Geographic variation in *Caluromys derbianus* and *Caluromys lanatus* (Didelphimorphia: Didelphidae)

Raul Fonseca[1,2] & Diego Astúa[1,3]

[1]*Departamento de Zoologia, Universidade Federal de Pernambuco. Avenida Professor Moraes Rêgo, s/n, Cidade Universitária, 50670-901 Recife, PE, Brazil.*
[2]*Departamento de Zoologia, Universidade do Estado do Rio de Janeiro. 20550-013 Rio de Janeiro, RJ, Brazil.*
[3]*Corresponding author. E-mail: diegoastua@ufpe.br*

ABSTRACT. We analyzed the geographic variations in the shape and size of the cranium and mandible of two woolly opossums, *Caluromys derbianus* and *Caluromys lanatus*. Using geometric morphometrics we analyzed 202 specimens of *C. derbianus* and 123 specimens of *C. lanatus*, grouped in 7 and 9 populations, respectively. We found sexual dimorphism in shape variables only in the dorsal view of the cranium of *Caluromys derbianus*, which is not associated with geographical origin. We detected geographic variation in the size of the mandible in two populations (Nicaragua and Northern Panama), but no geographic variation in shape. The size of the cranium of *C. lanatus* varies significantly, with clinal variation in peri-Amazon populations, with a break between two populations, Bolivia and Paraguay. Shape analyses also revealed some separation between the Paraná population and all other populations. Our results suggest that the available name, *Caluromys derbianus*, should be maintained for all individuals throughout the geographic range of the species. The same is true for *Caluromys lanatus*, which can be separated into two distinct morphologic units, *Caluromys lanatus ochropus*, from the Amazon and Cerrado, and *Caluromys lanatus lanatus*, from the Atlantic forest.

KEY WORDS. Caluromyinae; geometric morphometrics; marsupial; Neotropics; skull; size and shape analysis.

The morphology and/or physiology of organisms usually vary across their distribution range. This is particularly true for species that are distributed over different biomes or biogeographic provinces (THORPE 1987). Such variation in intraspecific characters throughout a species' range is known as geographic variation (MAYR 1977). The study of geographic variation is key for understanding speciation and the role that ecological and geographical features may play in shaping biodiversity (HAFFER 1969, GOULD 1972, EMMONS 1984). Furthermore, geographic variation has been a central theme in evolutionary biology, from the works of Darwin to modern analyses based on molecular approaches (HALLGRÍMSSON & HALL 2005).

Morphological variation across geographical and environmental discontinuities occur in different small mammal groups, such as rodents (e.g., MACÊDO & MARES 1987, LESSA et al. 2005) and marsupials (e.g., LÓPEZ-FUSTER et al. 2000, HIMES et al. 2008). In the latter, variation can be found in external and cranial morphology and morphometric data (LEMOS & CERQUEIRA 2002, LÓPEZ-FUSTER et al. 2002, LÓSS et al. 2011), as well as in genetic characters (COSTA 2003, STEINER & CATZEFLIS 2004, BRAUN et al. 2005).

Woolly opossums of the genus *Caluromys* Allen, 1900 are part of a basal lineage within the living New World Didelphidae opossums (VOSS & JANSA 2009). *Caluromys* currently includes three species, *Caluromys derbianus* (Waterhouse, 1841), *Caluromys lanatus* (Olfers, 1818) and *Caluromys philander* Linnaeus, 1758 which are widely distributed in forest areas of Central and South America (GARDNER 2008). Variation in external morphological traits has been found in *Caluromys lanatus* (Thomas, 1913) throughout its geographic range. Venezuelan populations of *Caluromys* species (LÓPEZ-FUSTER et al. 2008) also present morphometric variation. This phenotypic diversity lead to the recognition of a number of morphologically distinct groups: eight subspecies of *C. derbianus* (BUCHER & HOFFMANN 1980, GARDNER 2008), four of *C. philander* (CABRERA 1958, GARDNER 2005) and six of *C. lanatus* (CÁCERES & CARMIGNOTTO 2006, GARDNER 2008).

The purpose of this study was to evaluate and to quantify the morphological variation in the size and shape of the cranium and mandible of *Caluromys derbianus* and *Caluromys lanatus* throughout their geographic range. We used geometric morphometric tools to evaluate whether the variation supports the taxonomic status of each species and their currently recognized subspecies.

MATERIAL AND METHODS

We obtained 2D images of the crania in three views (dorsal, ventral and lateral), and lateral images of the mandibles. Only complete adult specimens, i.e., specimens with all three premolars and four molars fully erupted and functional (TRIBE

1990, Astúa & Leiner 2008) were photographed. Specimens analyzed were from the following institutions: Museu Nacional – Universidade Federal do Rio de Janeiro (MN), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Paraense Emílio Goeldi (MPEG), Coleção de Mamíferos do Departamento de Zoologia da Universidade Federal de Minas Gerais (UFMG), Museu de História Natural Capão da Imbúia (MHNCI), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Louisiana State University, Museum of Natural Science (LSUMZ), Museum of Southwestern Biology (MSB), Museum of Vertebrate Zoology (MVZ), Kansas University, Museum of Natural History (KU) and National Museum of Natural History (USNM).

We digitized a total of 92 landmarks – 28 in dorsal, 28 in ventral, 22 in lateral views of the cranium, and 14 landmarks on the mandible – using TPS Dig (Rohlf 2006) (Fig. 1, Appendix 1). All landmarks were tested for repeatability (Falconer & Mackay 1996), which was set at 85% for inclusion in subsequent analyses.

We applied a a Generalized Procrustes Analysis (GPA) to all landmark configurations (Rohlf & Slice 1990), to remove the effects of isometric size, orientation and position. Conse-quently, only shape information was retained (Adams et al. 2004, 2013). We obtained two formally independent set of variables, used in the subsequent analyses. One set includes centroid size for all specimens. Centroid size is the univariate size variable resulting from the squared-root of sums of the squared distances between each landmark and the centroid of its configuration. This set was used in the analyses of geographic variation in the size of the studied structures (for more details see Zelditch et al. 2012). GPA also yields the partial warps and uniform components, a set of variables that retain all the information on the shape of the landmark configuration of the studied structures that were used in the analyses of geographic variation in shape. Further detail on the geometric morphometric procedures can be found in Zelditch et al. (2012).

We obtained the geographic coordinates of the collecting localities of each specimen from their skin tags. When coordinates were not in the tags, we used standard ornithological gazetteers (Paynter 1982, 1989, 1992, 1993, 1995, 1997) to recover them. Specimens from different localities were grouped into populations based on the features of the ecoregions (Olson et al. 2001) found in the distribution of both species (specimens from geographically close localities in the same ecoregion were pooled into populations). Next, to increase the sample size of populations resulting from the classification using ecoregions,
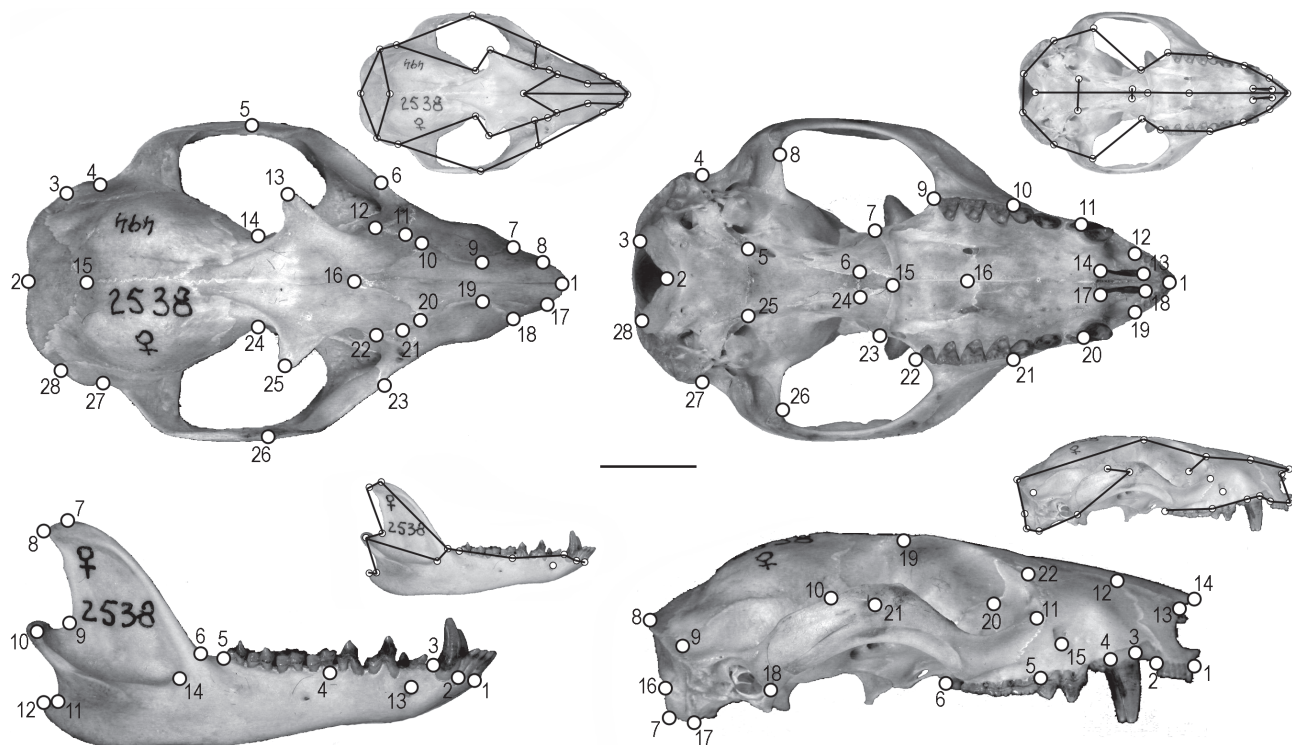

Figure 1. Landmarks used in the cranium and mandible. Smaller versions of each view include landmarks with links, as used deformation grids in subsequent figures. See Appendix 1 for detailed description of landmark locations. Scale bar: 1 cm.

we decided to pool the populations that were geographically closer to each other and which lacked morphometric divergence.

We examined a total of 202 specimens of *Caluromys derbianus* (the number of specimens analyzed in each view may vary because missing structures in one view may preclude the use of a photograph, while the photographs of the same specimen from other views can be used). The specimens were divided into seven populations: Colombian, Ecuadorian and Peruvian individuals (n = 9), Panama-Colombia (n = 16), Southern Panama (n = 22), Northern Panama (n = 51), Nicaragua (n = 54), Honduras (n = 37) and Mexico (n = 15) (Fig. 2). Likewise, we examined a total of 123 specimens of *Caluromys lanatus*, which were divided into 9 populations: Northern Venezuela (n = 11), Southern Venezuela (n = 8), Colombia (n = 17), Northern Peru (n = 22), Iquitos (n = 22), Peru-Bolivia (n = 15), Paraná (n = 8), Trombetas (n = 13), and Cerrado (n = 7) (Fig. 3). The list of all examined specimens with localities is presented in Appendix 2.

Literature information on the absence of sexual dimorphism in both species (ASTÚA 2010) was obtained from a smaller and geographically restricted dataset. With this in mind we re-evaluated the existence of sexual size dimorphism through a t-test on centroid size, and the existence of sexual shape dimorphism through a Hotteling T^2 test on shape variables. Since several populations were represented by only a few specimens, we pooled all males into one group and all females into another regardless of their geographic origin, in order to increase sample size and to avoid a type I error. To evaluate geographic variation in size, we compared populations with ANOVAs on centroid sizes, followed by Tukey *a posteriori* tests. To evaluate geographic variation in shape we compared shape variables between populations using Canonical Variates Analyses (CVA), following WEBSTER & SHEETS (2010), given that our total sample size was much larger than $[(2k – 4) + (G – 1)]$, where k is the number of variables and G is the amount of groups analyzed. For each view, this parameter ranged from 30 to 58 for *Caluromys derbianus*, and 32 to 60 for *C. lanatus*, indicating that running a CVA is appropriate. Because all analyses were repeated on four views of both species, we employed Bonferroni correction again, using a significant p-value of 0.0125 (0.05/4).

RESULTS

Sexual dimorphism

Neither species presented sexual dimorphism in size. Sexual dimorphism was observed only in the shape of the dorsal portion of the cranium of *Caluromys derbianus* (Hotteling
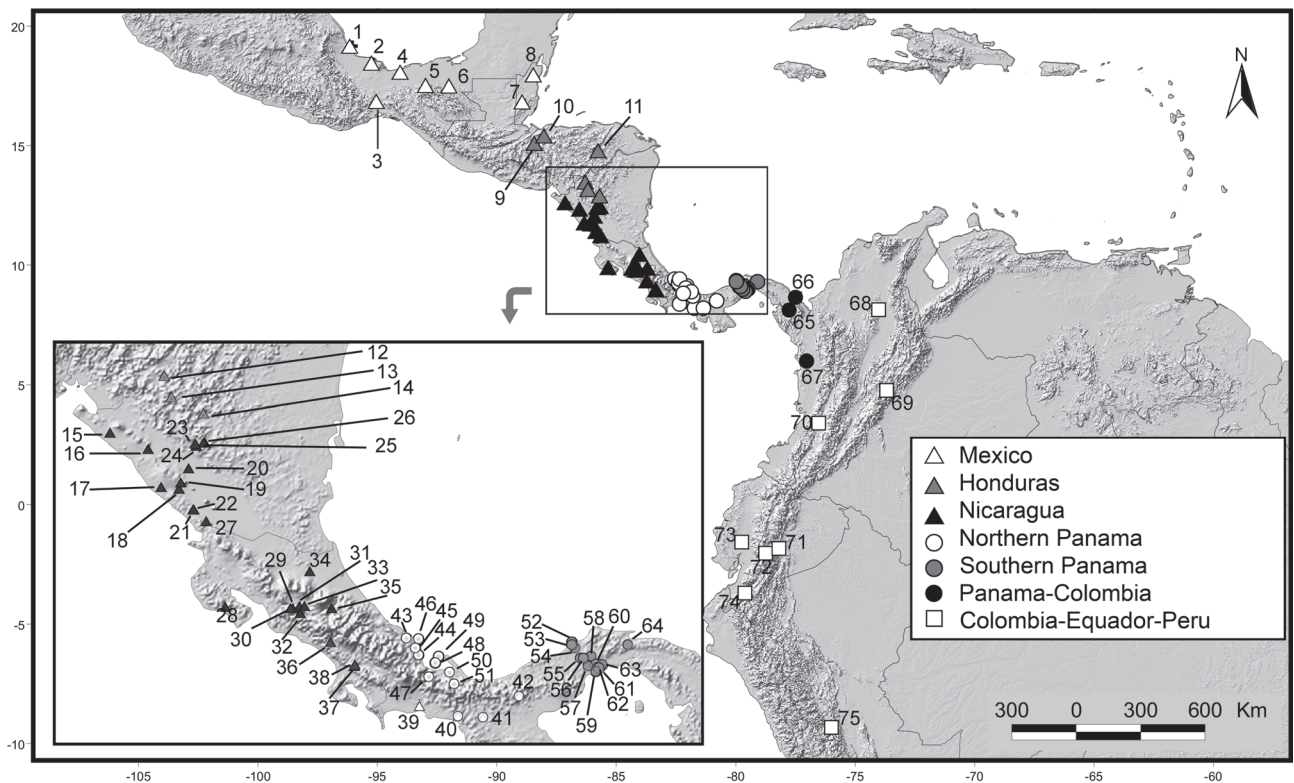

Figure 2. Distribution of the localities of *Caluromys derbianus* with specimens included in this study. Localities were grouped in populations for subsequent analyses, and are labelled accordingly. Numbers indicate localities as listed in Appendix 2.
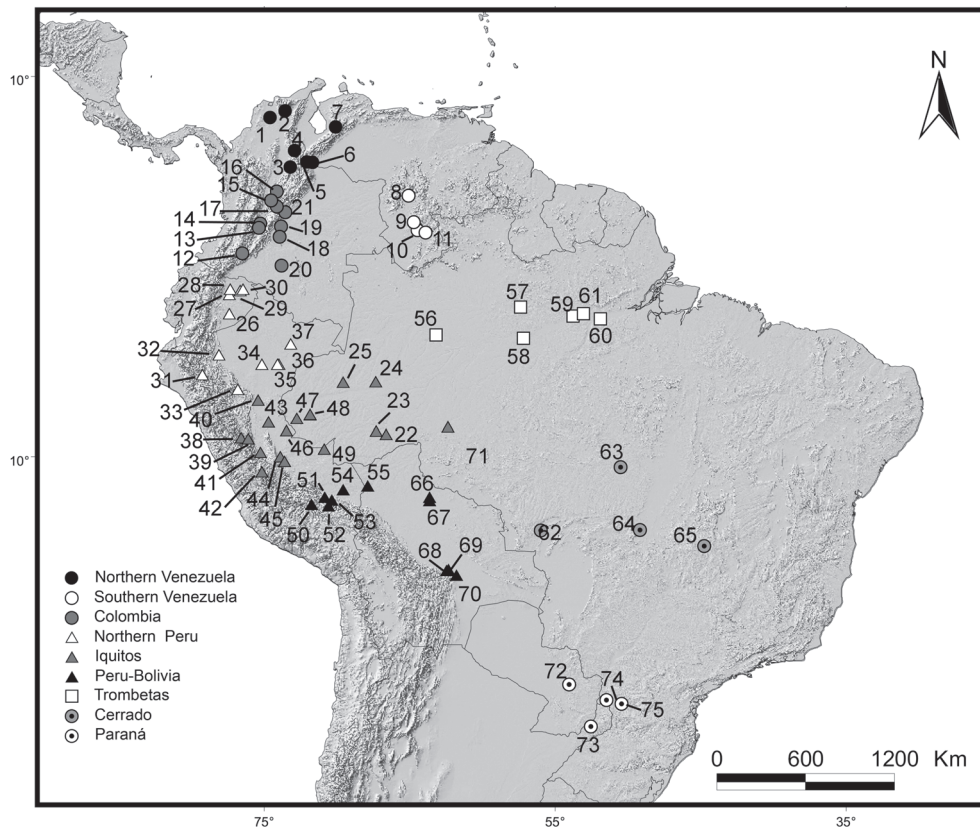
Figure 3. Distribution of the localities of *Caluromys lanatus* with specimens included in this study. Localities were grouped in populations for subsequent analyses, and are labelled accordingly. Numbers indicate localities as listed in Appendix 2.

$T^2 = 0.858$, $F = 1.82$; d.f. = 56, p < 0.01, 85 males, 90 females). In view of the absence sexual dimorphism in size and shape variables among individuals in all other views of both species, we decided to pool the sexes together within populations for subsequent analyses. This allowed us to include in the analyses specimens for which the sex was unknown.

Geographic variation in *Caluromys derbianus*

When analyzing size variation, we only found a statistically significant difference in mandible size, between the Nicaragua and Northern Panama populations (ANOVA F = 2.89, p < 0.01031, p < 0.002, *post-hoc* Tukey test). As for shape variation, the CVA scores overlapped considerably, indicating little morphometric divergence in size (Fig. 4). Given that the variation within each population was equal to or larger than the variation between populations, we concluded that the variation is not geographically structured and that the populations cannot be considered morphologically distinct.

Geographic variation in *Caluromys lanatus*

Under all views, size varied geographically (ANOVA, Dorsal: F = 11.02, p < 0.0001; Lateral: F = 3.66, p < 0.001; Ventral:

F = 9.62, p < 0.0001; Mandible: F = 10.91, p < 0.0001), but no clear grouping was observed among populations. However, a north-south clinal variation in skull size can be inferred, with specimens increasing in size from Colombia (smallest) to Bolivia (largest), with Ecuadorian and Peruvian specimens presenting intermediate sizes. This trend is then interrupted in southern Bolivia, with specimens from southeastern Brazil, Paraguay and Argentina being smaller than their Bolivian counterparts (Fig. 5).

Caluromys lanatus has a conserved skull shape throughout its geographic range. CVA scores show a partial separation of the Paraná population from all others, due to a variation in the morphology of the occipital and posterior roots of the squamosal, which are larger in Paraná specimens than in other individuals. The morphology of the rostrum also varies, with short and narrow nasals and basicranium with short frontals and longitudinal elongation of parietals (visualized through displacement of landmarks at the postorbital constriction) in the dorsal view of the cranium (Fig. 6). Additionally, an increase in occipital width, a more horizontally aligned molar tooth row, and shorter and narrow rostrum are found in Paraná individuals, in lateral view of the cranium (Fig. 7).
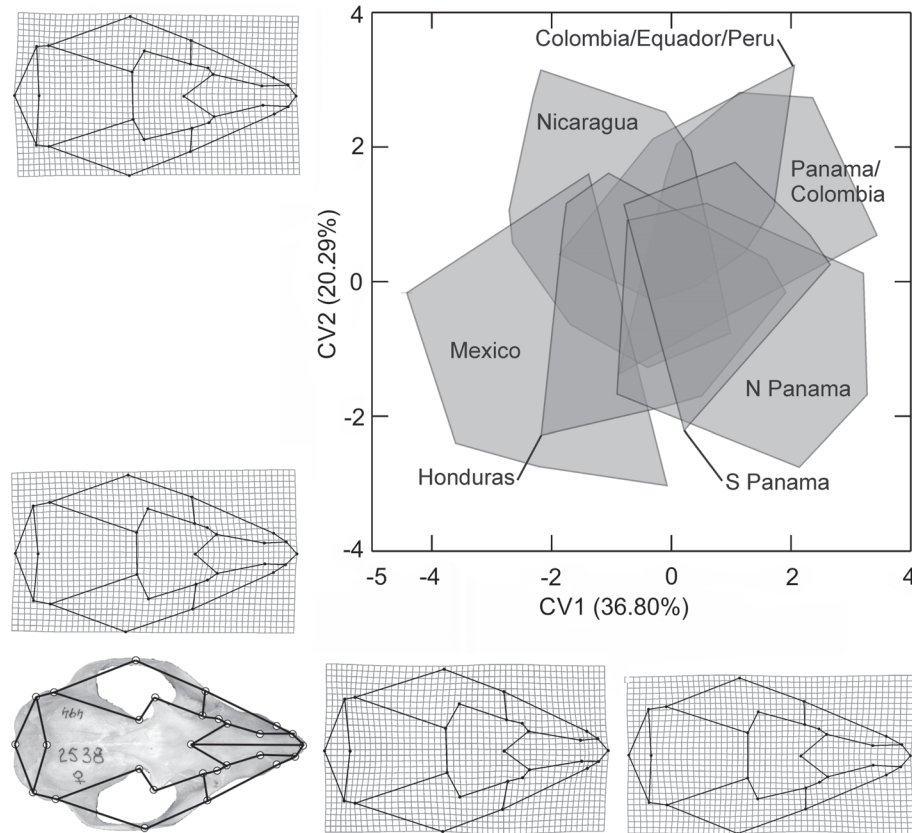
Figure 4. Canonical Variates Analysis on shape variables (partial warps and uniform components) of the skull in dorsal view of *Caluromys derbianus*, using localities as grouping factors, and percentage of variance explained by the first two CVs. Only the convex hulls for each population are shown. Grids indicate deformation associated with the extremes of each CV, from a multivariate regression of shape variables onto CV scores. Overlap for all other views are very similar, therefore only the dorsal view of the cranium is shown.

DISCUSSION

Structured geographic variation in cranial size and shape was not detected in *Caluromys derbianus*. However, it was observed in *Caluromys lanatus* populations. Despite the fact that subspecies have been recognized for *C. derbianus*, its populations belong to a single morphologic unit, which is spread throughout the geographic distribution of the species. Our results also corroborate that *Caluromys lanatus* is one species, but with two distinct morphological groups, one in the Amazon-Cerrado and the other in the Atlantic forest.

The absence of sexual size dimorphism in the skull of these species was already discussed (Astúa 2010), although that analysis, unlike ours, detected significant sexual shape dimorphism in both species.

Geographic variation in *Caluromys derbianus*

We did not find any evidence of structured geographical variation in the size of the skull of *Caluromys derbianus*, despite

its occurrence in the congeneric species *C. lanatus* (this study) and *C. philander* (Olifiers et al. 2004). We were also unable to detect a pattern in the geographic variation of the shape and size of the skull that would match the current taxonomic structures proposed for this species at the subspecific level. Bucher & Hoffmann (1980) and Gardner (2008) divided *Caluromys derbianus* into seven subspecies and one trans-Andean "unspecified" population. These populations were based on morphological differences such as fur color. As we used only cranial quantitative data, it is possible that other characters, particularly in the external morphology, may be the reason for the high number of subspecies. In particular, pelage color, which was not assessed in this study, is well known to vary geographically in this and other marsupial genera (Thomas 1913, Goodwin 1942) and might explain the discrepancy between the existing classification and the one that results from our quantitative results from skull morphology, which failed to support a separation.

The distribution of *Caluromys derbianus* represents a continuum of populations on a N-S stripe, most of which are in
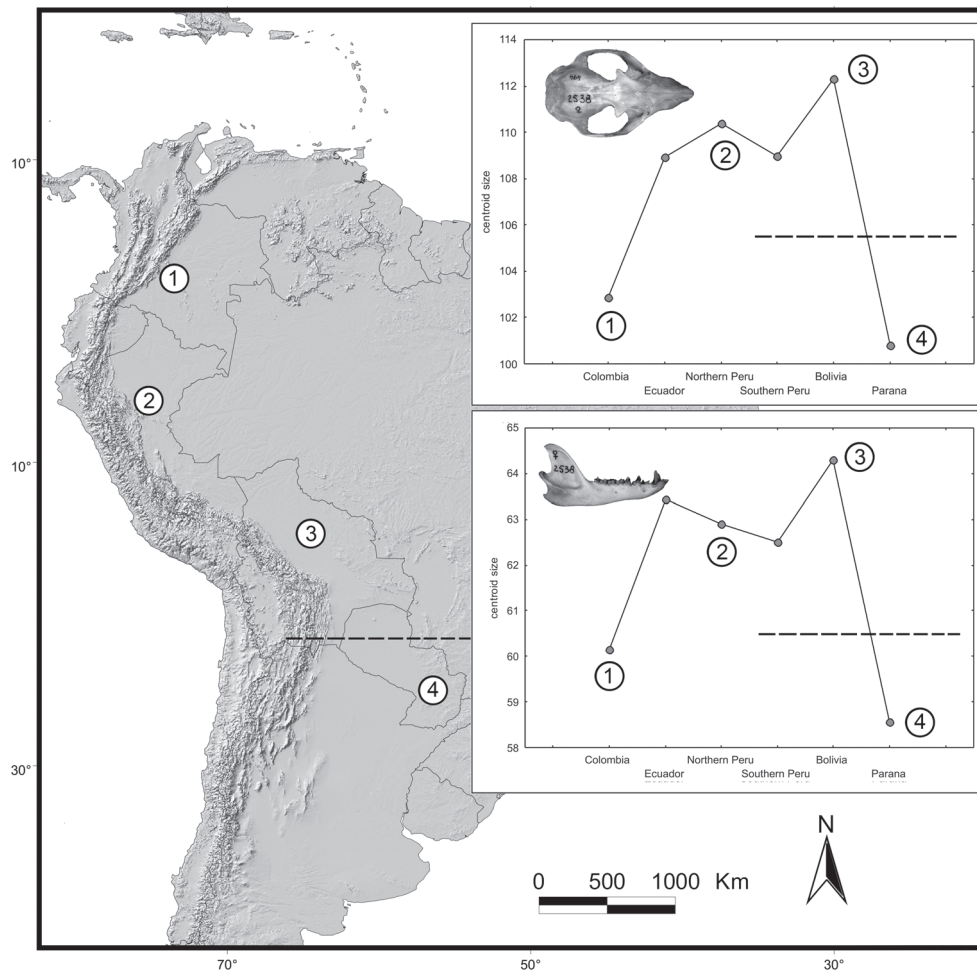
Figure 5. Clinal variation in size of the skull and mandible of populations of *Caluromys lanatus* along the east of the Andes, from Colombia to Bolivia, with a break between Bolivian and Northern Paraguay/Southern Brazil populations, indicated by the dashed line. Numbers in the map refer to the same points in the two graphs.

Central America and the remaining populations in the Andes in South America. The absence of geographic variation in the size of the cranium and mandible shape of this species is noteworthy, since several geographic and ecological discontinuities found throughout its distribution range are believed to cause variation among populations of other taxa (Savage 1987, Pérez-Emán 2005, Castoe et al. 2009).

Geographic variation in *Caluromys lanatus*

Clinal variation occurs throughout the range of many mammals (Storz et al. 2001, Cardini et al. 2007). We found clinal variation in the size of the skull of *Caluromys lanatus* from Andean populations, to the Bolivian-Paraguayan border, coinciding with those populations that overlap less in shape analyses. Even though we have not analyzed molecular data, we believe that the large overlap of CVA scores among all Amazon populations can be associated with reduced genetic divergence in this species. The latter has been already noted for populations distributed in this area (Patton et al. 2000, Patton & Costa 2003).

The divergence among the Paraná population and the others may correspond to the geographic differences between the Amazon and the Atlantic Rainforest. A similar variation pattern has also been observed to occur in *Didelphis*, *Marmosa*, *Caluromys philander* and *Metachirus nudicaudatus* (Costa 2003, Patton & Costa 2003). Both morphological and genetic divergence were observed in these species. Similar results were also recorded for rodent genera such as *Rhipidomys*, *Oecomys*, *Hylaeamys* and *Euryoryzomys* (Costa 2003). Populations from Paraná are ecologically separated from others by the Chaco – xerophytic plant cover, located in Argentina and Paraguay (Marco & Páezw 2002, Boletta et
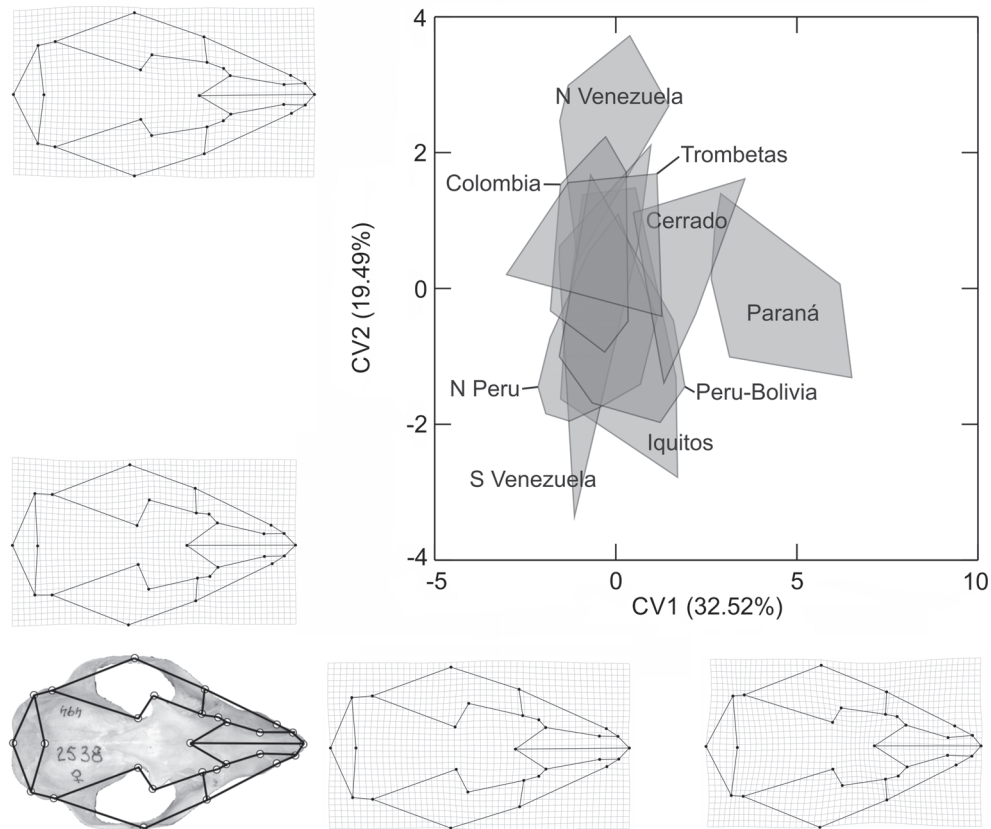
Figure 6. Canonical Variates Analysis on shape variables (partial warps and uniform components) of the cranium in dorsal view of *Caluromys lanatus*, using localities as grouping factors, and percentage of variance explained by the first two CVs. Only the convex hulls for each population are shown. Grids indicate deformation associated with the extremes of each CV, from a multivariate regression of shape variables onto CV scores.

al. 2006), which is characterized by medium and large trees such as Bignoniaceae, Leguminosae and grass fields (PENNINGTON et al. 2000). The increase in the Araucaria cover in the early Holocene (LEDRU 1993, SALGADO-LABOURIAU et al. 1998) over open areas may have served as a bridge between the forested areas of the Atlantic forest and the Amazon (AB'SABER 2000). This plant cover probably allowed the dispersion of *Caluromys lanatus* from the Amazon and Cerrado to the southern Atlantic Rainforest (COSTA 2003, PATTON & COSTA 2003), where these new populations were later isolated by open lands that arose between these areas (LEDRU et al. 1998, VAN DER HAMMEN & HOOGHIEMSTRA 2000, BEHLING 2002). This contact and subsequent isolation hypothesis is particularly likely for *Caluromys lanatus*, since this species is strictly arboreal. Environmental discontinuities that incur in canopy fragmentation may hinder population movements (PIRES et al. 2002), thus providing an effective ecological barrier like the one that has been associated with speciation of the congeneric *Caluromys philander* (LIRA et al. 2007). Morphologi-

cal similarities between populations from Central Brazil and the Amazon may be explained by the fact that Cerrado vegetation may not be uniformly affected by climatic changes (SALGADO-LABOURIAU et al. 1997). At higher altitudes the plant composition was less altered even in the dry periods of the Pleistocene and may have extended to lower areas during cold periods (BUSH et al. 2004). Grassland vegetation may have replaced only low-altitude forests (SALGADO-LABOURIAU et al. 1997, 1998). Due to climatic and pluviometric oscillations, eventual expansions of gallery forests may have created ecological corridors that allowed faunal and floristic population flow among Cerrado, Llanos, Amazonia and even Gran-Sabana (CERQUEIRA 1982, LEDRU 2002, OLIVEIRA-FILHO & RATTER 1995 apud DE OLIVEIRA et al. 2005). Gallery forests house twice as many forest-related species than the entire Cerrado *latu sensu* (JOHNSON et al. 1999). These forested areas may not have been totally affected by climatic changes and may have been used as a corridor that kept Amazonian and Cerrado populations in contact (CARDOSO & BATES 2002).
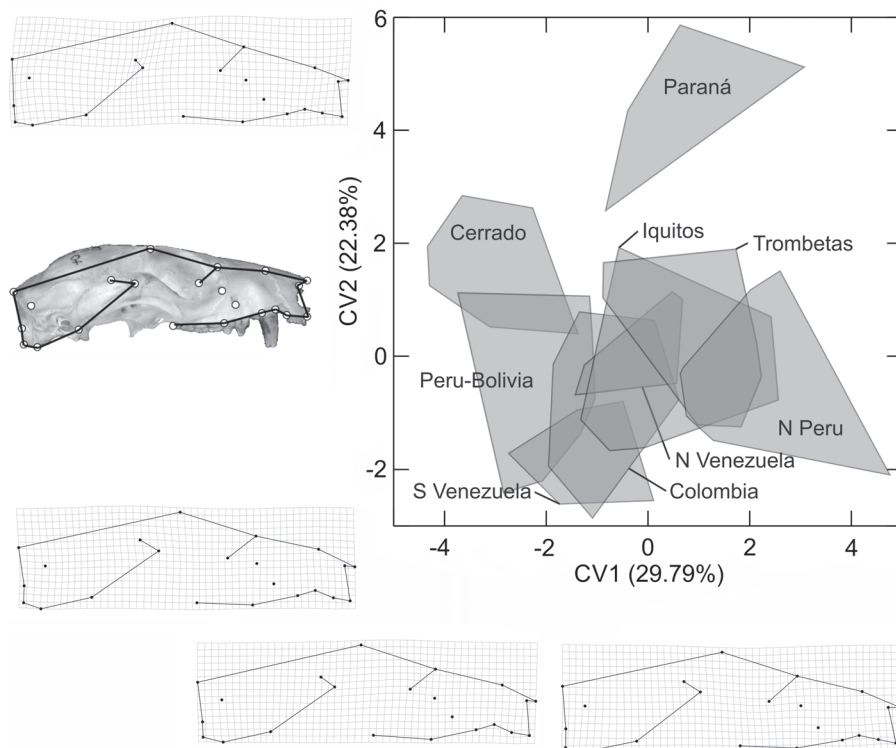
Figure 7. Canonical Variates Analysis on shape variables (partial warps and uniform components) of the cranium in lateral view of *Caluromys lanatus*, using localities as grouping factors, and percentage of variance explained by the first two CVs. Only the convex hulls for each population are shown. Grids indicate deformation associated with the extremes of each CV, from a multivariate regression of shape variables onto CV scores.

Potential implications for the taxonomic classification of *Caluromys derbianus* and *Caluromys lanatus*

The similar skull morphology shared by all populations of *Caluromys derbianus* suggest that the seven subspecies – *C. derbianus aztecus*, *C. d. canutus*, *C. d. centralis*, *C. d. derbianus*, *C. d. fervidus*, *C. d. nauticus* and *C. d. parvidus* – may be considered a unique species on morphometric grounds. Likewise, the lack of geographic variation among the Amazon and Cerrado populations of *Caluromys lanatus* suggest that three of the four subspecies recognized by CABRERA (1958) – *C. lanatus cicur*, *C. lanatus ornatus* and *C. lanatus ochropus* – and four of the six suggested by GARDNER (2008) – *C. lanatus cicur*, *C. lanatus ornatus*, *C. lanatus ochropus* and *C. lanatus vitalinus* can be lumped based on morphometrical data. The geographic variation found in skull morphometric data of individuals from the southern Atlantic Forest also suggest that two subspecies proposed by GARDNER (2008) – *C. lanatus lanatus* and *C. lanatus vitalinus* from southern Brazil can also be lumped.

All these subspecies were described based on external morphological characters, such as body, facial, dorsal, caudal or feet color, characters that usually present geographic variation (THOMAS 1899, 1913, ALLEN 1904, HOLLISTER 1914, GOODWIN 1942). *Caluromys* species were first described based on morphological characters of a single or a few individuals; subspecies were generally described after comparing individual variation with the holotype. For this reason, it cannot ruled out that these subspecies were based on individual variation. In all cases, pending a proper extensive review of coat color or other morphological variation in *Caluromys*, our extensive and quantitative results do not support separation of these taxa.

However, because phenotype is mainly the expression of the underlying genotype, morphological divergence is often interpreted as evidence of specific status. In didelphids, for example, morphological evidence has been used to support splitting of the black-eared and the white-eared opossums (CERQUEIRA & LEMOS 2000, LEMOS & CERQUEIRA 2002) of the genus *Didelphis*, and Bolivian species of *Marmosops* (VOSS et al. 2004). As such, it it possible that the morphologic groups found here may represent distinct species (see, however LÓSS et al. 2011, for a situation where morphologic differentiation does not coincide with species limits). The recognition of southern and southeastern populations of South American didelphids as distinct species appears to be a recurrent pattern that emerges after a deeper analysis of the existing variation, such as in *Phi-*

lander (Patton & da Silva 1997) and *Marmosa* (Patton & Costa 2003). Such changes are actually the reflection of our still incomplete knowledge on the taxonomy and systematics of didelphids.

A proper and definite appraisal of the taxonomic status of both woolly opossums would require an integrative approach (including other phenotypical and genetic characters) to unveil their actual status. Especially among *Caluromys lanatus* populations, a molecular approach may be useful to assess if these divergent groups constitute distinct evolutionary lineages that would ultimately validate their status as distinct species. Pending this, we suggest that the available name *Caluromys derbianus* (Waterhouse, 1841) is maintained for all individuals across the geographic distribution of its populations. The name *Caluromys lanatus* (Olfers, 1818) should also be considered valid, with at least two distinct morphometric units, namely *Caluromys lanatus ochropus*, representing Amazon and Cerrado populations, and *Caluromys lanatus lanatus*, encompassing Atlantic forest individuals.

ACKNOWLEDGEMENTS

LITERATURE CITED

Adams DC, Rohlf FJ, Slice DE (2004) Geometric morphometrics: ten years of progress following the 'revolution'. **Italian Journal of Zoology 71**(1): 5-16. doi: 10.1080/11250000409356545

Adams DC, Rohlf FJ, Slice DE (2013) A field comes of age: geometric morphometrics in the 21st century. **Hystrix, the Italian Jornal of Mammalogy 24**(1): 7-14. doi: 10.4404/hystrix-24.1-6283

Ab'saber AN (2000) Spaces occupied by the expansion of dry climates in South America during the Quaternary ice ages. **Revista do Instituto Geológico 21**(1/2): 71-78.

Allen JA (1904) Mammals from southern Mexico and Central and South America. **Bulletin American Museum of Natural History 20**(4): 29-80.

Astúa D (2010) Cranial sexual dimorphism in New World marsupials and a test of Rensch's rule in Didelphidae. **Journal of Mammalogy 91**(4): 1011-1024. doi: 10.1644/09-MAMM-A-018.1

Astúa D, Leiner NO (2008) Tooth eruption sequence and replacement pattern in woolly opossums, genus *Caluromys* (Didelphimorphia: Didelphidae). **Journal of Mammalogy 89**(1): 244-251. doi: 10.1644/06-MAMM-A-434.1

Behling H (2002) South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. **Palaeogeography, Palaeoclimatology, Palaeoecology 177**: 19-27. doi: 10.1016/S0031-0182(01)00349-2

Boletta PE, Ravello AC, Planchuelo AM, Grilli M (2006) Assessing deforestation in the Argentine Chaco. **Forest Ecology and Management 228**: 108-114. doi: 10.1016/j.foreco.2006.02.045

Braun JK, Van den Bussche RA, Morton PK, Mares MA (2005) Phylogenetic and biogeographic relationships of mouse opossums *Thylamys* (Didelphimorphia, Didelphidae) in southern South America. **Journal of Mammalogy 86**(1): 147-159. Available online at: http://jmammal.oxfordjournals.org/content/86/1/147 [Accessed: 20 April 2015]

Bucher JE, Hoffmann RS (1980) *Caluromys derbianus*. **Mammalian Species 140**: 1-4.

Bush MB, De Oliveira PE, Colinvaux PA, Miller MC, Moreno JE (2004) Amazonian paleoecological histories: one hill, three watersheds. **Palaeogeography, Palaeoclimatology, Palaeoecology 214**(4): 359-393. doi: 10.1016/j.palaeo.2004.07.031

Cabrera A (1958) Catalogo de los mamiferos de America del Sur. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas 4**(1): 1-46.

Cáceres NC, Carmignotto AP (2006) *Caluromys lanatus*. **Mammalian Species 803**: 1-6. doi: 10.1644/803.1

Cardini A, Jansson A, Elton S (2007) A geometric morphometric approach to the study of ecogeographical variation in vervet monkeys. **Journal of Biogeography 34**: 663-678. doi: 10.1111/j.1365-2699.2007.01731.x

Cardoso JMD, Bates JM (2002) Biogeographic patterns and conservation in the South American Cerrado: A tropical Savanna spot. **BioScience 52**(3): 225-233. doi http://dx.doi.org/10.1641/0006-3568(2002)052[0225:BPACIT]2.0.CO;2

Castoe TA, Daza JM, Smith ER, Sasa MM, Kuch U, Campbell JA, Chippindale PT, Parkinson CL (2009) Comparative phylogeography of pitvipers suggests a consensus of ancient Middle American highland biogeography. **Journal of Biogeography 36**: 88-103. doi: 10.1111/j.1365-2699.2008.01991.x

Cerqueira R (1982) South American landscapes and their mammals, p. 539-539. In: Mares MA, Genoways HH (Eds.). **Mammalian Biology in South American.** Pittsburg, University of Pittsburg, Special Publication Pymatuning Laboratory of Ecology.

Cerqueira R, Lemos B (2000) Morphometric differentiation between Neotropical black-eared opossums, *Didelphis marsupialis* and *D. aurita* (Didelphimorphia, Didelphidae). **Mammalia 64**: 319-327. doi: 10.1515/mamm.2000.64.3.319

Costa LP (2003) The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. **Journal of Biogeography 30**(1): 71-86. doi: 10.2307/827350

De Oliveira PE, Behling H, Ledru M-P, Barberi M, Bush M, Salgado-Labouriau ML, Medeanic S, barth OM, Barros MA, Schell-Yhert R (2005) Paleovegetação e paleoclimas do Quaternário do Brasil, p. 52-74. In: Souza CRG, Suguio K, Oliveira AMS, De Oliveira PE (Ed.). **Quaternário do Brasil.** São Paulo, Holos, Associação Brasileira de Estudos do Quaternário.

Emmons L (1984) Geographic variation in densities and diversities of non-flying mammals in Amazonia. **Biotropica 16**(3): 210-222. doi: 10.2307/2388054

Falconer DS, Mackay TFC (1996) **Introduction to Quantitative Genetics.** Harlow, Longman.

Gardner AL (2005) Order Didelphimorphia, p. 3-18. In: Wilson DE, Reeder DM (Ed.). **Mammal species of the world: a taxonomic and geographic reference.** Baltimore, Johns Hopkins University Press, 3rd ed.

Gardner AL (2008) **Mammals of South America.** Chicago, The University of Chicago Press.

Goodwin GG (1942) Mammals of Honduras. **Bulletin American Museum of Natural History 79**: 107-195.

Gould SJ, Johnston RF (1972) Geographic variation. **Annual Review of Ecology and Systematics 3**: 457-499. doi: 10.1146/annurev.es.03.110172.002325

Haffer J (1969) Speciation in Amazonian forest birds. **Science 165**: 131-137. doi: 10.1126/science.165.3889.131

Hallgrímsson B, Hall BK (2005) **Variation. A Central Concept in Biology.** Elsevier Academic Press.

Himes CMT, Gallardo MH, Kenagy GJ (2008) Historical biogeography and post-glacial recolonization of South American temperate rain forest by the relictual marsupial *Dromiciops gliroides* **Journal of Biogeography 35**: 1415-1424. doi: 10.1111/j.1365-2699.2008.01895.x

Hollister N (1914) Four new mammals from tropical America. **Proceedings of the Biological Society of Washington 27**: 103-106.

Johnson MA, Saraiva PM, Coelho D (1999) The role of gallery forests in the ditribution of Cerrado mammals. **Revista Brasileira de Biologia 59**(3): 421-427. doi: 10.1590/S0034-71081999000300006

Ledru M-P (1993) Late Quaternary environment and climatic changes in Central Brazil. **Quaternary Research 39**: 90-98. doi: 10.1006/qres.1993.1011

Ledru M-P, Salgado-Labouriaub ML, Lorscheitterc ML (1998) Vegetation dynamics in southern and central Brazil during the last 10,000yr. B.P. **Review of Palaeobotany and Palynology 99**: 131-142. doi: 10.1016/S0034-6667(97)00049-3

Ledru MP (2002) Late Quaternary history and evolution of the Cerrados as revealed by palynological records, p. 33-50. In: Oliveira PS, Marquis RJ (Eds.). **The Cerrados of Brazil: ecology and natural history of a Neotropical Savanna.** New York, Columbia University Press.

Lemos B, Cerqueira R (2002) Morphological differentiation in the white-eared opossum group (Didelphidae: *Didelphis*). **Journal of Mammalogy 83**(2): 354-369. Available online at: http://jmammal.oxfordjournals.org/content/83/2/354 [Accessed: 20 April 2015]

Lessa G, Gonçalves PR, Pessôa LM (2005) Variação geográfica em caracteres cranianos quantitativos de *Kerodon rupestris* (Wied, 1820) (Rodentia, Caviidae). **Arquivos do Museu Nacional 63**(1): 75-88.

Lira PK, Fernandez FAS, Carlos HSA, Curzio PL (2007) Use of fragmented landscape by three species of opossum in southeastern Brazil. **Journal of Tropical Ecology 23**: 427-435. doi: 10.1017/S0266467407004142

Lopez-Fuster MJ, Perez-Hernandez R, Ventura J (2008) Morphometrics of genus *Caluromys* (Didelphimorphia: Didelphidae) in northern South America. **Orsis 23**: 97-114.

López-Fuster MJ, Pérez-Hernandez R, Ventura J, Salazar M (2000) Effect of environment on skull-size variation in *Marmosa robinsoni* in Venezuela. **Journal of Mammalogy 81**(3): 829. doi: 10.1093/jmammal/81.3.829

López-Fuster MJ, Salazar M, Pérez-Hernández R, Ventura J (2002) Craniometrics of the orange mouse opossum *Marmosa xerophila* (Didelphimorphia: Didelphidae) in Venezuela. **Acta Theriologica 47**(2): 201-209. doi: 10.1007/BF03192460

Lóss S, Costa LP, Leite YLR (2011) Geographic variation, phylogeny and systematic status of *Gracilinanus microtarsus* (Mammalia: Didelphimorphia: Didelphidae). **Zootaxa 2761**: 1-33.

Macêdo RH, Mares MA (1987) Geographic variation in the South American cricetine rodent *Bolomys lasiurus*. **Journal of Mammalogy 68**(3): 578-594. doi: 10.2307/1381594

Marco D, Páezw SA (2002) Phenology and phylogeny of animal-dispersed plants in a Dry Chaco forest (Argentina). **Journal of Arid Environments 52**: 1-16. doi: 10.1006/jare.2002.0976

Mayr E (1977) **Populações, espécies e evolução.** São Paulo, Companhia Editora Nacional, Editora da Universidade de São Paulo.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the World: a new map of life on Earth. **BioScience 51**(11): 933-938. doi: http://dx.doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Olifiers N, Vieira MV, Grelle CEV (2004) Geographic range and body size in Neotropical marsupials. **Global Ecology and Biogeography 13**(5): 439-444. doi: 10.1111/j.1466-822X.2004.00115.x

PATTON JL, COSTA LP (2003) Molecular phylogeography and species limits in rainforest didelphid marsupials of South America, p. 63-81. In: JONES ME, DICKMAN CR, ARCHER M (Eds.). **Predators with pouches: The Biology of Carnivorous Marsupials.** Collingwood, CSIRO Publishing.

PATTON JL, DA SILVA MNF, MALCOM JR (2000) Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. **Bulletin of the American Museum of Natural History 244**: 1-306.

PATTON JL, DA SILVA MNF (1997) Definition of species of pouched four-eyed opossums (Didelphidae, *Philander*). **Journal of Mammalogy 78**(1): 90. doi: 10.2307/1382642

PAYNTER JR RA (1982) **Ornithological Gazetteer of Venezuela.** Cambridge, Museum of Comparative Biology, Harvard University.

PAYNTER JR RA (1989) **Ornithological Gazetteer of Paraguay.** Cambridge, Museum of Comparative Biology, Harvard University.

PAYNTER JR RA (1992) **Ornithological Gazetteer of Bolivia.** Cambridge, Museum of Comparative Biology, Harvard University.

PAYNTER JR RA (1993) **Ornithological Gazetteer of Ecuador.** Cambridge, Museum of Comparative Biology, Harvard University.

PAYNTER JR RA (1995) **Ornithological Gazetteer of Argentina.** Cambridge, Museum of Comparative Biology, Harvard University.

PAYNTER JR RA (1997) **Ornithological Gazetteer of Colombia.** Cambridge, Museum of Comparative Biology, Harvard University.

PENNINGTON RT, PRADO DE, PENDRY CA (2000) Neotropical Seasonally Dry Forests and Quaternary vegetation changes. **Journal of Biogeography 27**(2): 261-273. doi: 10.1046/j.1365-2699.2000.00397.x

PÉREZ-EMÁN JL (2005) Molecular phylogenetics and biogeography of the Neotropical redstarts (*Myoborus*; Aves, Parulinae). **Molecular Phylogenetics and Evolution 37**: 511-528. doi: 10.1016/j.ympev.2005.04.013

PIRES AS, LIRA PK, FERNANDEZ FAS, SCHITTINI GM, OLIVEIRA LC (2002) Frequency of movements of small mammals among Atlantic Coastal Forest fragments in Brazil. **Biological Conservation 108**(2): 229-237. doi: 10.1016/S0006-3207(02)00109-X

ROHLF FJ (2006) **TpsDig.** Stony Brook, Department of Ecology and Evolution, State University of New York.

ROHLF FJ (2011) **TpsRegr.** Stony Brook, Department of Ecology and Evolution, State University of New York.

ROHLF FJ, SLICE D (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. **Systematic Zoology 39**: 40-59. doi: 10.2307/2992207

SALGADO-LABOURIAU ML, BARBERI M, FERRAZ-VICENTINI KR, PARIZZI MG (1998) A dry climatic event during the late Quaternary of tropical Brazil. **Review of Palaeobotany and Palynology 99**: 115-129. doi: 10.1016/S0034-6667(97)00045-6

SALGADO-LABOURIAU ML, CASSETI V, FERRAZ-VICENTINI KR, MARTIN L, SOUBIÉS F, SUGUIO K, TURCQ B (1997) Late Quaternary vegetacional and climatic changes in Cerrado and palm swamp from Central Brazil. **Palaeogeography, Palaeoclimatology, Palaeoecology 128**: 215-226. doi: 10.1016/S0031-0182(96)00018-1

SAVAGE JM (1987) Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactyllus gollmeri* group (Amphibia: Leptodactylidae). **Fieldiana, Zoology, 33**: 1-57.

STEINER C, CATZEFLIS FM (2004) Genetic variation and geographical structure of five mouse-sized opossums (Marsupialia, Didelphidae) throughout the Guiana Region. **Journal of Biogeography 31**(6): 959-973. doi: 10.1111/j.1365-2699.2004.01102.x

STORZ JF, BALANSINGH J, BHAT HR, NATHAN PT, DOSS DPS, PRAKASH AA, KUNZ TH (2001) Clinal variation in body size and sexual dimorphism in an India fruit bat, *Cynopterus sphinx*, (Chiroptera, Pteropodidae). **Biological Journal of Linnean Society 72**: 17-31. doi: 10.1111/j.1095-8312.2001.tb01298.x

THOMAS O (1899) Descriptions of new Neotropical mammals. **Annals and Magazine of Natural History 4**(7): 278-288. doi: 10.1080/00222939908678198

THOMAS O (1913) The geographical races of the woolly opossum (*Philander laniger*). **Annals and Magazine of Natural History 12**(8): 358-361. doi: 10.1080/00222931308693409

THORPE RS (1987) Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. **Bolletino di Zoologia 54**: 3-11. doi: 10.1080/11250008709355549

TRIBE CJ (1990) Dental age classes in *Marmosa incana* and other didelphoids. **Journal of Mammalogy 71**(4): 566-569. doi: 10.2307/1381795

VAN DER HAMMEN T, HOOGHIEMSTRA H (2000) Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. **Quaternary Science Reviews 19**: 725-742. doi: 10.1016/S0277-3791(99)00024-4

VOSS R, JANSA S (2009) Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. **Bulletin American Museum of Natural History** (322): 1-177. doi: 10.1206/322.1

VOSS RS, TARIFA T, YENSEN E (2004) An introduction to *Marmosops* (Marsupialia: Didelphidae), with the description of a new species from Bolivia and notes on the taxonomy and distribution of other Bolivian forms. **American Museum Novitates 3466**: 1-40. doi: 10.1206/0003-0082(2004)466<0001:AITMMD>2.0.CO;2

WEBSTER M, SHEETS HD (2010) A practical introduction to landmark-based geometric morphometrics. p. 163-188. In: ALROY J, HUNT G (Eds). **Quantitative methods in Paleobiology.** Boulder, The Paleontological Society, Paleontological Society Papers, vol. 16.

ZELDITCH ML, SWIDERSKI DL, SHEETS HD, FINK WL (2012) **Geometric morphometrics for biologists: a primer.** Boston, Elsevier Academic Press.

Appendix 1. Definition of landmarks illustrated in Fig. 1.

Dorsal view of the cranium. 1: Anteriormost point of suture between left and right nasal bones; 2: Posteriormost point of interparietal at the sagital and nuchal crests intersection; 3 and 28: Intersection between interparietal-parietal suture and outline of the brain-case, at the nuchal crest; 4 and 27: Main curve of the squamosal, anteriorly to the post-tympanic process; 5 and 26: Tip of the frontal process of the jugal, on the zygomatic arch; 6 and 23: Lateralmost point of sutures between lacrimal and jugal; 7 and 18: Lateralmost point of sutures between maxilla and premaxilla; 8 and 17: Anteriormost point of suture between nasal and premaxilla; 9 and 19: Point of intersection between sutures of nasal, premaxilla and maxilla; 10 and 20: Intersection between sutures of nasal, frontal and maxilla; 11 and 21: Intersection of sutures between lacrimal, frontal and maxilla; 12 and 22: Posteriormost point of the suture between frontal and lacrimal; 13 and 25: Tip of the orbital process of the frontal; 14 and 24: Postorbital constriction; 15: Intersection between sutures of both parietals and interparietal; 16: Posteriormost point of sutures between both nasals.

Lateral view of the cranium. 1: Anterior base of I1; 2: Posterior base of I5; 3: Anterior base of C, at the junction with maxilla; 4: Posterior base of C, at the junction with maxilla; 5: Anterior base of M1 and posterior base of P3, at the junction with maxilla; 6: Posterior base of M4 at the juction with maxila (posteriormost point of molar series); 7: Posteroventral end of occipital condyle; 8: Posterodorsal end of braincase (posteriormost point of sagital line, junction with nuchal crest); 9: Intersection between sutures of infraparietal, parietal and squamosal; 10: Suture between jugal and squamosal at the dorsal border of the zygomatic arch; 11: Intersection between sutures of jugal, lacrimal and maxilla; 12: Intersection between sutures of nasal, premaxilla and maxilla; 13: Anteriormost point of the sutures of nasal and premaxilla; 14: Anterior tip of nasal; 15: Ventral end oftheinfraorbital fossa; 16: Intersection between exoccipital and occipital condyle; 17: Ventral end of occipital condyle; 18: Tip of postglenoid process; 19: Tip of orbital process of frontal; 20: Intersection of sutures between lacrimal, frontal and palate; 21: Anteriormost point of suture between jugal and squamosal; 22: Intersection of sutures between lacrimal, frontal and maxilla.

Ventral view of the cranium. 1: Point between right and left I1; 2: Anteriormost point of foramem magnum, at the basioccipital; 3 and 28: Posterior end of occipital condyle, at the basioccipital; 4 and 27: Exterior border of braincase, anterior to the posttympanic process; 5 and 25: Sutures between basioccipital, basephenoid and promontorium; 6 and 24: Posterolateral end of sutures between palateandpterigoyd; 7 and 23: Posterolateral tip of palate; 8 and 26: Anterior base of squamosal process; 9 and 22: Posterolateral base of M4; 10 and 21: Posterolateralbase or M3; 11 and 20: Posterolateral base of C; 12 and 19: Posterolateral base of I5; 13 and 18: Anterior end of incisive foramen; 14 and 17: Posterior end of incisive foramen; 15: Posterior end of suture between palates; 16: Intersection of sutures between maxilla and palate.

Mandible. 1: Anterior base of i1; 2: Anterior base of i4; 3: Anterior base of p1; 4: Anterior base of m1; 5: Posterior base of m4; 6: Intersection between horizontal ramus of the mandible and coronoid process; 7: Uppermost point of coronoid process; 8: Posterior tip of coronoid process; 9: Major curvature between articular process and posterior part of coronoid crest; 10: Labial tip of articular condyle; 11: Posterior base of angular process; 12: Caudal tip of angular process; 13: Upper end part of mental foramen; 14: Anteroventral end of masseteric fossa.

Appendix 2. Specimens examined, by country and locality. Numbers refer to Figs. 2 and 3.

Caluromys derbianus

Belize. 7. Baking Pot (88W55'12"; 16S49'48") FMNH 106529; **8**. Kate'sLagoon (88W27'36"; 17S58'48") FMNH 63886.

Colombia. 67. Unguia (77W; 6N) FMNH 69800, 69801, 69802, 69803, 69804; **70**. Cauquita River, South of Cali (76W31'12"; 3S25'12") AMNH 14189; **68**. Alto Rio Sinú (74W01'12"; 8S09') FMNH 69327; **69**. Rio Raposo (73W40'48"; 4S46'12") USNM 334676, 334678.

Costa Rica. 28. Escazu (85W19'48"; 9S55'12") AMNH 131708, 131710, 131711, 131712, 135329, 137287, 139278; **29**. Piedras Negras (84W19'12"; 9S54') AMNH 139781, 139783; **30**. Finca La Lola (84W16'48"; 9S54') LSUMZ 9337; **31**. 2 km NWSanta Ana (84W10'48"; 9S55'48") LSUMZ 12633; **32**. San Ignacio (84W10'12"; 9S49'12") USNM 250280; **33**. San Jose (84W06'; 9S55'48") AMNH 19202, 131709, KU 39247, 60447; **35**. 5 km SE Turrialba (83W40'48"; 9S54') KU 26927; **37**. Cerro Plano (83W19'48"; 9N) KU 157578, 157579; **38**. Puerto Cortez (83W19'12"; 9S01'12") AMNH 10057, 139678; **34**. La Selva Biologica Reserve, 35 km S Puerto Viejo, Heredia (83W50'; 10S26') FMNH 128385; **36**. San Isidro, San Jose (84W17'; 9S54'). **Ecuador. 73**. Vinces (79W43'48"; 1S33') AMNH 63526; **74**. Zaruma (79W36'; 3S40'48") AMNH 47194; **72**. Puente delChimbo (78W43'48"; 2S01'12") AMNH 63525; **71**. Inaza Range (78W10'48"; 1S49'12") AMNH 10058.

Honduras. 9. Santa Barbara (88W24'; 15S07'12") AMNH 126134; **10**. Chamelecon (88W; 15S25'12") USNM 148749; **11**. Olancho (85W45'; 14S48') AMNH 126980.

Mexico. 1. 20 km ESE San Jesus Carranza (96W07'12"; 19S10'12") KU 93192; **2**. 3 km SE San AndresTuxtla (95W13'12"; 18S27') KU 23367, 23368, 23369, 23370, 23371, 23372, 23373;**3**. 16 mi. SMatias Romero, Sarabia, Juchitán (95W01'12"; 16S52'12") AMNH 185756; **4**. La Venta (94W01'48"; 18S04'48") USNM 271105, 271106; **5**. 1 mi. E Teapa (92W57'; 17S31'48") LSUMZ 8105; **6**. Mayan Ruiz (91W58'12"; 17S30') FMNH 66918.

Nicaragua. 15. Chinandega (87W07'12"; 12S37'12") KU 110661, 105904; **16**. Lake Jiloa (86W31'48"; 12S22'12") AMNH 176710, 176711, 176712, 176714, 176715; **17**. 3 km S4 km WDiriamba (86W19'48"; 11S46'48") KU 110681, 110675, 110679, 114606;**12**. 5 mi. S, Managuá (86W16'48"; 13S30') KU 70160, 70161, 70162, USNM 253050;**13**. 5 km SSabana Grande (86W10'12"; 13S10'12") KU114604, 114605, 96201, 96203, 96208, 97359, 97360, 97361, 97367, 97381, 97382, 97388, 98379, 114603, 116700, 116701, 96209, 96213, 97362, 97365, 97369, 97376, 97377, 97383; **18**. La Calera (86W03'; 11S45') KU 108167,104503,96200, USNM 339889, 339892, 339893; **19**. Chinandega (86W01'12"; 11S51) KU 110661; **20**. Los Cocos, 14 km S Boaco (85W54'; 12S04'12") KU 114597, 114592, 114598, 114599; **21**. Finca Santa Cecilia, 6,5 km NE Guanacaste (85W49'48"; 11S25'48") KU 105906, 105907; **22**. Rivas (85W49'12"; 11S25'48") KU 97389, 105908; **23**. Rio Mico (85W48'; 12S27') KU 105901; **24**. 4 km WTeustepe (85W46'48"; 12S25'12") KU 114591; **25**. Santa Rosa, 17 km S15 km E Boaco (85W40'12"; 12S28'12") KU 110682,110684,110685;**14**. Matagalpa (85W40'12"; 12S55'12") AMNH 28831, 41395, KU 70156, 70157, 114575, 114576, 114580, 114585; **26**. 12 km S13 km E Boaco (85W39'; 12S28'12") KU 114590; **27**. Mecatepe (85W37'48"; 11S15') KU 108165, 108166.

Panama. 43. 7 km SSWChanguinola (82W31'12"; 9S25'48") USNM 315012; **44**. Almirante (82W22'48"; 9S16'48") USNM 315009; **45**. Isla Parida (82W19'48"; 9S10'12") AMNH 18911, 18912; **46**. Bocas del Drago (82W19'48"; 9S25'12") USNM 315011; Divala (82W19'12"; 8S22'48") USNM 243413; **39**. Boquerón (82W19'12"; 8S24') AMNH 18909,18910; **47**. Bocas del Toro (82W10'12"; 8S49'48") USNM 290878, 322943, 322944, 335004, 335005, 335009, 335010, 335011, 335012, 335013, 335014, 335017, 335019, 335020, 449560, 449562, 464247, 578118, 578119, 578934, 578935, 578936, 578939, 578940, 578941, 578942, 578944, 578945, 578946, 578947, 578948, 578950, 578951, 578953, 578954, 578955, 578956, 578957; **48**. Sibube (82W04'12"; 9S03') USNM 335001, 335003; **49**. Cayo Agua (82W01'12"; 9S09') USNM 578116, 335018; **50**. Bisira (81W51'; 8S54') USNM 575393; **51**. Bohio Peninsula, 4,5 km NWFrijoles (81W46'48"; 8S43'12") USNM 503420; **40**. 1/4 mi. WGuabalá (81W43'12"; 8S13'12") USNM 331068;**41**. Isla Cébaco (81W19'48"; 8S12') USNM 360134, 360135, 360136; **42**. La Cascadas (80W46'12"; 8S31'48") USNM 257328; **53**. Fort Sherman, 6 km WCristobal (79W57'; 9S19'48") USNM 456809; **52**. Camp Pina (79W57'; 9S22'12") USNM 306379; **54**. Fort Davis (79W54'; 9S16'48") USNM 297876; **55**.Tabernilla (79W49'12"; 9S07'12") USNM 171033; **56**.Darién (79W46'12"; 9S07'12") USNM 309256, 309257, 309258, 337951, 337952, 337953, 362315, 362316; **57**.Fort Clayton (79W42'; 9N) USNM 302329; **58**.Chagres River station (79W39'; 9S09') AMNH 164491; **59**.Fort Kobbe (79W34'48"; 8S55'12") USNM 301131, 301133, 301134; **60**. Chiva-Chiva (79W34'48";9S01'48") USNM 296344; **61**. Curundu (79W33'; 8S58'48") USNM 296188; **62**. Canal Zone (79W31'48"; 8S58'12") MVZ 183321, 183319, FMNH 30279; **63**. Panama City (79W28'48"; 9S01'12") MVZ 135231, 135233; **64**. France Field (79W04'48"; 9S19'48") USNM 303233; **65**. Jaqué (77W43'48"; 8S07'12") USNM 309256, 309257, 309258, 337951, 337952, 337953, 362315, 362316; **66**. Quebrada Venado (77W28'12"; 8S39') USNM 335021, 335026, 335023, 335024. **Peru. 75**. NE Tingo Maria (75W58'48"; 9S16'48") LSUMZ 17681.

Caluromys lanatus

Argentina. 73. Parque Iguazu (55W; 27S) MACS 21378.

Bolivia. 55. Isla Gargantua (68W34'48"; 12S22'48") MSB 56998; **66**. San Joaquín (64W49'12"; 13S04'12") FMNH 114649; **67**.Estancia Yutiole, 20 km S San Joaquín (64W48'; 13S15') AMNH 215001; **68**.Ichilo (63W46'12"; 17S30') MACS 50181, 50188; **69**.Buena Vista (63W40'12"; 17S27') FMNH 25265; **70**. Santa Cruz de La Sierra (63W10'12"; 17S48') AMNH 133205.

Brazil. 47. Nova Vida, Right bank Juruá river, Acre (72W49'12"; 8S22'12") MVZ 190250, 190251; **48**. Igarapé Porongaba, left bank Juruá river; Acre (72W46'48"; 8S40'12") MVZ 190249; **25**. right bank Juruá river, Amazonas (70W51'; 6S45') MVZ 190247; **24**. Altamira, rightbank, Juruá river, Amazonas (68W54'; 6S34'48") MPEG 28000; **23**. Niteroi, 2o Distrito, Acre (68W24'; 9S02'24") USNM 546177; **22**. Igarapé Grande, Juruá river, Amazonas (67W27'; 9S15') MZUSP 4532; **56**. Estação Ecológica Mamirauá, Japurá river, leftbank, Amazonas (64W25'12"; 3S13'12") MPEG 24566; **71**. UHE Samuel, Rondônia (63W; 11S) MZUSP 27389, 27390; **57**. Balbina, Amazonas (59W16'48"; 1S31'48") MHNCI 1727, 1728; ca. 8 km SLago Sampaio, Wbank Madeira river, Amazonas (59W04'48"; 3S25'12") AMNH 92760; **62**. Jauru river, 2days upper Porto Esperidião, Porto Esperidião, Mato Grosso (57W27'36"; 16S13'12") MS1222; **59**. Villa Bella Imperatriz, Amazonas (56W26'24"; 2S21'36") AMNH 92882, 92883, 92884, 93967; **60**. Rightbank Tapajós river, Pará (54W24'36"; 2S14'24") AMNH 133208; **74**. Flor da Serra, Boa Vista da Aparecida, Paraná (53W24'; 25S25'48") MHNCI 4206, 4207, 4208, 4209; **63**. Baixo Kuluene, Jacaré, Alto Xingu, São Félix do Araguaia, Mato Grosso (53W10'48"; 11S13'48") MS11705; **75**. UH Salto Caxias, Cruzeiro do Iguaçu, Paraná (53W07'48"; 25S37'12") MHNCI 4210, 4211; **64**. Fazenda São Luis, 30 km SBarra do Garças, Mato Grosso (52W09'; 15S31'48") UFMG 2538; **61**. Ilha Boiuçu, Pará (55W27'; 01S55') MZUSP 4531, 4533, 4534, 4883; **65**. Anápolis, Goiás (48W34'48"; 16S12') AMNH 133200, MS20963, 4599, 4782, 4785.

Colombia. 12. Valle de Suaza (76W10'12"; 1S45') FMNH 70994, USNM 541855, 541856; **13**. 5 km SVillavieja, Huila (75W10'12"; 3S19'12") MVZ 114227, 113831, 114223; **14**. Natagaima (75W04'48"; 3S34'48") AMNH 75886, 76768, 76769; **1**. Magdalena (74W30'; 10N) USNM 271317, 280900, 280906; **15**. Cundinamarca (74W25'48"; 4S58'12") USNM 544394, 544395; **16**. Boyaca (74W06'; 5S31'48") FMNH 70995, 70996; **17**. VolcanesTupana, Bogotá (74W04'48"; 4S36') AMNH 143522; **18**. La Macarena, Meta (73W55'12"; 2S45') FMNH 87931; **19**. San Juan de Arama, Meta (73W49'12"; 3S24') FMNH 87927; **2**. Valledupar Distr., Magdalena (73W34'48"; 10S25'12") USNM 280903, 280904, 280907; **21**. Restrepo, Meta (73W34'12"; 4S15') AMNH 136161; **3**. San Gil,

Santander (73W15'; 7N) FMNH 140239; **4**. Sarcula, Norte de Santander (73W; 8N) FMNH 140237; **5**. Toledo (72W15'; 7S18') USNM 544393; **20**. Merida (73W48'; 1N) MZUSP 2529, AMNH 78101.

Ecuador. 26. Pastaza (77W; 1S55'12") FMNH 41444, 43176, 43177; **27**. San Jose, Napo (77W; 0S43'48") AMNH 182938; **28**. Santa Maria, Napo (76W55'12"; 0S25'12"), AMNH 68282, FMNH 58952; **29**. Marián, Napo (76W19'12"; 0S31'12") FMNH 124595; **30**. Limon Cocha, Napo (76W09'; 0S25'12") USNM 528318. **Peru. 31**. Bagua Chica (78W37'48"; 5S37'48") LSUMZ 21880; **32**. La Poza, Rio Santiago (77W37'12"; 4S25'12") MVZ 157608, 157611, 157612; **33**. Tarapoto (76W28'12"; 6S30') MUSM 89, 90, LSUMZ 28420; **38**. Huánuco (76W16'12"; 9S27') FMNH 55409; **39**. Tingo Maria (75W49'48"; 9S30') FMNH 24142, MVZ 140041; **40**. Ucayali (75W15'; 7S10'12") FMNH 55502, 62069, 62070; **41**. Oxapampa (75W04'48"; 10S19'48") USNM 364160; **42**. San Ramon (75W; 11S30') MUSM 1303, FMNH 20787, AMNH 71979, 71984; **34**.Loreto (75W; 5S) AMNH 71979, 71983, 71984, 230001, 273038, 273059; **43**.Yarinacocha (74W36'; 8S30') LSUMZ 14024; **35**. Requena (73W58'48"; 4S58'48") MUSM 11024; **44**. Lagarto, Ucayali (73W52'48"; 10S34'48") AMNH 78951; **45**.Llillapichia river, near "Panguana" Biol. St. (73W37'48"; 10S52'12") MUSM 79; **36**.Nauta (73W33'; 4S31'48") FMNH 87134, 122749; **46**.Santa Rosa (73W30'; 9S) AMNH 75912; **37**. Iquitos (73W15'; 3S46'12") FMNH 87130, 87132, 87133; **50**. Cuzco (72W; 13S30') MUSM 13407; **49**. Balta, Curanja river (71W13'12"; 10S07'48") LSUMZ 14025; **51**. Cosñipata (71W10'48"; 13S04'12") FMNH 84245, 84246; **52**. Marcapata (70W58'12"; 13S34'48") FMNH 68333, 68334; **53**. Quince Mil (70W45'; 13S13'12") FMNH 75087, 75088, 75089; **54**. Albergue, Madre de Diós (70W04'48"; 12S36') MVZ 168852.

Paraguay. 72. Villa Rica, Guairá (56W18'; 24S27') AMNH 66780.

Venezuela. 6. 3 km SNula (71W55'12"; 7S16'48") USNM 416932; **7**. Trujillo (70W30'; 9S25'12") USNM 371280; **8**. San Juan (66W04'12"; 5S15') USNM 406875, 406878; **9**. Amazonas (65W46'12"; 3S39') USNM 388327, 380330; **10**. Esmeralda (65W31'48"; 3S10'12") AMNH 76970; **11**. Boca Mavaca, 68 km SE Esmeralda (65W03'; 3S01'12") USNM 388331, 388332, 388333, 388334.