteriorly and posteriorly: these characteristics of the mandible are more marked in other Margaritan specimens than in the holotype (Fig. 2B). In m1, the talonid is much longer than trigonid.

Comparisons (Table 1, Figs. 2 and 5)

We compare the new subspecies first with its geographic neighbor, and likely closest relative, then with species of *Conepatus* distributed from north to south in the Nearctic and Neotropical regions.

Compared to *C. s. semistriatus* from the Venezuelan mainland east of the Andes (this study), the new subspecies is much smaller, with no overlap in several cranial measurements. Its rostrum is proportionally shorter, narrower, and lower, with a rostral angle of less than 50°, as opposed to more than 50°. The coronoid process is narrow-tipped, and much bowed forwards, as opposed to broad tipped, and moderately bowed or straight. In the new subspecies, each mandible usually has a single mental foramen, sometimes surrounded by one or two poorly developed accessory foramina, as opposed to one mental foramen accompanied by one to four, often well-developed, accessory foramina. Little is known about the external appearance of the new subspecies, but the study skin of the holotype, which is the only one available, has two features not observed in *C. s. semistriatus*, namely numerous dark spots on the dorsal stripes, and a dark tail, as opposed to totally white stripes, and a tail having at least a white tip (in most cases the distal half or two-thirds are white). The tail also has shorter hairs.

Compared to *C. leuconotus*, the new subspecies possesses a hypoglossal foramen well separated from the posterior lacerate foramen, as opposed to confluent with it. In m1, the talonid is much longer than trigonid, as opposed to the talonid slightly longer than the trigonid. Dorsally, the pelage shows two white stripes, as opposed to a single and central white stripe.

Compared to Central American *C. semistriatus*, on dorsal view of the cranium, the incisive and interincisive foramina of the new subspecies are fully exposed, as opposed to partly covered by the nasals, which extend farther frontally. The precanine and postdental regions are pro-

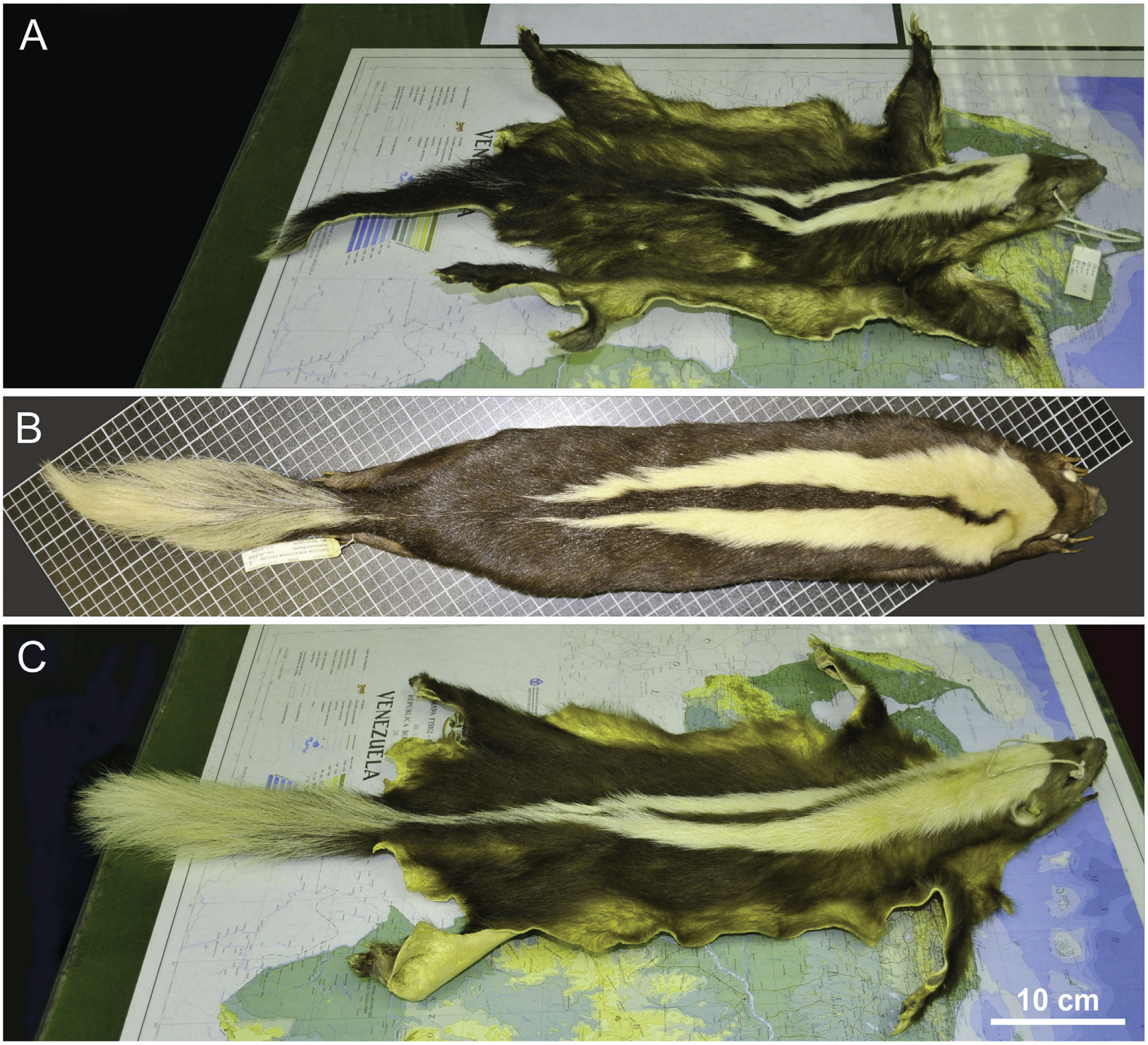

Figure 5. Comparison of study skins. A) holotype of *C. semistriatus elieceri* **ssp. nov.** (EBRG 3138). B) *C. s. semistriatus* (FMNH 38061). C) *C. s. semistriatus* (EBRG 3009). The scale (bottom) applies to the three skins. Note the uniformly dark tail, and the dark spots on the dorsal stripes of the study skin of the holotype, which is the only one available for the new subspecies.

portionally longer with respect to the rest of the palate. The anterior opening of the infraorbital foramen is usually single, as opposed to double or triple. Each mandible usually has a single mental foramen, as opposed to one mental foramen accompanied by up to six accessory foramina. In contrast with the holotype of the new subspecies, specimens of Central American *C. semistriatus* possess distally white (one-third to more than one-half the length) tails.

Compared to Ecuadorian and Peruvian *C. semistriatus* (*C. s. taxinus*, and *C. s. zorrino*) and *C. chinga* (*C. c. quitensis*, *C. c. rex*), the new subspecies is smaller. On dorsal view of the cranium, its incisive and interincisive foramina are fully exposed, as opposed to partly or totally covered by the nasals. Its postorbital region is not as narrowly constricted, its sagittal crest and nasal spine are less developed, and its upper molars and fourth upper premolars (P4) are proportionally larger. The holotype of the new subspecies has dorsal stripes that are less separated from each other than those of Ecuadorian and Peruvian specimens.

Compared to *C. chinga amazonicus* and southern South American members of the *C. chinga*-group, the new subspecies has a short or absent nasal spine with the nasal septum fully inside the nasal cavity, as opposed to a well-developed nasal spine with a nasal septum that typically (*C. c. amazonicus*), or sometimes (southern South American material), continues into a keel posterior to the nasal spine. Its zygomatic arches are from moderately to strongly bowed upwards, as opposed to moderately bowed or almost straight. It has a less inflated tympanic bulla. Compared only to *C. c. amazonicus*, the new subspecies is smaller. Unlike the holotype of the new subspecies, *C. c. amazonicus* typically has a predominantly white tail. Compared only to southern South American specimens, the new subspecies is larger. On dorsal view of the cranium, its incisive and interincisive foramina are fully exposed, as opposed to partly or, more typically, covered by the nasals, which extend anteriorly causing the nasal cavity to open frontally through a comparatively small and rounded orifice. The holotype of the new subspecies has narrowly-separated dorsal stripes, as opposed to widely-separated dorsal stripes (often reduced or absent). The *C. semistriatus* from Venezuela, Colombia, and Central America always have well-developed dorsal stripes. This seems to be also de case of *C. c. amazonicus*.

Distribution (Fig. 1)

Endemic to Margarita Island, Venezuela. Occurring in both geographic subdivisions (Macanao Peninsula, Paraguachoa) of the island.

Etymology

The epithet *elieceri*, a masculine noun in the genitive case, honors the Venezuelan researcher Eliécer E. Gutiérrez, in recognition of his outstanding contributions to Neotropical mammalogy.

DISCUSSION

Cranially, species of the genus *Conepatus* lack highly distinctive characters, and can be distinguished from each other mainly based on size and proportions. In addition, at the intraspecific level they are variable in coloration (Van Gelder 1968, Dragoo *et al.* 2003, Schiaffini *et al.* 2013, Teta *et al.* 2020, Ferguson *et al.* 2022). Perhaps it is for these reasons that Hershkovitz (1959) suggested all members of the genus to be conspecific, which the genetic data now available (Dragoo *et al.* 2003, Schiaffini *et al.* 2013, Rodrigues 2013) show not to be the case. In this context, the finding that the Margaritan skunk is 100% distinguishable from its nearby mainland congener, not only morphometrically but also to the naked eye, is remarkable. In fact, the differences in raw measurements, and PCA and LDA scores, between both forms are similar or greater to those found in interspecific comparisons within genera of several carnivoran families (*e.g*., Van Valkenburgh & Wayne 1994, Taylor & Matheson 1999, Bertrand & Morisot 2012, Bornholdt *et al.* 2013, Srinivas & Jhala 2021). We are assigning the subspecies rank to this skunk based on the findings that it is highly diagnosable, and that its morphometric differences are large; we are not assigning the species rank because such differences involve mainly size (Molinari 2023b).

Middle-sized carnivorans often evolve dwarfism after colonizing islands, either by over-water dispersal or glacial-period vicariance. Examples include insular endemics such as the Channel Islands fox, *Urocyon littoralis* (Baird, 1858) (Coonan *et al.* 2010), the Pygmy Raccoon, *Procyon pygmaeus* Merriam, 1901 (Villa-Meza *et al.* 2011), the Dwarf Coati, *Nasua nelsoni* Merriam, 1901 (Cuarón *et al.* 2009), the Cozumel Island fox, genus *Urocyon* Baird, 1857 (Gompper *et al.* 2006), and the Margaritan Hog-nosed Skunk, *C. s. elieceri* (this study). The latter is the first known case of insular dwarfism in extant skunks: a dwarfed fossil skunk, *Promephitis majori* Pilgrim, 1933, has been found on the Greek island of Samos (Pilgrim 1933). Exceptions include the Tres Marías Raccoon, *Procyon lotor insularis* Merriam, 1898 (Wilson 1991), and the extinct Falkland Islands wolf, *Dusicyon australis* (Kerr, 1792) (Lyras *et al.* 2010), which are (or were) similar-sized to their mainland ancestors. Thus, the Margaritan skunk is not alone among carnivorans in following the island rule (Foster 1964, Van Valen 1973).

The suite of morphological, functional, and behavioral changes often observed in insular organisms has been referred to as the 'island syndrome' (Adler & Levins 1994, Baeckens & Damme 2020). These changes may involve traits such as body size (considered by the island rule), cranial shape, limb proportions, coloration, diet, and escape behavior (Adler & Levins 1994, Sánchez-Villagra *et al*. 2016, van der Geer 2019, Baeckens & Damme 2020). To some degree, *C. s. elieceri* also complies with the island syndrome since it differs from *C. s. semistriatus* in a cranial shape parameter (rostral angle) that could not be quantified using linear measurements.

Along the last 500,000 years, on four times global sea level was more than 100 m below the present level: about 20,000 (Last Glacial Maximum), 140,000 (Penultimate Glacial Period), 250,000, and 340,000 YBP (Waelbroeck *et al.* 2002, Siddall *et al.* 2007, Lichter *et al.* 2010). At such times, many continental-shelf islands were connected to the mainland by land bridges, offering the opportunity of colonization to mainland populations. Animals can be expected to cross ecologically suitable land bridges every time that they are formed, and pre-established insular populations can be expected to retain at least part of their acquired differences even if genetic exchange takes place with more recent immigrants. Thus insular animals that are classifiable as endemic species or subspecies, such as the Margaritan skunk, are likely to have colonized the islands and started their separate evolution earlier than the Last Glacial Maximum. Examples exist for insular mammals of the Caribbean: the Pygmy Three-toed Sloth, *Bradypus pygmaeus* Anderson & Handley, 2001, from the Escudo de Veraguas Island (Panama) was estimated to have diverged at least 4.3 Mya (Ruiz-García *et al.* 2017); the pygmy raccoon and the dwarf coati from Cozumel Island (Mexico) were estimated to have been isolated since 50,000 YBP, and the fox from this island 'for a minimum of 5000–13000 years, and perhaps far longer' (McFadden 2004, Gompper *et al.* 2006); as already noted, the Margaritan White-tailed Deer was estimated to have diverged at least 118,000 YBP (Moscarella 2001, Molinari 2007).

As areas of endemism, the Margarita and Cozumel Islands show similarities. Both have about the same number of endemic species and subspecies, and are at a similar distances from the mainland. However, Margarita is twice as large (1,071 opposed to 478 km^2); and with mountains as high as 760 m (Cerro Macanao to the west) and 960 m (Cerro El Copey to the east) it has a greater environmental diversity than Cozumel, which has a maximum elevation of about 15 m. Margarita has a more complex biogeographic history: it has been emerged, intermittently connected to the mainland during glacial periods, for more than one million years, whereas Cozumel was under water about 120,000 YBP; relatively to the mainland, Margarita was from 20 to 50 km to the west 1 Mya, whereas Cozumel has not shifted its position over the last 200,000 years (Gompper *et al.* 2006, Molinari 2007). More attention needs to be given to the protection of the Margaritan flora and fauna. The conservation status of the Margaritan skunk is undetermined, but the abundant material of the subspecies in museum collections suggests that it is common, that it suffers a high mortality rate, or both.

ACKNOWLEDGEMENTS

We are grateful to the museum staff that facilitated examination of specimens under their care, namely Robert Voss and Nancy Simmons (AMNH), Paula Jenkins and Roberto Portela Miguez (BMNH), Pascual Soriano and Johnny Murillo (CVULA), the late Francisco Bisbal, and Javier Sánchez (EBRG), Bruce Patterson (FMNH), Yaneth Muñoz-Saba (ICN), Mercedes Salazar-Candelle and Carmen Ferreira-Marques (MBUCV), Alexis Araujo (MCNG), Luis Albuja (MEPN), Jacques Cuisin, Christiane Denys, Jean-Marc Pons, Anne Previato, and Géraldine Veron (MNHN), Santiago F. Burneo and M. Alejandra Camacho (QCAZ), and Michael D. Carleton, Nicole Edmison, Alfred L. Gardner, Linda K. Gordon, Esther Langan, and Darrin Lunde (USNM). Verónica Vargas Muñoz (UV) sent photographs of two study skins and one skull of Colombian specimens. Guilherme Siniciato Terra Garbino (MZUFV) sent photographs and measurements of the skulls of two Brazilian specimens.

REFERENCES

Adler, G. H. & R. Levins. 1994. The island syndrome in rodent populations. *Quarterly Review of Biology* 69: 473–490. https://doi.org/10.1086/418744

ASM [American Society of Mammalogists]. 2024. *Mammal diversity database*, version 1.12.1. https://doi.org/10.5281/zenodo.10595931

Baeckens, S. & R. Damme. 2020. The island syndrome. *Current Biology* 30: 338–339. https://doi.org/10.1016/j.cub.2020.03.029

Belant, J. L., J. Schipper & J. Conroy. 2009. The conservation status of small carnivores in the Americas. *Small Carnivore Conservation* 41: 3–8.

Bertrand, A. S. & A. Morisot. 2012. Neotropical spotted cat species discrimination using morphometrics. *Natureza & Conservação* 10: 40–44. https://doi.org/10.4322/natcon.2012.007

Bisbal, F. J. 1983. Dos nuevos mamíferos para la Isla de Margarita, Venezuela. *Acta Científica Venezolan*a 34: 366–367.

Boher-Bentti, S. & G. A. Cordero-Rodríguez. 2000. Distribution of brown capuchin monkeys (*Cebus apella*) in Venezuela: a piece of the puzzle. *Neotropical Primates* 8: 152–153.

Boher-Bentti, S., M. Salazar-Candelle & C. Ferreira-Marques. 2023. Mamíferos de Venezuela: lista actualizada 2023 y comentarios taxonómicos. *Anartia* 36: 7–35. https://doi.org/10.5281/zenodo.10433912

Bornholdt, R., K. Helgen, K. P. Koepfli, L. Oliveira, M. Lucherini & E. Eizirik. 2013. Taxonomic revision of the genus *Galictis* (Carnivora: Mustelidae): Species delimitation, morphological diagnosis, and refined mapping of geographical distribution. *Zoological Journal of the Linnean Society* 167: 449–472. https://doi.org/10.1111/j.1096-3642.2012.00859.x

Cabrera, A. 1958. Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas* 4: 1–308.

Castillo, D. F. & N. C. Caruso. 2024. Potential distribution and conservation of the hog-nosed skunk (genus *Conepatus*, Mammalia: Mephitidae). *Journal for Nature Conservation* 77: 126519. https://doi.org/10.1016/j.jnc.2023.126519

Coonan, T. J., C. A. Schwemm & D. K. Garcelon. 2010. *Decline and recovery of the island fox - a case study for population recovery*. Cambridge, United Kingdom: Cambridge University Press, xi + 212 p.

Cuarón, A. D., D. Valenzuela-Galván, D. García-Vasco, M. E. Copa, S. Bautista, H. Mena, D. Martínez-Godínez, C. González-Baca, L. A. Bojórquez-Tapia, L. Barraza, P. C. De Grammont, F. Galindo-Maldonado, M. A. Martínez-Morales, E. Vázquez-Domínguez, E, Andresen, J. Benítez-Malvido, D. Pérez-Salicrup, K. W. McFadden & M. E. Gompper. 2009. Conservation of the endemic dwarf carnivores of Cozumel Island, Mexico. *Small Carnivore Conservatio*n 41: 15–21.

Dragoo, J. W., R. L. Honeycutt & D. J. Schmidly. 2003. Taxonomic status of white-backed hog-nosed skunks, genus *Conepatus* (Carnivora: Mephitidae). *Journal of Mammalogy* 84: 159–176. https://doi.org/10.1644/1545-1542(2003)084%3C0159:TSOWBH%3E2.0.CO;2

Dragoo, J. W. & S. R. Sheffield. 2009. *Conepatus leuconotus* (Carnivora: Mephitidae). *Mammalian Species* 827: 1–8. https://doi.org/10.1644/827.1

Emmons, L. H. 2005. A revision of the genera of arboreal Echimyidae (Rodentia: Echimyidae, Echimyinae), with descriptions of two new genera. pp. 247–310. *In*: Lacey, E. A. & P. Myers (eds). *Mammalian diversification: from chromosomes to phylogeography*. Berkeley, USA: University of California Publications in Zoology. https://doi.org/10.1525/california/9780520098534.003.0009

Ferguson, A. W., R. E. Strauss & R. C. Dowler. 2022. Beyond black and white: Addressing colour variation in the context of local environmental conditions for the aposematic North American Hog-nosed skunk. pp. 107–130. *In*: Do Linh San, E., J. J. Sato, J. L. Belant & M. J. Somers (eds). *Small carnivores: Evolution, ecology, behaviour, and conservation*. New York, USA: Wiley.

Floyd, C. H., D. H. Van Vuren, K. R. Crooks, K. L. Jones, D. K. Garcelon, N. M. Belfiore, J. W. Dragoo & B. May. 2011. Genetic differentiation of island spotted skunks, *Spilogale gracilis amphiala*. *Journal of Mammalogy* 92: 148–158. https://doi.org/10.1644/09-MAMM-A-204.1

Foster, J. B. 1964. Evolution of mammals on islands. *Nature* 202: 234–235. https://doi.org/10.1038/202234a0

García-Perea, R. 1996. Patterns of postnatal development in skulls of lynxes, genus *Lynx* (Mammalia: Carnivora). *Journal of Morphology* 229: 241–254. https://doi.org/10.1002/(SICI)1097-4687(199609)229:3%3C241::AID-JMOR1%3E3.0.CO;2-1

Gompper, M. E., A. E. Petrites & R. L. Lyman. 2006. Cozumel Island fox (*Urocyon* sp.) dwarfism and possible divergence history based on subfossil bones. *Journal of Zoology* 270: 72–77. https://doi.org/10.1111/j.1469-7998.2006.00119.x

Groves, C. P. 2001. *Primate Taxonomy*. Washington, USA: Smithsonian Institution Press, 350 pp.

Gutiérrez, E. E. & J. Molinari. 2008. Morphometrics and taxonomy of bats of the genus *Pteronotus* (subgenus *Phyllodia*) in Venezuela. *Journal of Mammalogy* 89: 292–305. https://doi.org/10.1644/06-MAMM-A-452R.1

Hall, E. R. 1981. *The mammals of North America*, 2nd ed. New York, USA: Wiley, xv + vi + 1181 pp.

Hammer, Ø. 2024. PAST, *Paleontological Statistics*, Version 4.16, Reference manual. Oslo, Norway: University of Oslo.

Hernández-Sánchez, A., A. Santos-Moreno & G. Pérez-Irineo. 2022. The Mephitidae in the Americas: A review of the current state of knowledge and future research priorities. *Mammalian Biology* 102: 307–320. https://doi.org/10.1007/s42991-022-00249-z

Hershkovitz, P. 1959. Nomenclature and taxonomy of the Neotropical mammals described by Olfers, 1818. *Journal of Mammalogy* 40: 337–353. https://doi.org/10.2307/1376558

Jolicoeur, P. & J. R. Mosimann. 1960. Size and shape variation in the painted turtle: A principal component analysis. *Growth* 24: 339–354.

Lichter, M., D. Zviely, M. Klein & D. Sivan. 2010. Sea-level changes in the Mediterranean: Past, present, and future –a review. pp. 3–17. *In*: Seckbach, J., R. Einav & A. Israel (eds). *Seaweeds and their role in globally changing environments (cellular origin, life in extreme habitats and astrobiology)*. Dordrecht, Netheerlands: Springer. https://doi.org/10.1007/978-90-481-8569-6_1

Linares, O. J. 1998. *Mamíferos de Venezuela*. Caracas, Venezuela: Sociedad Conservacionista Audubon de Venezuela, 691 pp.

Lyras, G. A., A. A. Van Der Geer & L. Rook. 2010. Body size of insular carnivores: evidence from the fossil record. *Journal of Biogeography* 37: 1007–1021. https://doi.org/10.1111/j.1365-2699.2010.02312.x

McDonough, M. M., A. W. Ferguson, R. C. Dowler, M. E. Gompper & J. E. Maldonado. 2022. Phylogenomic systematics of the spotted skunks (Carnivora, Mephitidae, *Spilogale*): Additional species diversity and Pleistocene climate change as a major driver of diversification. *Molecular Phylogenetics and Evolution* 167: 107266. https://doi.org/10.1016/j.ympev.2021.107266

McFadden, K. W. 2004. *The ecology, evolution, and natural history of the dwarf carnivores of Cozumel Island, Mexico*. New York, USA: Columbia University, 148 pp. [PhD Thesis]

McGarigal, K., S. Cushman & S. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. New York, USA: Springer, xiii + 283 pp.

Mead, R. A. 1967. Age determination in the spotted skunk. *Journal of Mammalogy* 48: 606–616. https://doi.org/10.2307/1377584

Meiri, S., T. Dayan & D. Simberloff. 2004. Body size of insular carnivores: Little support for the island rule. *American Naturalist* 163: 469-479. https://doi.org/10.1086/382229

Meza-Joya, F. L., E. Ramos, F. Cediel, V. Martínez-Arias, J. Colmenares & D. Cardona. 2018. Predicted distributions of two poorly known small carnivores in Colombia: The greater grison and striped hog-nosed skunk. *Mastozoología Neotropical* 25: 89–105. https://doi.org/10.31687/saremMN.18.25.1.0.09

Miller, A. 2015. *Skunk*. London, United Kingdom: Reaktion Books, 199 pp.

Molinari, J. 2007. Variación geográfica en los venados de cola blanca (Cervidae, *Odocoileus*) de Venezuela, con énfasis en

O. margaritae, la especie enana de la Isla de Margarita. *Memoria de la Fundación La Salle de Ciencias Naturales* 167: 29–72.

Molinari, J. 2023a. A global assessment of the 'island rule' in bats based on functionally distinct measures of body size. *Journal of Biogeography* 50: 1179–1190. https://doi.org/10.1111/jbi.14624

Molinari, J. 2023b. A bare-bones scheme to choose between the species, subspecies, and 'evolutionarily significant unit' categories in taxonomy and conservation. *Journal for Nature Conservation* 72: 126335. https://doi.org/10.1016/j.jnc.2023.126335

Molinari, J., E. E. Gutiérrez & B. K. Lim. 2023. Systematics and biogeography of *Anoura cultrata* (Mammalia, Chiroptera, Phyllostomidae): A morphometric, niche modeling, and genetic perspective, with a taxonomic reappraisal of the genus. *Zootaxa* 5297: 151–188. https://doi.org/10.11646/zootaxa.5297.2.1

Moscarella, R. A. 2001. *Filogeografía y genética de la conservación del venado caramerudo de Venezuela*. Caracas, Venezuela: Universidad Simón Bolívar, 87 pp. [MSc Thesis]

Pacheco, V., S. Diaz, L. Graham-Angeles, M. Flores-Quispe, G. Calizaya-Mamani, D. Ruelas & P. Sánchez-Vendizú. 2021. Lista actualizada de la diversidad de los mamíferos del Perú y una propuesta para su actualización. *Revista Peruana de Biología* 28: e21019. http://dx.doi.org/10.15381/rpb.v28i4.21019

Patten, M. A., & P. Unitt. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk* 119: 26–35. https://doi.org/10.1093/auk/119.1.26

Pilgrim, G. E. 1933. A fossil skunk from Samos. *American Museum Novitates* 663: 1–15.

Rodrigues, M. L. F. 2013. *História evolutiva de* Conepatus *(Carnivora: Mephitidae): padrões biogeográficos de diversificação, investigação filogenética e revisão taxonómica do gênero*. Porto Alegre, Brazil: Pontifícia Universidade Católica do Río Grande do Sul, 162 pp. [PhD Thesis]

Rossi, R. V., R. S. Voss & D. P. Lunde. 2010. A revision of the didelphid marsupial Genus *Marmosa* Part 1. The species in Tate's '*mexicana*' and '*mitis*' sections and other closely related forms. *Bulletin of the American Museum of Natural History* 334: 1–83. https://doi.org/10.1206/334.1

Ruíz-García, M., D. Chacón, T. Plese, I. Schuler & J. M. Shostell. 2017. Mitogenomics phylogenetic relationships of the current sloth's genera and species (Bradypodidae and Megalonychidae). *Mitochondrial DNA Part A* 29: 281–299. http://dx.doi.org/10.1080/24701394.2016.1275602

Sánchez-Villagra, M. R., Geiger, M., & R. A. Schneider. 2016. The taming of the neural crest: a developmental perspective on the origins of morphological covariation in domesticated mammals. *Royal Society Open Science* 3: 160107. http://dx.doi.org/10.1098/rsos.160107

Schiaffini, M. I., M. Gabrielli, F. J. Prevosti, Y. P. Cardoso, D. Castillo, R. Bo, E. Casanave & M. Lizarralde. 2013. Taxonomic status of southern South American *Conepatus* (Carnivora: Mephitidae). *Zoological Journal of the Linnean Society* 167: 327–344. https://doi.org/10.1111/zoj.12006

Siddall, M., J. Chappell & E. K. Potter. 2006. Eustatic sea level during past interglacials. pp. 75–92. *In*: Sirocko, F., M. Claussen, T. Litt & M. F. Sanchez-Goni (eds). *The climate of past interglacials*. Amsterdam, The Netherlands: Elsevier. https://doi.org/10.1016/S1571-0866(07)80032-7

Simpson, G. G. 1951. The species concept. *Evolution* 5: 285–298. https://doi.org/10.1111/j.1558-5646.1951.tb02788.x

Smith, J. D. 1972. Systematics of the chiropteran family Mormoopidae. *Miscellaneous Publication, Museum of Natural History, University of Kansas* 56: 1–132.

Smith, J. D. & H. H. Genoways. 1974. Bats of Margarita island, Venezuela, with zoogeographic comments. *Bulletin of the Southern California of Sciences* 73: 64–79.

Solari, S., Y. Muñoz-Saba, J. V. Rodríguez-Mahecha, T. R. Defler, H. E. Ramírez-Chaves & F. Trujillo. 2013. Riqueza, endemismo y conservación de los mamíferos de Colombia. *Mastozoología Neotropical* 20: 301–365.

Srinivas, Y. & Y. Jhala. 2021. Morphometric variation in wolves and golden jackal in India (Mammalia, Carnivora). *Biodiversity Data Journal* 9: e67677. https://doi.org/10.3897/BDJ.9.e67677

Taylor, M. E. & J. Matheson. 1999. A craniometric comparison of the African and Asian mongooses in the genus *Herpestes* (Carnivora: Herpestidae). *Mammalia* 63: 449–464. https://doi.org/10.1515/mamm.1999.63.4.449

Teta, P., G. D'Elía, P. Jayat, G. S. Libardi, J. A. Oliveira, R. Moratelli, A. R. Percequillo, J. R. Prado, P. E. Ortiz, N. Hurtado, M. E. Schiaffini, E. F. Abreu, Jr., E. A. Chiquito, A. L. Giménez & J. Torres. 2020. On the distinction and availability of the new taxa proposed by Agnolin *et al.,* (2019). *Mastozoología Neotropical* 27: 155–171. https://doi.org/10.31687/saremMN.20.27.1.0.20

Tirira, D. G., J. Brito, S. F. Burneo, C. M. Pinto & J. A. Salas. 2023. *Mamíferos del Ecuador: lista oficial actualizada de especies*. Quito, Ecuador: Asociación Ecuatoriana de Mastozoología, 83 pp.

van der Geer, A. A. E. 2019. Effect of isolation on coat colour polymorphism of Polynesian rats in Island Southeast Asia and the Pacific. *PeerJ* 7:e6894. http://doi.org/10.7717/peerj.6894

Van Gelder, R. G. 1959. A taxonomic revision of the spotted skunks (genus *Spilogale*). *Bulletin of the American Museum of Natural History* 117: 229–392.

Van Gelder, R. G. 1968. The genus *Conepatus* (Mammalia, Mustelidae): variation within a population. *American Museum Novitates* 2322: 1–37.

Van Valen, L. 1973. Body size and numbers of plants and animals. *Evolution* 27: 27–35. https://doi.org/10.1111/j.1558-5646.1973.tb059 14.x

Van Valkenburgh, B. & R. K. Wayne. 1994. Shape divergence associated with size convergence in sympatric East African jackals. *Ecology* 75: 1567–1581. https://doi.org/10.2307/1939618

Villa-Meza, A., R. Avila-Flores, A. D. Cuarón & D. Valenzuela-Galván. 2011. *Procyon pygmaeus* (Carnivora: Procyonidae). *Mammalian Species* 877: 87–93. https://doi.org/10.1644/877.1

Vivo, M. & A. P. Carmignotto. 2015. Family Sciuridae G. Fischer, 1817. pp. 1–48. *In*: Patton, J. L., U. F. Pardiñas & G. D'Elía (eds). *Mammals of South America, volume 2. Rodents*. Chicago, USA: University of Chicago Press.

Waelbroeck, C., L. Labeyrie, E. Michel, J. C. Duplessy, J. F. McManus, K. Lambeck, E. Balbon & M. Labracherie. 2002. Sea-level and deep water temperature changes derived from benthonic foraminifera isotopic records. *Quaternary Science Reviews* 21: 295–305. https://doi.org/10.1016/S0277-3791(01)00101-9

Wang, X. & Z. Qiu. 2004. Late Miocene *Promephitis* (Carnivora, Mephitidae) from China. *Journal of Vertebrate Paleontology* 24: 721–731. https://doi.org/10.1671/0272-4634(2004)024[0721:LMPCMF]2.0.CO;2

Wang, X., D. P. Whistler & G. T. Takeuchi. 2005. A new basal skunk *Martinogale* (Carnivora, Mephitinae) from late Miocene Dove Spring Formation, California, and origin of new world mephitines. *Journal of Vertebrate Paleontology* 25: 936–949. https://doi.org/10.1671/0272-4634(2005)025[0936:ANBSMC]2.0.CO;2

Wilson, D. E. 1991. Mammals of the Tres Marías Islands. *Bulletin of the American Museum of Natural History* 206: 214–250.

Wozencraft, W. C. 2005. Order Carnivora. pp. 532–562. *In*: Wilson, D. E. & D. M. Reeder (eds) *Mammal species of the world: A taxonomic and geographic reference*. Washington, USA: Smithsonian Institution Press, 2142 pp.

APPENDIX 1
Additional specimens of *Conepatus* examined

Specimens are grouped according to current classification (ASM 2024), which must be deemed provisional because the genus has never been reviewed. Adult specimens whose skulls were examined are indicated with an asterisk. All other specimens consist of immature skulls with or without study skin, or study skins only.

C. chinga (*n* = 272).— **ARGENTINA: Buenos Aires,** 25 de Mayo (CFA 9752); Bonifacio (BMNH 17.9.15.3); Bonifacio (Laguna Alsina) (BMNH 17.9.15.1*); Estación Ombucta (BMNH 28.12.11.9); Estancia Los Angeles, 64 Mi SE Azul (USNM 331066); Estancia Los Ingleses, near Mar de Ajó (BMNH 20.2.7.10, 20.2.7.8, 20.2.7.9, 9.12.1.16, 9.12.1.17, 9.12.1.18*); Gándara (MACN 29.912); Mar del Plata (BMNH 13.2.24.1, 16.10.3.6); N of Necochea (USNM 172792*); near Henderson (FMNH 24354*); San José Ranch, 32 km SSW San Blas (USNM 171957, 171958, 172791). **Catamarca,** 'Otro Cerro', Sierra de Ambato, aprox. 35 km N Chumbicha (BMNH 19.2.7.1*, 19.2.7.2, 19.2.7.3*, 20.3.17.2); Belén (BMNH 34.11.4.6, 34.11.4.7). **Chubut,** 100 km NW Comodoro Rivadavia (AMNH 94317*); Barrancas Blancas, 5.5 km al SW Puerto Madryn (MNHN 1897-1244*); La Concepción (Laguna) (BMNH 28.12.11.6, 28.12.11.7); Lago Colhue Huapi (AMNH 94328, 94330*); Pico Salamanca (BMNH 28.12.11.3–28.12.11.5); Rawson (MACN 28.72); Río Chubut (BMNH 99.2.22.10); Sarmiento (AMNH 94329*); unknown locality (BMNH 96.10.7.3); Valle del Lago Blanco (BMNH 3.7.9.13–3.7.9.15). **Córdoba,** Cruz del Eje (BMNH 2.2.5.2, 2.2.5.3*, 2.2.5.4–2.2.5.6, 2.2.5.9); El Carrizal, Villa Dolores (BMNH 17.6.29.5–17.6.29.7); Noetinger (BMNH 17.1.25.8, 17.1.25.9); unknown locality (AMNH 36933). **Corrientes,** Manantiales (MACN 13.714). **Entre Ríos,** Paraná (AMNH 36932). **Formosa,** 'Formosa, Paso de las Niñas, Río Teuco' [39 km SSW Ingeniero Suárez, Río Teuco-Bermejo] (MACN 47.119); Fortín Nuevo Pilcomayo (MACN 43.58). **Jujuy,** Alfarcito (BMNH 21.11.1.3); Humahuaca (MACN 26.182); Maimara (BMNH 12.12.12.1*, 12.12.12.2). **La Rioja,** Desiderio Tello (USNM 172793*, 172794). **Mendoza,** Colonia Alvear (BMNH 10.9.12.2); Tupungato (BMNH 21.7.5.3*). **Neuquén,** Chos Malal (BMNH 26.10.11.1); Collón Curá (BMNH 27.6.4.68); 16 km SE of La Rinconada (BMNH 27.5.1.1*); San Martín de los Andes (BMNH 27.5.1.119); Sierra de Pil Pil (BMNH 27.5.1.2). '**Patagonia**', unknown locality (BMNH 1899.2.41, 3.11.5.10, 3.11.5.11). **Río Negro,** Estancia Huanu-Luan (FMNH 34193*); Huanuluan (MCZ 19110–19114); Pichi Mahuida (BMNH 27.6.21.1–27.6.21.9); Pilcaniyeu (BMNH 19.1.5.2, 19.1.5.22, 20.11.4.3); S shore of Lake Nahuel Huapi (BMNH 3.11.5.9). **Salta,** Cachi (BMNH 6.5.8.12–6.5.8.14, 6.5.8.16); Metán (La Cañada) (BMNH 34.11.4.14); Metán (La Represa) (BMNH 34.11.4.10–34.11.4.12, 34.11.4.8, 34.11.4.9). **San Juan,** Pedernal (BMNH 21.6.19.2–21.6.19.4). **Santa Cruz,** 40 km SW Puerto Santa Cruz (AMNH 17446*); Estancia Alta Vista, Lago Argentino (BMNH 28.12.11.8); Puerto Santa Cruz (CFA 9926); Río Chico, Departamento Corpen Aike (AMNH 25669*); Río Gallegos (USNM 264479); Santa Cruz (BMNH 99.2.4.2); unknown locality (MNHN 1883-163*). **Santa Fe,** Esperanza (BMNH 1.2.4.5, 1.2.4.7); Las Rosas (BMNH 17.5.2.2–17.5.2.4); San Cristóbal (BMNH 17.5.3.5). **Santiago del Estero,** Clodomira (CFA 9459); Lavalle (AMNH 41530*, 41531*, 41532, 41533, 41534*); Roversi (BMNH 34.11.4.13); Villa La Punta (CFA 10803). **Tucumán,** Tafi Viejo (AMNH 41529*). **BOLIVIA: Cochabamba,** 32 km S Tiraque (USNM 271410*); 43 km ESE of Iquisivi (BMNH 2.1.1.11*); Cochabamba (BMNH 2.1.1.15*); El Choro (BMNH 2.1.1.12–2.1.1.14); Tujma, near Mizque (AMNH 39011*). **La Paz,** 34 km NNE Nevado Sajama (BMNH 98.3.16.4*); 5 km E Ulla Ulla (AMNH 247712); Nevado Sajama (BMNH 3.2.9.2). **Oruro,** Pampa Aulliaga (BMNH 2.2.2.11). **Santa Cruz,** Comarapa (BMNH 34.9.2.53). **Tarija,** Carlazo (BMNH 26.1.1.2, 26.1.1.3); Tapecua, 13.5 k, WSW Palos Blancos (AMNH 264464*). **Santa Cruz,** 5 km SE Tita (AMNH 260327*). **BRAZIL: Bahia,** Lamarão (BMNH 3.9.5.45, 3.9.5.46, 3.9.5.47*, 3.9.5.48). **Goias,** Anapolis (AMNH 133948*). **Mato Grosso do Sul,** Maracaju (AMNH 133946*). **Minas Gerais,** Arinos (MZUFV 3471*); Itapecerica (MZUFV 4422*); Rio Jordão (BMNH 1.11.3.24, 1.11.3.25*). **Piauí,** Central Piauí (MCZ 24828). **Unknown state** (BMNH 68.a*). **Rio Grande do Sul,** Quinta (AMNH 235512*, 235513*, AMNH 235514*); Santana da Boa Vista (AMNH 235993*); Uruguaiana (AMNH 235994*). **CHILE: Araucania,** 2.5 km NNE Angol (AMNH 93324); Maquehue, 9.5 km WSW Temuco (AMNH 33290*, 33291*). **Talca?,** San Rafael? (BMNH 45.11.18.17). **Arica y Parinacota,** Parinacota (USNM 391849, 391850). **Magallanes,** Punta Arenas (AMNH 130053, 130068, 130095); Strait of Magellan (BMNH

66.a). **Valdivia,** Riñihue (FMNH 24350*). **Valparaíso,** Cerro Castillo, Viña del Mar (BMNH 10.7.23.1); Curaumilla Farm-Coast Hills (BMNH 0.10.2.2). **COLOMBIA: Nariño,** Vereda El Espino, 5.2 km SW Túquerres (UV 13287*). **ECUADOR: Bolívar,** Sinche (= Hacienda Sinche), 6 km NNE Guaranda (AMNH 67085*, BMNH 99.9.9.7*). **Chimborazo,** Hacienda Alao (MCZ 52661); Volcán Chimborazo (QCAZ 642). **Imbabura,** Hacienda La Vega, 5 km ESE San Pablo del Lago (FMNH 125113*); Volcán Imbabura (QCAZ 2046*). **Napo,** Baeza (MEPN 8169*); Cuyuja (QCAZ 726* = '638'); Probably Volcán Antisana (1923 expedition, H. E. Anthony and G. H. H. Tate) (AMNH 66244*); Volcán Antisana (AMNH 66719*). **Pastaza,** Río Pastaza, Mera (MNHN 1932-2884*). **Pichincha,** 40 km S Quito (AMNH 187838*); Alóag (AMNH 66722*); Cumbre del Monte Quitoloma (QCAZ 8338); El Castillo, vía Esmeraldas (FMNH 44336*); Hacienda Antisanilla, 33 km SE Quito (AMNH 63577, 66721*); Mindo (MEPN 8305*); Northwest side of Mindo (MCZ 27341); Pichincha Volcano (AMNH 36462*, 36463*); Quito (AMNH 36464–36466, BMNH 99.2.18.13*); San José de Minas (QCAZ 640); Santa Rosa above Río Pita (AMNH 66720*); unknown locality (BMNH 34.9.10.81*). **Tungurahua,** Montaña de Runtún, near Baños de Agua Santa (MCZ 38732). **Unknown province** (AMNH 66723, 66724, MEPN 2862, 6864, MNHN 1904-774). **PARAGUAY: Boquerón,** 50 km WSW Fortín Madrejón (AMNH 248467*, 248468*, 248469*, 248470*); Guachalla, Río Pilcomayo, 5.4 km SW San Agustín (FMNH 54329*, 54330*). **PERU: Ancash,** Carpa (AMNH 238425*). **Arequipa,** 2 km NE Yura Viejo (FMNH 106007*); 2.9 km NW Sumbay (FMNH 49720*); 5.3 km NW Salinas Moche (FMNH 49732, 49733*, 49734*); Caylloma (BMNH 3.8.4.1*, FMNH 49721, 49722, 49723*); Sumbay (BMNH 0.10.1.2). **Cajamarca,** Celendín (BMNH 26.4.1.116); Hacienda Limón, 60 km NE Cajamarca (FMNH 19680*). Hacienda Taulis (AMNH 73123). **Callao,** Callao (BMNH 0.5.7.34*). **Cusco,** Chospyoc (BMNH 22.1.1.19); Chospyoc, Río Huarocondo (USNM 194322); Ocobamba Valley (BMNH 22.1.1.20, USNM 194319*, 194320*); Orca, Near Calca (USNM 194324*); San Miguel Bridge, near Matchu Picchu (USNM 194323*). **Huánuco,** 4 km E Ambo (FMNH 24355*, FMNH 24356*). **Lima,** Near Huarochiri (USNM 176320*); Surco (BMNH 0.5.7.35–0.5.7.37). **Puno,** 2.2 km ESE Huacullani (FMNH 52486); Azángaro ('Sangero') (BMNH 1.1.1.10); Hacienda Checayani, near Azángaro (MNHN 1957-1293*, 1957-1294, 1957-1295, 1957-1296, 1957-1297*, 1970-301*, 1970-302*); Hacienda Collacachi, 12 km SSE Puno (FMNH 49724*, 49725*, 49726*, 49727*, 49728, 49729*, 49730*, 49731*); West shore of Lake Titicaca (MCZ 5257–5259). **URUGUAY: Artigas,** 6 km NNW Belén (in neighboring Departamento de Salto) (AMNH 205833–205835). **Cerro Largo,** 20 km NW Paso del Dragón (AMNH 205839); Estancia Las Marías, 6 km SE Melo (AMNH 205837, 205838). **Lavalleja,** 12 km WSW Zapicán (AMNH 205843, 205844). **Paysandú,** Arroyo Negro stream, 15 km S Paysandú (AMNH 205849, 205866). **Rocha,** Rocha, 24 km N San Vicente De Castillos (USNM 259436*). **Treinta y Tres,** 16 km SSW Tacuarí River mouth (AMNH 205895). **Unknown department** (BMNH 91.4.24.4, MHNM 3382*, 4298*, 4299*).

C. leuconotus (*n* = 21).— **Honduras: Francisco Morazán,** El Caliche (AMNH 127569*). **Olancho,** Catacamas (AMNH 128125*). **MEXICO: Jalisco,** Garabatos (Tepatitlán de Morelos) (AMNH 25171*); La Estancia (Arandas) (AMNH 25178*). **Oaxaca,** La Concepción, 11 km NE San Miguel Tenango (AMNH 145973*); San Pedro Tapanatepec (AMNH 176665*, 176668*). **Sinaloa,** Escuinapa de Hidalgo (AMNH 24707*). **Veracruz,** 11 km NW Alvarado (AMNH 172187*); 39 km S Veracruz (AMNH 204288*, 204289*); Córdoba (AMNH 30526*). **NICARAGUA: Jinotega,** San Rafael del Norte (AMNH 29282). **UNITED STATES: Arizona,** Near Fort Verde (AMNH 1921*, 1922*). '**California**', erroneous state (BMNH 55.12.24.221). **New Mexico,** Cliff (Grant Co.) (AMNH 127112*); Gila (Grant Co.) (AMNH 127110*). **Texas,** Juniper Canyon, Chisos Mountains (AMNH 136415*); Rockport (Aransas Co.) (AMNH 5130, 5883).

C. semistriatus (*n* = 111).— **BELIZE: Belize District,** 3.55 mi Northern Hwy (FMNH 58560*). **Cayo,** Red Creek, Before Santa Elena (FMNH 121557). **Stann Creek,** Stann Creek Valley (FMNH 63902). **COLOMBIA: Cesar,** Colonia Agrícola de Caracolicito, 9.3 km E Pamparejo (USNM 281452*, 281453, 281454); El Orinoco, Río Cesar, 37 km SSW Valledupar (USNM 281455, 281456*). **Córdoba,** Catival, upper Río San Jorge (FMNH 68904, 68905). **Cundinamarca,** Choachí (MCZ 27218, MCZ 27219); Finca El Soche, 4.0 km E Granada (UV 8103); Laguna de Fúquene (ICN 283); Las Balsillas (currently Bogotá) (AMNH 38423*, 38424*). **La Guajira,** Las Marimondas, 4 km ESE Conejo (USNM 281464*, 281465*); Sierra Negra, 8.5 km ENE Villanueva (USNM 281457*, 281458*, 281459*, 281460*); Villanueva (USNM 281461*, 281462*, 281463*). **Magdalena,** Bonda (AMNH 14632); Cuchilla de San Lorenzo (IAvH-M 1759). **Norte de Santander,** Parque Nacional Natural El Tamá, Maraña site (IAvH-M 3117). **COSTA RICA: Cártago,** Ricardo Jiménez Ranch, Irazú Volcano (AMNH 19206*). **Limón,** Jiménez (AMNH 2794). **Puntarenas,** Pozo Azul de Pirrís, plains of the Río Grande de Pirrís

(AMNH 19205*). **San José,** Escazú (AMNH 135269, 135271*, 137282*, 137283*); La Hondura, 22.5 km NE San José (AMNH 135270*); Santa Teresa (currently San José) (AMNH 141858*). **Unknown province** (USNM 19646, 19647, 61205*, 61275*). **ECUADOR: Sto. Domingo de los Tsáchilas,** Río Palenque Science Center, 1.7 km SSE Consumulo (USNM 568103*). **MEXICO: Quintana Roo,** La Vega, on mainland coast opposite Isla Cancún (USNM 108502*, 108503*). **Unknown state** (BMNH 2001.5). **Veracruz,** Achotal (FMNH 13825*); Catemaco (USNM 65762*, 65763*, AMNH 172190); Paso Nuevo (AMNH 17201*, 17202); Pérez (USNM 132512*). **Yucatán,** Mérida (USNM 8610*). **NICARAGUA: Chontales,** Villa Somoza (= Villa Sandino) (USNM 337832*). **Jinotega,** Hacienda La Trampa, 16 km E, 5.5 km N Jinotega (USNM 338870*). **Río San Juan,** La Esperanza, 9.5 km SE San Carlos (USNM 361359*). **PANAMA: Bocas del Toro,** Sibube (USNM 335773*). **Chiriquí,** 3.2 km NE El Volcán (USNM 332037*); Boquerón (AMNH 18900); Boquete (BMNH 4.7.6.5*, MCZ 10115, 10116); Cerro Punta (USNM 324236); Progreso (USNM 363346*). **PERU: Amazonas,** Chachapoyas (BMNH 24.7.11.10*, 24.7.11.11–24.7.11.13, 24.7.11.8, 24.7.11.9). **La Libertad,** Chicama Valley (USNM 172857*); Menocucho, 23.5 km ENE Trujillo (FMNH 19976*); San Pedro de Lloc (AMNH 73220). **Lambayeque,** Eten (BMNH 0.3.1.39*). **VENEZUELA: Falcón,** 20.5 km SSE Tucacas (USNM 372745*); 3.5–6.0 km NE Capatárida (EBRG 3309*, 3310*,3311*, 3312*, 443290*, 443291*, 443295*); Capatárida (USNM 443285*, 443286*, 443289*, 443293*, 443294*, 443296*); Dabajuro to Mene de Mauroa road, 25.6 km WSW Dabajuro (CVULA 8544*); Muaco, 3.5 km ENE Vela de Coro (MBUCV 4170*); Península de Paraguaná, 5.5 km WNW Adícora (CVULA 8545*); Península de Paraguaná, Cueva de Piedra Honda (EBRG 20237*, 20241*); Península de Paraguaná, Near Moruy, 15 km SSW Pueblo Nuevo (USNM 443414*); Península de Paraguaná, Reserva Biológica de Monte Cano (RBMC unnumbered); Pueblo Nuevo to Adícora road (CVULA 8542); Urumaco to Dabajuro road, 17 km WSW Urumaco (CVULA 8543*). **Mérida,** Casa del Ángel del Sol, 9.7 km ENE Mérida (CVULA 9130*); El Mirabel, 3 km SSE La Azulita (CVULA 6210*); La Hechicera, 3 km NNW Mérida (CVULA 8537*); Mountains W of Mérida (FMNH 22202*, 22203); Near Chorrera de las González, 5.1 km WSW Jají (CVULA 1025); unknown locality (AMNH 21634, AMNH 21635, BMNH 5.2.5.10*, 5.4.5.4*, 5.4.5.5*. **Yaracuy,** El Hacha (AMNH 32073). **Zulia,** El Rosario, 39 Km WNW Encontrados (USNM 443576*); Río Aurare, 12.5 km ESE Maracaibo (FMNH 18770*).

APPENDIX 2

Results of the Principal Component Analysis (PCA). Measurement loadings and percent variance explained by components are shown. Components 17 to 25 are omitted because together they explain less than 2% of total variance and 5% of total 'shape' (PC2 to PC25) variance. The measurements are ordered according to their communality values.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	Communality (PC2–PC16)
Precanine length	0.12	0.16	-0.52	0.58	0.05	-0.14	0.23	-0.14	0.96
Width of interpterygoid fossa	-0.07	0.15	0.70	0.50	-0.07	0.19	0.28	0.06	0.95
Length of PM4	0.20	-0.22	0.07	-0.03	-0.16	0.08	0.09	0.53	0.92
Post-notch length	0.06	0.65	0.06	-0.09	0.47	-0.08	-0.08	0.33	0.91
Heigth of cranium	0.20	0.17	0.13	-0.27	0.15	0.02	0.11	-0.35	0.91
Length of PM3	0.17	0.12	-0.11	0.23	-0.13	0.69	-0.31	-0.10	0.88
Postorbital breadth	0.19	-0.14	0.25	0.21	0.13	-0.21	-0.46	-0.26	0.87
Width across incisors	0.20	0.00	-0.08	0.23	0.19	0.03	-0.27	0.26	0.87
Height of coronoid	0.17	0.18	0.02	0.14	-0.55	-0.45	-0.07	-0.03	0.84
Length of mandible	0.20	0.23	-0.07	-0.05	-0.31	-0.15	0.13	0.22	0.79
Diameter of canine	0.21	-0.04	0.07	-0.14	-0.19	0.01	-0.34	0.17	0.72
Length of lower carnassial	0.21	-0.15	0.03	0.09	0.18	-0.07	0.40	0.17	0.67
Interorbital breadth	0.22	0.11	0.18	0.00	-0.01	-0.05	0.01	-0.23	0.60
Zygomatic breadth	0.22	0.06	0.10	-0.16	0.12	-0.10	0.02	-0.12	0.59
Width of molar	0.19	-0.35	0.07	-0.05	0.23	-0.07	0.09	0.10	0.50
Postpalatal length	0.22	-0.01	0.06	-0.15	-0.14	0.13	0.25	-0.20	0.48
Length of molar	0.19	-0.35	-0.08	0.19	0.24	-0.08	0.02	-0.08	0.46
Notch to canine length	0.22	-0.02	-0.13	-0.10	-0.13	0.17	0.04	-0.02	0.44
Length of maxillary toothrow	0.22	-0.13	0.01	-0.05	-0.04	0.12	0.05	0.12	0.43
Width across canines	0.23	0.01	0.07	0.03	0.01	-0.13	-0.18	0.14	0.34
Width across molars	0.23	-0.07	0.14	0.11	0.05	-0.05	-0.07	-0.03	0.28
Palatilar length	0.23	0.13	-0.16	-0.01	0.10	0.14	0.02	0.07	0.21
Mastoid breadth	0.23	0.06	0.03	-0.04	0.07	-0.10	0.00	-0.19	0.15
Basilar length	0.23	0.06	-0.04	-0.09	-0.04	0.16	0.14	-0.07	0.15
Condylobasal length	0.23	0.07	-0.02	-0.09	-0.01	0.08	0.17	-0.08	0.10
EIGENVALUE	17.36	1.65	1.24	0.76	0.72	0.63	0.52	0.36	
% TOTAL (PC1–PC25) VARIANCE	69.44	6.61	4.95	3.05	2.87	2.50	2.10	1.43	
% SHAPE (PC2–PC25) VARIANCE	0.00	21.63	16.18	9.98	9.38	8.20	6.86	4.68	

APPENDIX 2. (*Continuation*)

	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	Communality (PC2–PC16)
Precanine length	0.20	-0.28	0.29	0.08	0.03	0.07	0.07	0.08	0.96
Width of interpterygoid fossa	0.00	0.05	0.15	0.07	0.05	0.17	-0.03	0.01	0.95
Length of PM4	0.20	-0.34	-0.12	0.21	-0.09	-0.33	0.24	0.39	0.92
Post-notch length	0.23	0.20	0.00	0.03	-0.04	-0.17	-0.13	0.03	0.91
Heigth of cranium	-0.11	0.04	0.10	-0.06	0.32	0.14	0.52	0.46	0.91
Length of PM3	0.21	0.09	-0.28	-0.21	0.08	-0.09	0.06	-0.01	0.88
Postorbital breadth	0.08	0.06	0.01	0.01	-0.58	0.04	0.23	0.09	0.87
Width across incisors	-0.74	-0.06	0.01	0.11	0.18	-0.02	0.11	-0.13	0.87
Height of coronoid	-0.04	0.31	-0.16	0.00	0.23	-0.09	-0.18	0.23	0.84
Length of mandible	0.07	0.18	-0.14	-0.09	-0.20	0.16	0.46	-0.44	0.79
Diameter of canine	0.09	-0.08	0.65	-0.08	-0.05	0.16	-0.21	0.02	0.72
Length of lower carnassial	-0.23	0.03	-0.18	-0.42	-0.31	0.09	-0.14	0.14	0.67
Interorbital breadth	-0.09	-0.20	-0.12	0.53	0.03	-0.32	-0.09	-0.23	0.60
Zygomatic breadth	0.17	-0.46	-0.26	-0.02	0.06	0.33	-0.20	-0.23	0.59
Width of molar	0.28	0.30	0.16	0.10	0.28	-0.04	0.00	-0.10	0.50
Postpalatal length	-0.10	-0.01	0.27	-0.18	-0.11	-0.36	-0.01	-0.21	0.48
Length of molar	0.15	0.37	-0.08	0.06	0.12	-0.15	0.02	-0.12	0.46
Notch to canine length	-0.12	0.15	-0.10	0.20	-0.12	0.24	-0.37	0.26	0.44
Length of maxillary toothrow	0.08	0.05	-0.07	0.29	0.10	0.50	0.09	-0.13	0.43
Width across canines	0.02	-0.23	0.06	-0.35	0.28	-0.03	0.07	-0.08	0.34
Width across molars	0.07	-0.06	-0.13	-0.31	0.25	-0.04	-0.22	0.00	0.28
Palatilar length	-0.05	0.16	0.07	0.13	-0.15	0.14	-0.08	0.16	0.21
Mastoid breadth	0.03	-0.14	-0.16	-0.01	-0.11	-0.06	-0.11	0.15	0.15
Basilar length	-0.08	0.08	0.18	-0.03	-0.08	-0.14	-0.06	-0.07	0.15
Condylobasal length	-0.02	0.04	0.10	0.05	-0.10	-0.10	-0.02	-0.12	0.10
EIGENVALUE	0.32	0.26	0.20	0.18	0.16	0.15	0.12	0.12	
% TOTAL (PC1–PC25) VARIANCE	1.28	1.02	0.79	0.72	0.62	0.60	0.48	0.46	
% SHAPE (PC2–PC25) VARIANCE	4.20	3.35	2.60	2.37	2.03	1.97	1.56	1.52	