Morphological variation in the skull of *Nephelomys meridensis* (Rodentia, Cricetidae): evidence for cryptic species in andean populations from northern South America

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The genus *Nephelomys* comprises at least 13 taxa with altitudinal distribution ranging from 900 to 4,000 meters above sea level. Three species are currently known to occur in Venezuela, but some authors suggest that two additional taxa are present in Venezuelan Andes populations and consider *N. meridensis* as a species complex. We conducted geometric morphometric analyses of skulls and jaws from populations assignable to the monotypic species *N. meridensis* from the Venezuelan Andes, in order to examine and compare morphological variations in this species. We compared four localities (including the type locality of *N. meridensis*) situated in northern, central, and western portions of Cordillera de Mérida and the Tamá páramo. We created morphological landmarks on dorsal, ventral, lateral, and jaw views of each skull using the tpsDIG software. Significant differences were found in skull shape and isometric size in most of the populations examined. The discrimination and morphological differentiation of some of these groups with respect to the population from the type locality (Mérida) were aligned with the results from multivariate and cytogenetic analyses carried out previously by other authors. Our data support recognizing *N. meridensis* as a species complex, comprising at least three still undescribed taxa from the Yacambú National Park (cordillera de Mérida), La Trampita (cordillera de Mérida) and the Tamá páramo (Tamá massif). A more detailed taxonomic study of *Nephelomys* from Venezuela, molecular and linear morphometric analyses, and revision of morphological characters, are necessary to describe potential new taxa and determine the geographical distribution of the species in this genus.

El género *Nephelomys* contiene al menos 13 taxa con distribuciones altitudinales desde los 900 metros sobre el nivel del mar hasta 4,000. Actualmente, tres especies ocurren en Venezuela, pero algunos autores sugieren la existencia de dos taxa adicionales en los Andes venezolanos, considerando a la especie monotípica, *N. meridensis* como un complejo de especies. En este estudio, se usó morfometría geométrica para comparar la forma y tamaño del cráneo en poblaciones de roedores andinos de Venezuela, asignables a la especie monotípica, *N. meridensis*. Se compararon cuatro localidades de *N. meridensis* (incluyendo la localidad tipo), ubicadas en el norte, centro y oeste de la Cordillera de Mérida y en el Páramo El Tamá. Se colocaron hitos morfológicos en las vistas dorsal, ventral, lateral y mandíbula, empleando el programa tpsDIG. Nuestros datos mostraron diferencias significativas en el tamaño isométrico (tamaño centroide) y en la forma del cráneo para la mayoría de las poblaciones evaluadas, resaltando que para algunas, su discriminación y diferenciación morfológica con la población de la localidad tipo (Mérida), coincidió con resultados multivariados y citogenéticos previamente realizados por otros autores. El presente estudio corrobora que *N. meridensis* tiene que ser tratado como un complejo de especies, incluyendo al menos tres taxa no descritos, ubicados geográficamente en el Parque Nacional Yacambú (Cordillera de Mérida), La Trampita (Cordillera de Mérida) y Páramo El Tamá (Macizo El Tamá). Se plantea la necesidad de hacer un estudio taxonómico más detallado para *Nephelomys* de Venezuela en combinación con técnicas moleculares, morfometría lineal y revisión de caracteres morfológicos, entre otros; todo esto con el propósito de describir posiblemente nuevos taxa y delimitar la distribución geográfica de las especies del género.

Key words: cranial morphology; geometric morphometrics; *Nephelomys albigularis* group; Oryzomyini; species complex.

Introduction

The genus *Nephelomys* had been previously included in the genus *Oryzomys* and has been subject to taxonomic, systematic, and molecular studies in recent years, leading to the delimitation of species and new hypotheses about their phylogenetic relationships (*e. g.*, Musser *et al.* 1998; Bonvicino *et al.* 2001; Percequillo 2003; Weksler 2003, 2006; Weksler *et al.* 2006).

Nephelomys comprises at least 13 taxa whose altitudinal distribution ranges from 900 to 4,000 masl (Weksler *et al.* 2006; Percequillo 2015). These rodents inhabit humid montane and cloudy forests in the Andes mountain range, from Bolivia to Colombia. They can also be found along the mountain ranges of northern Venezuela and in the Central American mountain ranges in Panama and Costa Rica (Aguilera *et al.* 1995; Percequillo 2003, 2015; Weksler *et al.* 2006; Anderson *et al.* 2012).

Three species, all included in the *Nephelomys albigularis* group (*sensu* Weksler *et al.* 2006), are currently known to occur in Venezuela, one being endemic to the country (García *et al.* 2019). Their geographical distribution is as follows: *N. caracolus* (endemic) has been recorded in the central and western portions of Cordillera de la Costa (Aguilera *et al.* 1995; Márquez *et al.* 2000; Percequillo 2003, 2015; Anderson and Raza 2010) and in the Lara-Falcón hill systems (Anderson *et al.* 2012); *N. meridensis* is found in the Andes at Cordillera de

Mérida and the Tamá massif (Aguilera *et al.* 1995; Soriano *et al.* 1999; Márquez *et al.* 2000; Percequillo 2003, 2015; Anderson and Raza 2010); *N. maculiventer* was recently recorded in Sierra de Perijá (García *et al.* 2019). However, some authors recognize *N. meridensis* as a species complex, suggesting the existence of two additional taxa in the populations from the Venezuelan Andes (Aguilera *et al.* 1995; Rivas and Péfaur 1999a; Márquez *et al.* 2000; Percequillo 2003).

The use of geometric morphometrics on bony structures (mainly skulls) of cricetid rodents has increased lately as a means to examine intra- and interspecific morphological variation, and to identify and diagnose cryptic species within the group (Cordeiro-Estrela *et al.* 2006, 2008; García and Sánchez-González 2013; Astúa *et al.* 2015; Boroni *et al.* 2017; García *et al.* 2018). Geometric morphometrics is a biologically based statistical analysis method that decomposes variations in size and shape in a two- or three-dimensional space (Bookstein 1991).

Since the Andean populations of *N. meridensis* are considered as taxonomically unstable, we deemed appropriate to collect further evidence that might help to discriminate the species or subspecies currently clustered together into *N. meridensis*. In this work, skulls from Andean populations of this rodent were morphologically characterized and compared using geometric morphometrics techniques. Our objective was to contribute to the delimitation of potentially different taxa currently included within the *N. meridensis* complex of Venezuela.

Materials and Methods

We examined a total of 65 adult specimens (age class 3, as per the classification based on the molar wear pattern; Percequillo 2003) (Appendix 1). These specimens are deposited in the following Venezuelan collections: Museo de la Estación Biológica de Rancho Grande (EBRG, Aragua State), Museo de Historia Natural La Salle (MHNLS, Capital District) and the Colección de Vertebrados de la Universidad de los Andes (CVULA, Merida State).

Given the lack of sexual dimorphism, male and female specimens were pooled together for analyses (Rivas and Péfaur 1999a, b; Percequillo 2003). The specimens were then sorted into groups or morphotypes, according to their geographic distribution (Figure 1): *N. meridensis* (Mérida and adjacent areas), Cordillera de Mérida, Mérida State; *N. meridensis* A (Yacambú National Park), Cordillera de Mérida, Lara State; *N. meridensis* B (La Trampita), Uribante, Cordillera de Mérida, Táchira State; *N. meridensis* C (El Tamá) El Tamá massif, Táchira State; and *N. meridensis* D (Dinira National Park), Cordillera de Mérida, Lara and Trujillo States.

Dorsal, ventral, and lateral views of each skull, as well as the labial view of the jaw, were selected for digitization. All photographs were captured by the same person using a digital camera Nikon D3000 16MP 24X and a tripod; a ruler graduated in millimetres was placed next to each skull as reference. Type-I and -II bidimensional homolo-
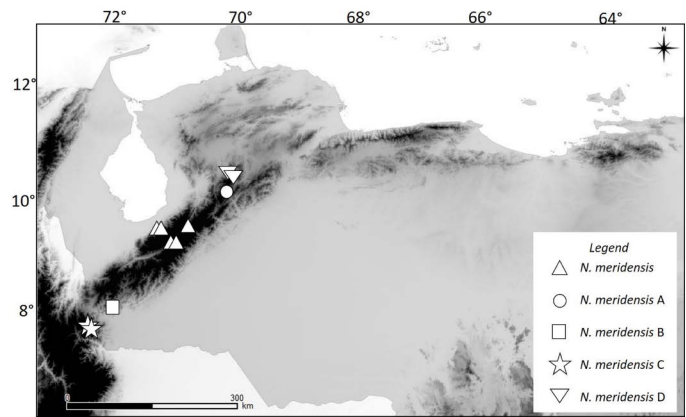

Figure 1. Geographic distribution of the Andean populations of the rodent *Nephelomys* in Venezuela. A darker coloration indicates an elevation higher than 1000 m above sea level.

gous morphological landmarks were digitized (Bookstein 1991; Figure 2) using the software tpsDig (Rohlf 2006); the total number of landmarks digitized on each view were as follows: dorsal (12), ventral (15), lateral (11), and jaw (10). Landmark locations were selected to encompass the skull zones that have taxonomic diagnostic value for this group (Rivas and Péfaur 1999a, b; Márquez *et al.* 2000; Percequillo 2003). Landmark names correspond to those documented by Astúa et al. (2015).

Morphological landmarks were associated with Cartesian coordinates (x, y) that represent the geometric configuration of each skull. The coordinates were subject to a Procrustes adjustment, using the MorphoJ program, which removes the variations in size due to the position, orientation, and scale of each image (Klingenber 2011). Additionally, to detect a potential allometric correlation between the structures analysed, a Multivariate Regression Analysis (based on Goodall's F statistic) was carried out, using the Regress7a program implemented in the series IMP7 (Sheets 2010). The independent variable was the centroid size and the dependent variables were the shape variables (Meloro *et al.* 2008).

The Procrustes residuals produced two matrices; the partial deviations matrix was used for exploratory analyses (Canonical Variable and Discriminant Function analyses) aimed to identify correlations between the different
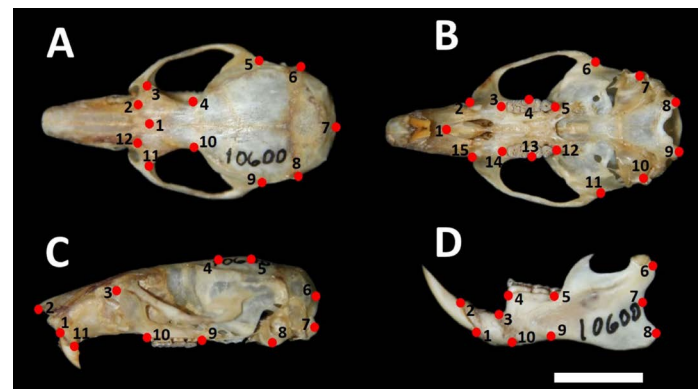
Figure 2. Position of the morphological landmarks selected in the different views of skulls from Andean populations of *Nephelomys* in Venezuela. A Dorsal view. B Ventral view. C Lateral view, and C Mandible. The reference scale is 10 mm.

groups in the morphospace, as well as their shape-related differences. These analyses were conducted using the IMP7 and MorphoJ programs. The groups formed based on the geographic distribution of specimens were used as *a-priori* groups for these analyses. The results from these analyses were estimates of Wilks' λ and Mahalanobis and Procrustes distances, with their statistical significance evaluated by permutations tests with α ≤ 0.05; the *a-priori* groups were reclassified as per the Discriminant Function Analysis (in percentages) and evaluated with a cross-validation test (*post hoc* classification, also in percentages).

The second matrix was used to document isometric size by the centroid size, using the Past program ([Hammer and Happer 2011](#)). Centroid sizes in the different views were compared using a non-parametric Kruskal-Wallis test with the Bonferroni correction ($P \leq 0.05$), as implemented in Past. Finally, MorphoJ ([Klingenber 2011](#)) was used to examine changes in shape in the different skull regions, by comparing the average shape superimposed on the groups.

Results

No significant correlation between centroid size and the shape variables was found in any of the skull views: dorsal ($F_{20, 1220} = 2.235$, $P < 0.002$, explained variation = 3.53 %); ventral ($F_{26, 1482} = 4.091$, $P < 0.002$, explained variation = 6.69 %); lateral ($F_{18, 1098} = 3.339$, $P < 0.006$, explained variation = 5.19 %); jaw ($F_{16, 960} = 3.154$, $P < 0.002$, explained variation = 3.53 %).

There were significant differences in the centroid size of some groups in the following views: Dorsal: *N. meridensis - N. meridensis* A, and *N. meridensis* A - *N. meridensis* B; Ventral: *N. meridensis - N. meridensis* A; *N. meridensis - N. meridensis* B; *N. meridensis - N. meridensis* C, and *N. meridensis* A - *N. meridensis* C; Jaw: *N. meridensis* A - *N. meridensis* B. These comparisons are detailed in in Table 1.

Figure 3 shows the separation of the groups in the morphospace, with the groups that are significantly different from each other in each view. In all views, the first two axes account for over 50% of the total variation: Dorsal view (variation = 73.01 %; Wilks' λ = 0.2542; $X^2 = 68.0873$;

Table 1. Significant differences in the values of the centroid size estimator for Andean populations of *Nephelomys meridensis* in Venezuela. Descriptive statistics were tested with a probability value less than or equal to 0.05 ($P \leq 0.05$). x̄ = Arithmetic mean, σ = standard deviation. Values expressed in millimeters.

Views of the Skull	x̄	σ	P
Dorsal			
N. meridensis - N. meridensis A	31.95–30.33	2.23–1.37	0.032
N. meridensis A - *N. meridensis* B	30.33–32.18	1.37–2.87	0.019
Ventral			
N. meridensis - N. meridensis A	37.03–32.28	4.35–1.14	0.001
N. meridensis - N. meridensis B	37.03–33.52	4.35–1.04	0.001
N. meridensis - N. meridensis C	37.03–33.71	4.35–1.04	0.005
N. meridensis A - *N. meridensis* C	32.28–33.71	1.14–1.04	0.037
Mandible lateral wiew			
N. meridensis A - *N. meridensis* B	18.99–19.84	1.26–1.27	0.049
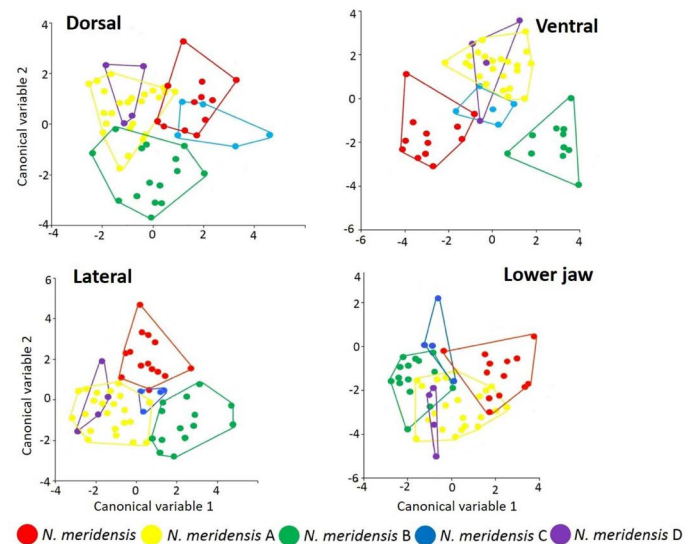
Figure 3. Factorial diagram of the Canonical Variable Analysis showing the spatial distribution and correlation between the different groups identified in the Andean populations of *Nephelomys meridensis* in Venezuela.

d. f. = 38; $P = 0.0002$); ventral (variation = 76.59 %; Wilks' λ = 0.1732; $X^2 = 76.2631$; d. f. = 52; $P = 0.015$); lateral (variation = 79.79 %; Wilks' λ = 0.2241; $X^2 = 77.0203$ d. f. = 36; $P = 0.0001$) and jaw (variation = 79.18 %; Wilks' λ = 0.2786; $X^2 = 65.8128$; d. f. = 32; $P = 0.0003$).

There were statistically significant differences in skull configuration between *N. meridensis - N. meridensis* A and *N. meridensis* A - *N. meridensis* B in all views (Table 2). The *post hoc* reclassification percentages of these groups were high, with *N. meridensis* A being better classified after the validation tests (Table 2). In addition, there were significant differences between *N. meridensis* and *N. meridensis* B in the ventral, lateral and jaw views; between *N. meridensis* A and *N. meridensis* C in the dorsal and lateral views; and between *N. meridensis* and *N. meridensis* C in the labial view of the jaw (Table 2). Figures 4 to 7 show the separation between these groups.

Regarding cranial morphology by view, the *N. meridensis* population from Mérida and adjacent areas differs from *N. meridensis* A by having a skull slightly longer in the posterior region (morphological landmarks 6 and 7; Figures 4C and 6C, respectively), with nasal bones slightly longer (landmark 2; Figure 6C). Maxillary toothrow slightly shorter (landmarks 9 and 10; Figure 6C); and palate wide between the incisive foramen (landmarks 2 and 15), narrow between the anterior base of the first molar (landmarks 3 and 14), the outer margin of the second molar (landmarks 4 and 13), and the posterior base of the last molar (landmarks 5 and 12; Figure 5C). Basicranium slightly wider at the posterior part of the zygomatic bones (landmarks 6 and 11) and the tympanic bullae (landmarks 7 and 10; Figure 5C). Jaw narrow and more extended, both on the anterior end (landmarks 1, 2 and 3), and by the coronoid and angular processes (landmarks 6 and 8; Figure 7C).

*Nephelomys meridensis* differs from *N. meridensis* B in that the skull is lower in the parietal-interparietal region

Table 2. Statistical comparison and subsequent differentiation between the different Andean populations of the genus *Nephelomys* (class 3) from Venezuela. Procrustes and Mahalanobis distances were tested with a value of $P \leq 0.05$. The subsequent reclassification was tested with a cross-validation test, also with a value of $P \leq 0.05$. The asterisk indicates statistically significant differences between groups.

| Views of the Skull	Procrustes distances	Mahalanobis distances	Reclassification discriminant function	Reclassification cross validation
Dorsal				
N. meridensis - N. meridensis A*	0.02339096*	3.7598*	100 % – 100 %	64 % – 75 %
N. meridensis - N. meridensis B	0.02022337	5.7221	100 % – 100 %	41 % – 73 %
N. meridensis - N. meridensis C	0.02210766	5.0693	100 % – 100 %	83 % – 40 %
N. meridensis - N. meridensis D	0.01950156	1.8399	83 % – 100 %	33 % – 33 %
N. meridensis A - *N. meridensis* B*	0.01595765*	3.1648*	90 % – 94 %	79 % – 63 %
N. meridensis A - *N. meridensis* C*	0.01670396*	3.1271*	90 % – 87 %	78 % – 66 %
N. meridensis A - *N. meridensis* D	0.01166001	5.2342	100 % – 100 %	67 % – 0 %
N. meridensis B - *N. meridensis* C	0.02665050	7.1853	100 % – 100 %	60 % – 86 %
N. meridensis B - *N. meridensis* D	0.02479904	1.5076	80 % – 100 %	80 % – 33 %
Ventral				
N. meridensis - N. meridensis A*	0.02199053*	8.2665*	100 % – 100 %	58 % – 93 %
N. meridensis - N. meridensis B*	0.02218107*	11.8822*	100 % – 100 %	75 % – 83 %
N. meridensis - N. meridensis C	0.03218275	3.2676	91 % – 80 %	91 % – 60 %
N. meridensis - N. meridensis D	0.02115735	1.9478	83 % – 100 %	58 % – 33 %
N. meridensis A - *N. meridensis* B*	0.01669937*	5.7588*	100 % – 100 %	82 % – 67 %
N. meridensis A - *N. meridensis* C	0.02193730	4.5667	96 % – 100 %	62 % – 0 %
N. meridensis A - *N. meridensis* D	0.02081512	16.8012	100 % – 100 %	74 % – 33 %
N. meridensis B - *N. meridensis* C	0.02193730	4.5667	100 % – 91 %	20 % – 58 %
N. meridensis B - *N. meridensis* D	0.03506906	2.2241	100 % – 66 %	100 % – 66 %
Lateral				
N. meridensis - N. meridensis A*	0.02243218*	5.1764*	100 % – 100 %	86 % – 93 %
N. meridensis - N. meridensis B*	0.04068574*	4.6594*	100 % – 100 %	50 % – 72 %
N. meridensis - N. meridensis C	0.03906102	23.6338	100 % – 100 %	50 % – 80 %
N. meridensis - N. meridensis D	0.01788145	5.0564	100 % – 100 %	50 % – 0 %
N. meridensis - N. meridensis B*	0.03523493*	4.1682*	100 % – 100 %	82 % – 72 %
N. meridensis A - *N. meridensis* C*	0.03335329*	6.4908*	100 % – 100 %	85 % – 80 %
N. meridensis A - *N. meridensis* D	0.01985321	4.4808	100 % – 100 %	70 % – 33 %
N. meridensis B - *N. meridensis* C	0.01769165	31.2413	100 % – 100 %	60 % – 78 %
N. meridensis B - *N. meridensis* D	0.03622074	3.6542	100 % – 100 %	80 % – 33 %
Mandible lateral wiew				
N. meridensis - N. meridensis A*	0.02952130*	2.6267*	92 % – 85 %	58 % – 70 %
N. meridensis - N. meridensis B*	0.03814583*	4.7765*	100 % – 100 %	75 % – 73 %
N. meridensis - N. meridensis C*	0.03675974*	48.3824*	100 % – 100 %	58 % – 80 %
N. meridensis - N. meridensis D	0.03746015	11.8451	100 % – 100 %	83 % – 33 %
N. meridensis A - *N. meridensis* B*	0.02030497*	3.2410*	96 % – 93 %	85 % – 67 %
N. meridensis A - *N. meridensis* C	0.02402845	4.4597	100 % – 100 %	85 % – 40 %
N. meridensis A - *N. meridensis* D	0.02343556	2.3998	88 % – 75 %	70 % – 33 %
N. meridensis B - *N. meridensis* C	0.02817338	8.8376	100 % – 100 %	80 % – 66 %
N. meridensis B - *N. meridensis* C	0.03109383	2.5269	100 % – 75 %	80 % – 50 %

(landmarks 5, 6, 7 and 8) and has a longer nasal and premaxillae (landmarks 1, 2, and 11; Figure 6C). Maxillary toothrow (landmarks 9 and 10) slightly shorter (Figure 6C) and palate somewhat narrower between the first and second molars (landmarks 3, 14 and 4, 13; Figure 5C). Basicranium wide between the posterior bases of the zygomatic arches (landmarks 6 and 11) and narrow between the tympanic bullae (landmarks 7 and 10; Figure 5C). Jaw narrow and extended, both anteriorly (landmarks 2, 3 and 4) and in the posterior region by the coronoid and angular processes (landmarks 6 and 8; Figure 7C).

Nephelomys meridensis differs from *N. meridensis* C only in its jaw (Figure 7C), which is narrower in the posterior region of the diastema (landmarks 3 and 4) and has extended angular processes aligned with the coronoid processes (landmarks 6 and 8).
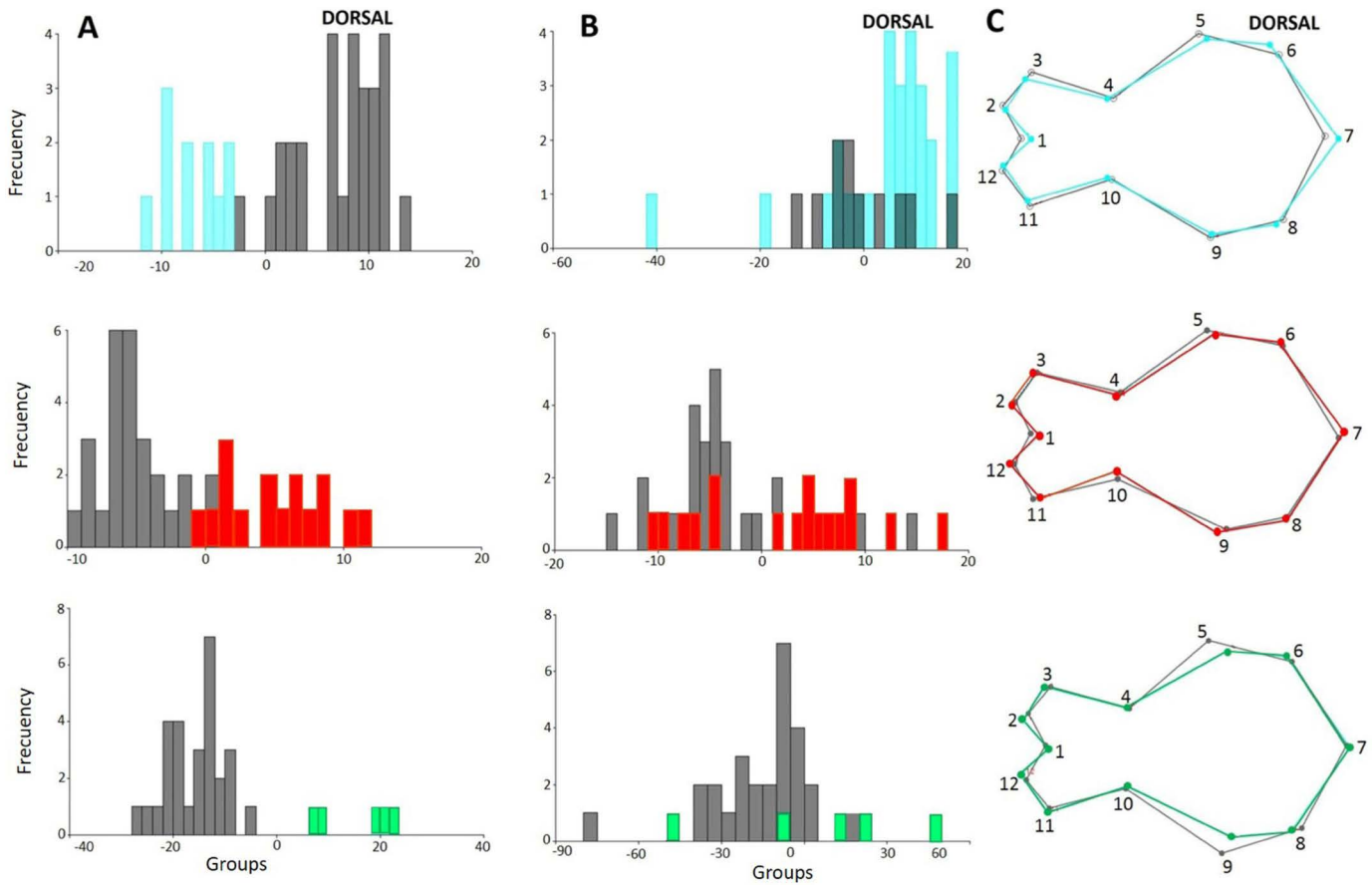
Figure 4. Visual representation of the skull differentiation (dorsal view) in Andean populations of the genus *Nephelomys* in Venezuela. A Histogram resulting from the Discriminant Function Analysis. B Histogram resulting from the cross-validation. C Between-group comparison of the average shape.
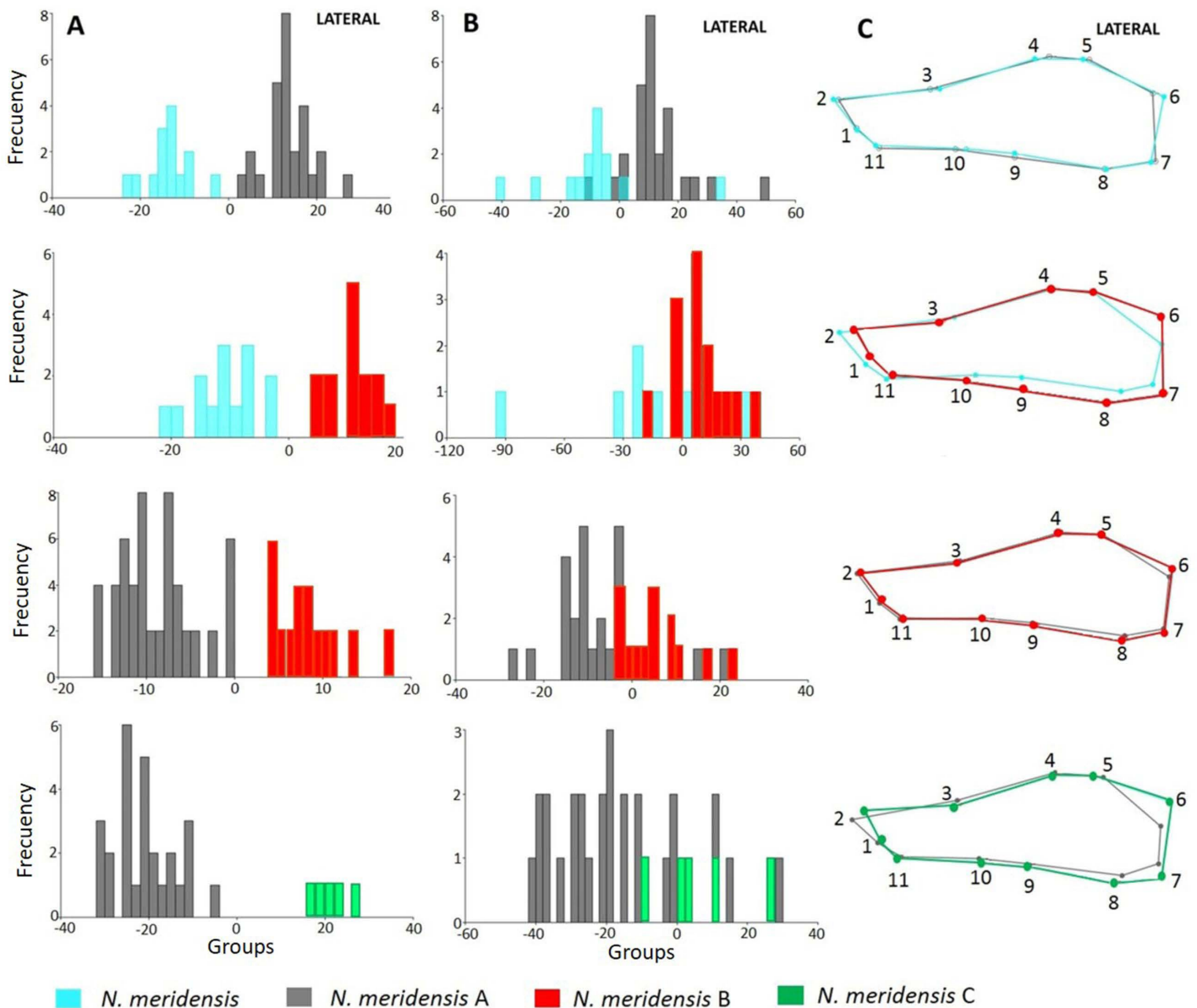

N. meridensis   N. Meridensis A   N. Meridensis B
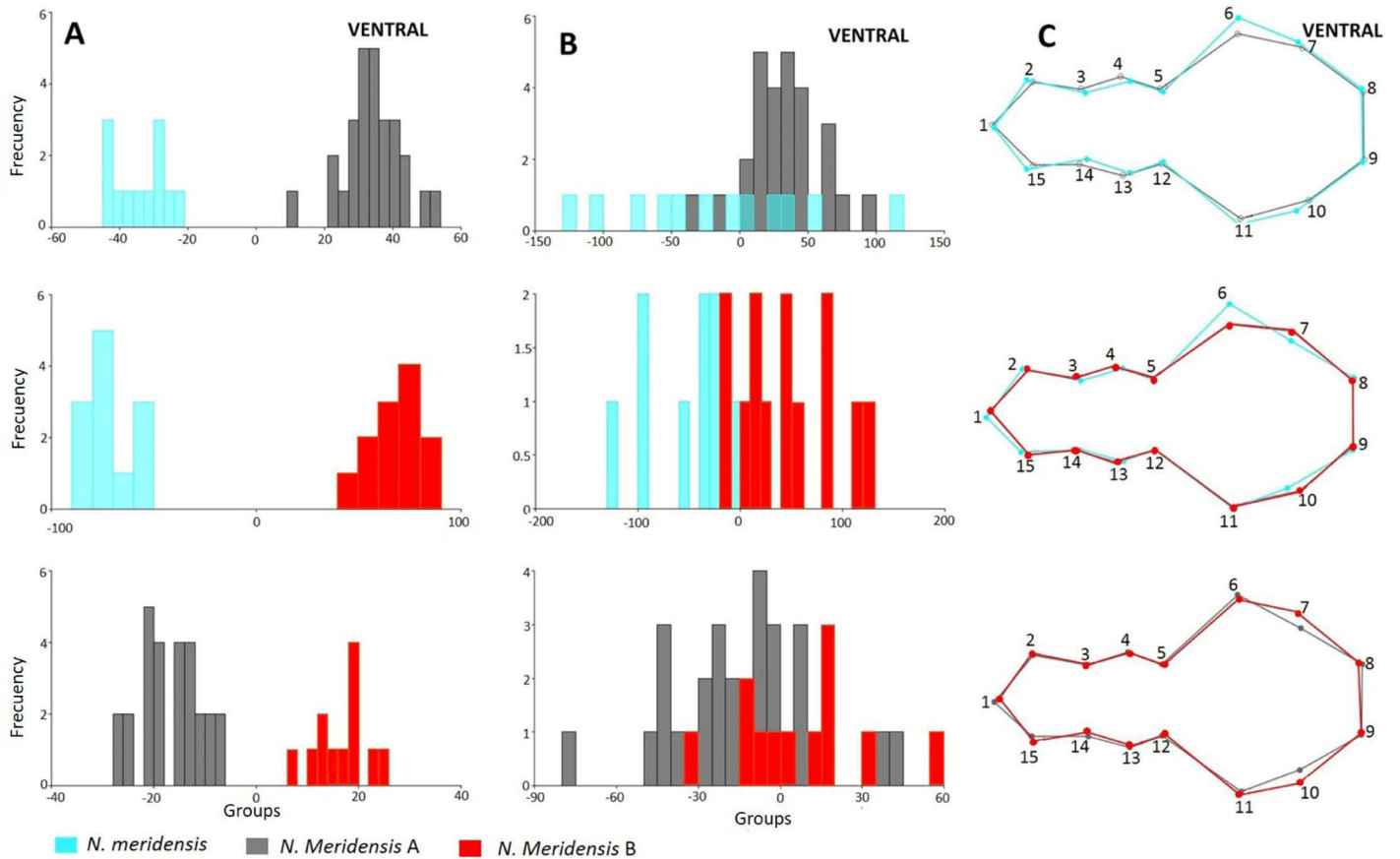
Figure 5. Visual representation of the skull differentiation (ventral view) in Andean populations of the genus *Nephelomys* in Venezuela. A Histogram resulting from the Discriminant Function Analysis. B Histogram resulting from the cross-validation. C Between-group comparison of the average shape.

The frontal bones of *Nephelomys meridensis* A are slightly wider (landmarks 1, 3 and 11) than those of *N. meridensis* B towards the anterior region (Figure 4C). Interorbital region (landmarks 4 and 10) slightly wider in *N. meridensis* A (Figure 4C). Posterior part of the skull in the interparietal region (landmarks 5, 6, 7 and 8) higher in *Nephelomys meridensis* B than in *N. meridensis* A (Figure 6C). Both groups share a maxillary toothrow (landmarks 9 and 10) of similar length (Figure 6C) and a similar morphology in the posterior part of the palate (between the incisive foramen and between the anterior base of the first molar and the posterior base of the last molar; landmarks 2, 3, 4, 5, 12, 13, 14 and 15, Figure 5C). Basicranium of *N. meridensis* A narrower between the bullae (landmarks 7 and 10; Figure 5C) and jaw similar in both groups in the anterior region (in the incisors alveoli), but a little higher at the toothrow base (landmarks 4 and 5) and narrow towards the posterior part, with the coronoid processes (landmark 6) more extended in *N. meridensis* A (Figure 7C).

Nephelomys meridensis A and *N. meridensis* C differed from each other in skull metrics; skull of *N. meridensis* A wider in the posterior part of the zygomatic arches (landmarks 5 and 9; Figure 4C), with longer nasal bones (landmark 2), and posterior part of the skull narrower (landmarks 5, 6, 7 and 8; Figure 6C).

Discussion

Our results show that specimens from the type locality of *Nephelomys meridensis* exhibit a cranial conformation different from that of other populations of the Venezuelan Andes (Yacambú National Park [Cordillera de Mérida, Lara State]), La Trampita [Cordillera de Mérida, Mérida State] and El Tamá massif, Táchira State, respectively). The population herein referred to as *N. meridensis* D (Dinira National Park) was not different, in any of the views, from the other groups compared, contrary to the results obtained by Rivas and Péfaur (1999a) using morphometrics based on linear distances.

Figure 6. Visual representation of the skull differentiation (lateral view) in Andean populations of the genus *Nephelomys* in Venezuela. A Histogram resulting from the Discriminant Function Analysis. B Histogram resulting from the cross-validation. C. Between-group comparison of the average shape.
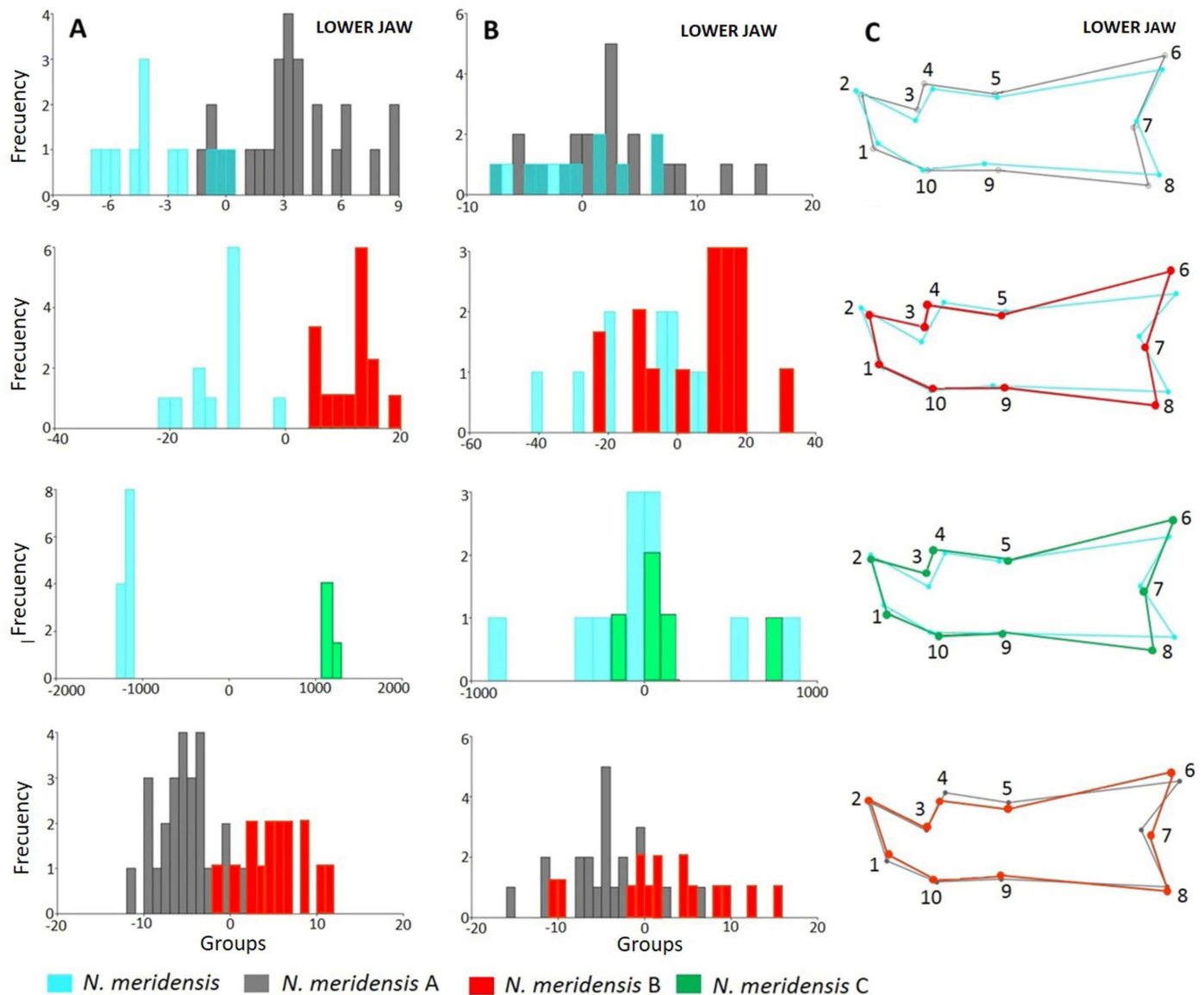
Figure 7. Visual representation of the skull differentiation (jaw view) in Andean populations of the genus *Nephelomys* in Venezuela. A. Histogram resulting from the Discriminant Function Analysis. B. Histogram resulting from the cross-validation. C. Between-group comparison of the average shape.

The clear separation and differentiation of the cranial model in most populations currently recognized as monotypic within *N. meridensis* provides further evidence supporting the hypothesis that this taxon should be treated as a species complex (Rivas and Péfaur 1999a; Soriano *et al.* 1999; Márquez *et al.* 2000). In its current delimitation, *N. meridensis* could include at least one species (karyotype 2n = 66, FN = 92, occurring in the La Trampita and El Tamá localities in Venezuela and Colombia; Aguilera *et al.* 1995; Márquez *et al.* 2000; Percequillo 2003, 2015) and two new subspecies (one from Yacambú National Park, with the same karyotype that the Mérida populations: 2n = 66, FN = 104; Aguilera *et al.* 1995; Rivas and Péfaur 1999a; Márquez *et al.* 2000 and another in the Tamá populations, as per the morphological differences described in this work).

Our morphogeometric data are consistent with morphometrics studies based on linear distances on skulls of *Nephelomys* rodents (Rivas and Péfaur 1999a; Percequillo 2003). Percequillo (2003) studied the systematics of the *Nephelomys albigularis* group and suggested that the El Tamá population should correspond taxonomically to the La Trampita population (although he did not examine specimens from the latter locality). Rivas and Péfaur (1999a) explored the geographic variation in skulls of specimens of the genus *Nephelomys* from Venezuela using multivariate analyses; their results supported the differentiation of the populations from Yacambú National Park and Mérida. Our results using geometric morphometrics demonstrate the validity of this tool for taxonomic studies and for the identification or detection of cryptic species (Cordeiro-Estrela *et al.* 2006, 2008; Astúa *et al.* 2015; Boroni *et al.* 2017).

From a biogeographic viewpoint, the Andes is considered a mega-diverse region that harbors a high species richness and a high level of endemisms of flora and fauna (Josse *et al.* 2009). The Venezuelan Andean system encompasses three mountain ranges: Sierra de Perijá, El Tamá massif (which are part of the eastern Andes of Colombia), and Cordillera de Mérida (Soriano *et al.* 1999). Cordillera

de Mérida is the main mountain range of the Venezuelan Andean system; it is approximately 400 km long by 80 km wide and runs in a southwest-northeast direction starting at the Táchira depression and ending at the Barquisimeto depression (La Marca 1997). The Táchira depression separates Cordillera de Mérida from the Colombian Andes; its particular conditions of low elevation (< 1,000 m above sea level), high temperature, and arid (deciduous and xerophytic) vegetation likely function as ecological and geographic barriers that may foster isolation and speciation of some mammalian taxa (*e.g.*, shrews of the genus *Cryptotis*; Woodman 2002). However, it has been reported that the Táchira depression does not act as a natural barrier restraining gene flow in other mammals (Gutiérrez *et al.* 2015).

Cordillera de Mérida encompasses various mountain formations and branches, the most important being Sierra Nevada de Mérida, Sierra de La Culata, Cordillera de Trujillo, Guaramacal massif, Sierra de Barbacoas, and Sierra de Portuguesa (La Marca 1997). These branches are separated by valleys or depressions that may also act as natural barriers (as is the case of the Táchira depression), thus preventing the dispersal and promoting vicariant speciation of rodents of the genus *Nephelomys*. The recent description of the species *Aepeomys reigi* (Rodentia: Cricetidae), which had been previously included in *Aepeomys lugens* (Ochoa *et al.* 2001), and *Cryptotis dinirensis* (Eulipotyphla: Soricidae), previously included in *Cryptotis meridensis* (Quiroga-Carmona and Do Nascimiento 2016), are clear examples of evolutionary processes in small non-flying mammals that took place in Cordillera de Mérida.

Finally, our work highlights the need to gather complete wildlife inventories in biogeographically important zones of the Venezuelan Andes, such as Sierra de Perijá, where the presence of *N. maculiventer* was recently reported (García *et al.* 2019); the protected areas of the Venezuelan System of National Parks located in Cordillera de Mérida (*e.g.*, Dinira National Park, Guache, Páramo Batallón and la Negra, etc.); as well as other areas within the distribution range of the non-Andean species *N. caracolus* in Cordillera de la Costa and the Lara-Falcón hill systems in northern Venezuela. This would allow obtaining a more representative sample that could be used for comprehensive taxonomic reviews using a combination of (geometric and linear) morphometrics techniques, analyses of morphological characters, cytogenetics and DNA sequencing, as well as biogeographic and niche-modeling studies (Anderson and Raza 2010).

Acknowledgements

Literature cited

Aguilera, M., A. Pérez-Zapata, and A. Martino. 1995. Cytogenetics and karyosystematics of *Oryzomys albigularis* (Rodentia, Cricetidae) from Venezuela. Cytogenetics and Cell Genetics 69:44–49.

Anderson, R. P., and A. Raza. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. Journal of Biogeography 37:1378–1393.

Anderson, R. P., E. E. Gutiérrez, J. Ochoa-G., F. J. García, and M. Aguilera. 2012. Faunal nestedness and species–area relationship for small non-volant mammals in "sky islands" of northern Venezuela. Studies on Neotropical Fauna and Environment 47:157–170.

Astúa, D., I. Bandeira, and L. Geise. 2015. Cranial morphometric analyses of the cryptic rodent species *Akodon cursor* and *Akodon montensis* (Rodentia, Sigmodontinae). Oecología Australis 19:143–157.

Bonvicino, C. R., and M. A. M. Moreira. 2001. Molecular phylogeny of the genus *Oryzomys* (Rodentia: Sigmodontinae) based on cytochrome b DNA sequences. Molecular Phylogenetics and Evolution 18:282–292.

Bookstein, F. L. 1991. Morphometric tools for landmark data. Geometry and biology Cambridge University Press. New York, U.S.A.

Boroni, L. N., L. S. Lobo, P. S. R. Romanom and G. Lessa. 2017. Taxonomic identification using geometric morphometric approach and limited data: an example using the upper molars of two sympatric species of *Calomys* (Cricetidae: Rodentia). Zoologia 34:1–11.

Cordeiro-Estrela, P., M. Baylac, C. Denys, and J. Marinho-Filho. 2006. Interspecific patterns of skull variation between sympatric Brazilian vesper mice: geometric morphometrics assessment. Journal of Mammalogy 87:1270–1279.

Cordeiro-Estrela, P., M. Baylac, C. Denys, and J. Polop. 2008. Combining geometric morphometrics and pattern recognition to identify interspecific patterns of skull variation: case study in sympatric Argentinian species of the genus *Calomys* (Rodentia: Cricetidae: Sigmodontinae). Biological Journal of the Linnean Society 94:365–378.

García, F. J., and E. Sánchez-González. 2013. Morfometría geométrica craneal en tres especies de roedores arbóricolas neotropicales (Rodentia: Cricetidae: *Rhipidomys*) en Venezuela. Therya 4:157–178.

García, F. J., E. Sánchez-González, M. Machado, G. Flórez, D. Araujo-Reyes, O. Vásquez-Parra, and D. Prieto-Torres. 2019. First record of the Santa Marta mouse, *Nephelomys maculiventer* (Mammalia, Rodentia, Cricetidae), for Venezuela. Mammalia 83:203–207.

García, F. J., E. Sánchez-González, D. Araujo-Reyes, M. Machado, and G. Flórez. 2018. Descripción de una nueva subespecie de ratón mochilero del género *Heteromys* (Mammalia, Rodentia,

Heteromyidae) en Venezuela. Revista de Biodiversidad Neotropical 8:41–54.

Gutiérrez, E. E., J. E. Maldonado, A. Radosavljevic, J. Molinari, B. D. Patterson, J. M. Martínez-C, A. R. Rutter, M. T. R. Hawkins, F. J. García, and J. Maldonado. 2015. The taxonomic status of *Mazama bricenii* and the significance of the Táchira depression for mammalian endemism in the Cordillera de Mérida, Venezuela. PLoS ONE 10:1–24.

Hammer, Ø., and D. A. T. Harper. 2011. PAST: PAlaeontological STAtistics, versión 2.10. http://folk.uio.no/ ohammer/past. Accesed in February 2020

Josse C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito, and A. Tovar. 2009. Ecosistemas de los Andes del Norte y Centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTA-UNALM, ICAE-ULA, CDC-UNALM, RUMBOL SRL. Lima, Perú.

Klingenber, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11:353–357.

La Marca, E. 1997. Origen y evolución geológica de la Cordillera de Mérida, Andes de Venezuela. Geografía 1:1–110.

Márquez, E. J., M. Aguilera M., and M. Corti. 2000. Morphometric and chromosomal variation in populations of *Oryzomys albigularis* (Muridae: Sigmodontinae) from Venezuela: multivariate aspects. Zeitschrift für Säugetierkunde 65:84–99.

Meloro, C, P. Raia, P. Piras, C. Barbera, and P. O' Higgins. 2008. The shape of the mandibular corpus in large fissiped carnivores: allometry, function and phylogeny. Zoological Journal of the Linnean Society 154:832–845.

Musser, G. G., M. D. Carleton, E. M. Brothers, and A. L. Gardner. 1998. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): diagnoses and distributions of species formerly assigned to *Oryzomys* "*capito*". Bulletin of the American Museum of Natural History 236:1–376.

Ochoa-G., J., M. Aguilera, V. Pacheco, and P. J. Soriano. 2001. A new species of *Aepeomys* Thomas, 1898 (Rodentia: Muridae) from the Andes of Venezuela. Mammalian Biology 66:228–237.

Percequillo, A. R. 2003. Sistemática de *Oryzomys* Baird, 1858: definicão dos grupos de espécies e revisão taxonômica do grupo *albigularis* (Rodentia, Sigmodontinae). PhD Thesis, Universidade de São Paulo, Brazil.

Percequillo, A. R. 2015. Genus *Nephelomys* Weksler, Percequillo and Voss 2006. Pp. 377–390 *in* Mammals of South America Volume 2. (Patton, J. L., Pardiñas, U. F. J., y G. D'Elía, eds). The University of Chicago Press. Chicago, U.S.A.

Quiroga-Carmona, M., and C. DoNascimiento. 2016. A new species of small-eared shrew of the genus *Cryptotis* Pomel, 1848 (Mammalia, Eulipotyphla, Soricidae) from the easternmost mountains of the Venezuelan Andes. Mammalian Biology 81:494–505.

Rivas, B. A., and J. E. Péfaur. 1999a. Variación geográfica en poblaciones venezolanas de *Oryzomys albigularis* (Rodentia: Muridae). Mastozoología Neotropical 6:47–59.

Rivas, B. A., and J. E. Péfaur. 1999b. Variación craneana entre sexo y edad en *Oryzomys albigularis* (Rodentia: Muridae). Mastozoología Neotropical 6:61–70.

Rohlf, F. J. 2006. tpsDig, Digitize landmarks and outlines. Version 2.05. New York: Stony Brook. Department of Ecology and Evolution, State University of New York. New York, U.S.A.

Sheets H. D. 2010. Integrated Morphometrics Package (IMP) 7. http://www3.canisius.edu/~sheets/imp7.htm. Accesed in February 2020.

Soriano, P. J., A. Díaz de Pascual, J. Ochoa-G., and M. Aguilera. 1999. Biogeographic analysis of the mammal communities in the Venezuelan Andes. Interciencia 24:17–25.

Weksler, M. 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae: Sigmodontinae) based on the nuclear IRBP exon. Molecular Phylogenetics and Evolution 29:331–349.

Weksler, M. 2006. Phylogenetic relationships of oryzomyine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. Bulletin of the American Museum of Natural History 296:1–149.

Weksler, M., A. R. Percequillo, and R. S. Voss. 2006. Ten new genera of oryzomyine rodents (Rodentia. Cricetidae). American Museum Novitates 3537:1–29.

Woodman, N. A. 2002. New species of small-eared shrew from Colombia and Venezuela (Mammalia: Soricomorpha: Soricidae: Genus *Cryptotis*). Proceedings of the Biological Society of Washington 115:249–272.

Appendix 1

Specimens used in the geometric morphometrics analyses in this study

Nephelomys meridensis: Mérida and adjacent areas: Mérida, La Azulita (8° 41' 05"N, -71° 25' 33"O; 2,000 msnm), CVULA –I - 6350, 1074; Mérida, La Carbonera (San Eusebio) (8° 38' 39"N, -71° 24' 57"O; 2,500 msnm), CVULA – I - 1070, 1077; Mérida, Monte Zerpa (8° 38' 16"N, -71° 09' 47" O; 2,000 – 2,200 msnm), CVULA – I - 1093, 1098, 1255, 1257, 1258, 2965, EBRG-28403, 28404; Mérida, Santa Rosa (8° 37' 40"N, -71° 09' 15" O; 2,100 msnm), EBRG - 14885; Mérida, El Baho (8° 50' 17"N, -70° 43' 34"O; 3,010 msnm), CVULA – I - 6178. *Nephelomys meridensis* A: Parque Nacional Yacambú, El Blanquito (9° 38' 30"N, -69° 30' 47"O; 1,500 msnm), 17 Km de Sanare, Estado Lara: EBRG - 10297, 10298, 10300, 10594, 10595, 10599, 10600, 10601, 10603, 10605, 10606, 10607, 10608, 10609, 10619, 10620, 10956, 10986, 21464, 21465, 21466, 21468, 21469, 21470, 21471, 21474, 21480, 28398. *Nephelomys meridensis* B: La Trampita, campamento Siberia, 12 Km SSE de Pregonero, Uribante, Estado Táchira (7° 35' 30"N, -72° 04' 36"O; 1,000 – 1,300 msnm), CVULA – I - 2317, 1528, 1963, 2190, 2307, 2316, 2318, 2471, 3539, 7043, MHNLS - 8749, 8750, 8751, 8753, 8764. *Nephelomys meridensis* C: Páramo El Tamá, Macizo El Tamá, Estado Táchira: 35 Km S, 22 Km O de San Cristobal, Buena Vista (7° 27' 43"N, -72° 22' 07"O; 2,460 msnm), EBRG – 14893. Páramo El Tamá (7° 27' 24"N, -72° 22' 05"O; 2,400 msnm), MHNLS - 4650, 4652, 4657, 4923. *Nephelomys meridensis* D: Parque Nacional Dinira, carretera La Peña-Carache, sector Las Torres, municipio Las Palmas (9° 41' 50"N, -70° 04' 26"O; 2,553 msnm), EBRG - 24669, 24670; Parque Nacional Dinira, sector Buenos Aires (9° 36' 27"N, -70° 04' 06"O; 1,900 msnm), EBRG - 24416.