

Alpha-taxonomy in the cricetid rodent *Neomicroxus*, a first assessment

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Neomicroxus, a recently named genus, comprises small-bodied cricetid rodents patchily distributed in high-Andean ranges from Ecuador to Venezuela. Currently, two species of *Neomicroxus* are recognized, *N. bogotensis*, endemic to the Cordillera Oriental in Colombia and Cordillera de Mérida and Páramo de Tamá in Venezuela, and *N. latebricola* that occurs northern Andes of Ecuador. The genus is among the most poorly understood Neotropical rodents and to date no formal assessment about its alpha taxonomy was conducted. Based on DNA evidence of the first portion of the mitochondrial cytochrome b gene (cytb) and the first exon of the interphotoreceptor retinoid binding protein (IRBP), as well as craniodental measurements, we explored the divergence degree, genetic structure and phyletic relationships of the two species currently allocated under *Neomicroxus*. Our analyses support the monophyly of the genus as well as its uncertain tribal affiliation. *Neomicroxus* was retrieved as structured in two main branches, in agreement with the traditional recognition of two species. The populations referred to *N. bogotensis* exhibit deep divergence values (> 6 %) pointing to the existence of undescribed species under its concept. In contrast, populations of *N. latebricola* show a shallow genetic structure although implying recognizable geographical breaks. A moderate degree of genetic and morphological differentiation supports a new subspecies for the western populations of *N. latebricola*. Our contribution is the first attempt to better understanding the alpha taxonomy of *Neomicroxus*, highlighting the importance of the geographic complexity as a barrier to the genetic flow in *N. bogotensis* and the significance of the subspecies concept to formalize the geographic variation recovered in *N. latebricola*.

Neomicroxus, un género recientemente nominado, agrupa roedores cricétidos de pequeño tamaño distribuidos en zonas altas de los Andes, desde Ecuador hasta Venezuela. Actualmente, se reconocen dos especies, *N. bogotensis* endémica de la Cordillera Oriental de Colombia, Cordillera de Mérida y Páramo de Tamá en Venezuela, y *N. latebricola*, que ocupa el norte de los Andes en Ecuador. Este género se encuentra entre los roedores neotropicales menos conocidos y, hasta la fecha, no se ha realizado ninguna evaluación formal sobre su taxonomía alfa. Basados en secuencias de ADN de la primera porción del gen mitocondrial del citocromo b (cytb) y el primer exón de la proteína de unión del interfotoreceptor del retinoide (IRBP) e información métrica cráneo-dentaria, exploramos el grado de divergencia, estructura genética y relaciones filogenéticas de las dos especies actualmente asignadas bajo *Neomicroxus*. Nuestros análisis apoyan la monofilia del género como así también su afiliación tribal incierta. Se recuperaron dos cladogramas principales en concordancia con las especies reconocidas dentro del género. Las poblaciones referidas a *N. bogotensis* muestran valores de divergencia profunda (> 6 %) que sugieren la existencia de una especie no descrita. En contraste, las poblaciones de *N. latebricola* muestran una estructura genética somera pero que implica quiebres geográficos reconocibles. La diferenciación genética y morfológica moderada apoyan la existencia de una nueva subespecie para las poblaciones occidentales de *N. latebricola*. Nuestra contribución es el primer intento de comprender la taxonomía alfa de *Neomicroxus*, destacando la importancia de la complejidad geográfica como barrera para el flujo genético en *N. bogotensis* y la importancia del concepto de subespecie para formalizar la variación geográfica observada en *N. latebricola*.

Keywords: Colombia; Ecuador; *Microxus*; *Neomicroxus bogotensis*; *Neomicroxus latebricola*.

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Introduction

Among the most poorly known high-Andean cricetids is *Neomicroxus*, a genus recently erected to encompass small-bodied akodont-like sigmodontines previously placed in *Akodon* and *Microxus*. *Neomicroxus* was based on *Microxus latebricola*, originally described from a single specimen collected in Ambato, on the eastern Cordillera in Ecuador (Anthony 1924). Another species, *Acodon bogotensis*, is also included in the genus, being up to date exclusive from Colombia and Venezuela (Alvarado-Serrano and D'Elía 2013, 2015).

Paradoxically, both species of *Neomicroxus* remained taxonomically unexplored, although they are abundant and easy to catch in high-Andean environments (e. g., [Corporación Suna Hisca 2003](#); [Vianchá et al. 2012](#); [Brito 2013](#); [Curay 2019](#); [Ojala-Barbour et al. 2019](#)). The deconstruction of the genus *Microxus*, after the peak of its complexity during the '30 (i. e., involving *affinis*, *bogotensis*, *iheringi*, *lanosus*, *latebricola*, *mimus*, and *torques*; [Gyldenstolpe 1932](#)), was a slow and hesitant process. As late as the beginnings of the present century, the taxonomic situation of *bogotensis* and *latebricola* was summarized by [Voss \(2003:21\)](#) as

follows “*This species [latebricola] closely resembles Akodon [sic] bogotensis Thomas (1895), another eastern-Andean species that was formerly referred to the genus Microxus. Among other shared similarities, both species differ from typical Akodon by their ... Although phylogenetic analyses of mitochondrial DNA sequences do not support the separate generic status of Microxus (as represented by the type species mimus Thomas; see Smith and Patton [1993] and references cited therein), sequence data from latebricola and bogotensis have not been analyzed. Despite their current generic classification, these two northern-Andean endemics clearly form a distinct clade that merits nomenclatural recognition.*” The advent of the first molecular data for *latebricola* was the keystone to crystallize what the acute morphological eye of Voss (2003) envisioned; *Neomicroxus* was erected with *latebricola* as type species (Alvarado-Serrano and D’Elía 2013). However, molecular findings retrieved an additional and previously unsuspected result; *N. latebricola* was neither an *Akodon* nor an *Akodontini* (Alvarado-Serrano and D’Elía 2013).

Almost nothing is known about the potential variability within *Neomicroxus* along the > 10° degrees of latitude which encompasses its range. Both species are found in the northern Andes at elevations above 2,400 masl and reaching as high as 3,900 masl (Alvarado-Serrano and D’Elía 2015). *N. bogotensis* is endemic to the Cordillera Oriental of Colombia and the Cordillera de Mérida and Páramo de Tamá in Venezuela, while *N. latebricola* occurs to high elevations of the eastern Andes in Ecuador, from Tungurahua to Carchi provinces (Alvarado-Serrano and D’Elía 2013, 2015). Recently, Curay (2019) revealed morphological variation within the Ecuadorian populations that supports the recognition of geographic structure in what is currently understood as *N. latebricola*. It is in agreement with the finding of populations of the species, traditionally known and restricted only to the eastern Andes, in western locations from the Cordillera Occidental such as the Páramo de Fraillejones (Brito 2013). In this contribution, we undertook a reappraisal of the systematics of *Neomicroxus*, including for the first time sequences of *N. bogotensis*. We analyzed two DNA markers and morphometric variables as a first attempt to explore of the alpha-taxonomy of the genus.

Materials and Methods

Sequence acquisition. We obtained DNA sequences from specimens of *Neomicroxus* from Colombia ($n = 3$, Cundinamarca and Santander departments) and Ecuador ($n = 2$, Carchi province; Appendix 1, Appendix 2). The new molecular data consisted of five nucleotide sequences of the first portion of the mitochondrial cytochrome b gene (cytb, 801bp) and four of the first exon of the interphotoreceptor retinoid binding protein (IRBP, 1514bp). Here, we included for the first time in any phylogenetic study sequences of three specimens of *Neomicroxus bogotensis*. The monophyly of the genus, the identity of the sister group, and its phylogenetic position into the Sigmodontinae have not been fully corroborated (Alvarado-Serrano and D’Elía 2013). There-

fore, we included sequences for representatives of the several tribes of Sigmodontinae and some outgroup taxa (other Cricetidae, Nesomyidae and Spalacidae) retrieved from GenBank. For those terminals that miss information, we completed the matrix with missing data or ambiguous state characters (*i.e.* N). All analyzed taxa as well as the vouchers of their cytb and IRBP sequences are listed in Appendix 2.

DNA of high molecular weight was extracted from the Ecuadorian specimens (*N. latebricola*) using the protocol of the Wizard Genomic DNA Purification kit, with fresh tissues as starting material. In the case of the Colombian specimens also DNA of high molecular weight was extracted from fresh tissues, as well as degraded DNA from ancient material (small fragments of rehydrated soft tissue adhered to cranial bones of museum specimens); a GeneJet Genomic DNA Purification Kit (Thermo Fisher Scientific) was used indistinctly for both processes. However, the ancient material was previously subjected to a repetitive washing protocol (Giarla *et al.* 2010) in order to remove foreign DNA and potential PCR inhibitors. Primer pairs used for amplification and sequencing of the mitochondrial fragment from the Ecuadorian specimens were MVZ05 and MVZ16 (Smith and Patton 1993), while for the IRBP locus we used the A1 and F1 (Jansa and Voss 2000). Amplification conditions followed Da Silva and Patton (1993) for cytb and Jansa and Voss (2000) for IRBP. For the Colombian specimens with DNA of high molecular weight (UIS-MZ 1299 and 1596), a fragment of + 800 bp of the cytb was amplified with the flanking primer L14724 (Irwin *et al.* 1991), and the internal primer O700 H (Handson and Bradley 2008), while for the specimen with degraded DNA (IAvH 5777), only + 400 base pairs of the gene were amplified with the flanking primer MVZ05, and the internal primer MVZ04 (Smith and Patton 1993). For these cytb sequences we modified the amplification conditions of Hanson and Bradley (2008). The IRBP locus only was amplified from the Colombian specimens with DNA of high molecular weight using the primers IRBP217 and IRBP1351 (Stanhope *et al.* 1992) and we followed the amplification conditions mentioned there. All reactions included negative controls. Amplicons from Ecuadorian specimens were purified and sequenced at the external service of Macrogen, Inc. (Seoul, Korea), whereas those from Colombian specimens at the Servicio de Secuenciación y Análisis Molecular SSiGMol, Universidad Nacional de Colombia (Bogotá, Colombia).

Descriptive and phylogenetic analysis. Before conducting phylogenetic analyses, we checked the quality of each DNA sequence in the edition process with CodonCode Aligner (Codon-Code 2014). Subsequently, sequences were aligned using default options in ClustalX 2.0 (Larkin *et al.* 2007). New DNA sequences were deposited in GenBank (accession numbers cytb: MT240520-MT240524, IRBP: MT249797-MT249800). Observed values of cytb sequence divergence (p distance) were calculated with MEGA7 (Kumar *et al.* 2016) ignoring those sites with missing data (Appendix 3). Phylo-

genetic analyses were conducted using the concatenated matrix and subjected to Maximum Parsimony (MP; [Farris 1982](#)), Maximum Likelihood (ML; [Felsenstein 1981](#)) and Bayesian Inference (BI; [Huelsenbeck et al. 2001](#)) approaches. MP analysis was carried out in PAUP* version 4.0 ([Swofford 2000](#)) with characters treated as unordered and equally weighted, 200 replicates of heuristic searches with random addition of sequences and tree bisection-reconnection (TBR) branch swapping. Nodal support was estimated by 1,000 bootstrap replicates with five replicates of sequence addition each (BT1). For the ML analysis, we used IQ-TREE version 1.6.0 software ([Nguyen et al. 2015](#)) implemented in the IQ-TREE webserver ([Trifinopoulos et al. 2016](#)) using LG+I+G4 substitution as the best-fit model. Statistical support for each individual node of the ML phylogenetic tree was estimated using 1,000 iterations of the ultrafast bootstrap value (BT2). Bayesian analyses were conducted in MrBayes 3.2 ([Ronquist et al. 2012](#)). We performed two independent runs, each with three heated and one cold Markov chains, were allowed to proceed for 10^7 iterations and were sampled every 1,000 generations. We used the GTR+G+I substitution model previously determined by Akaike information criterion (AIC) in jModeltest ([Posada 2008](#)). Log-likelihood values against generation time for each run were plotted in Tracer v1.7.1 ([Rambaut et al. 2018](#)). The first 25 % of the trees obtained were discarded as burn-in, and the remaining trees were used to construct a 50 % majority rule consensus tree and obtain the support for each clade as posterior probability (PP) values. Outgroups used in the phylogenetic analyses include taxa of Sigmodontinae and representatives of another rodents families (*i. e.*, Cricetidae, Nesomyidae and Spalacidae).

Studied specimens. We examined the external and craniodental morphology of 55 specimens of *Neomicroxus*, including skulls, skins, and fluid-preserved animals (see Appendix 1). Studied specimens are deposited in the following insti-

tutional collections: Argentina: Colección de Mamíferos del Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut). Colombia: Colección de Mamíferos del Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH; Villa de Leyva, Boyacá). Colección de Mamíferos “Alberto Cadena García” del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia (ICN; Bogotá). Colección de Mamíferos del Museo de Historia Natural de la Universidad Industrial de Santander (UIS-MZ; Bucaramanga, Santander). Ecuador: Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ; Quito). Instituto Nacional de Biodiversidad (INABIO-MECN; Quito). Instituto de Ciencias Biológicas de la Escuela Politécnica Nacional (MEPN; Quito). United States: National Museum of Natural History of Smithsonian Institute (USNM; Washington).

Morphometrics. Taking into account the important degree of hypsodonty showed by *Neomicroxus*, we established an ad-hoc classification composed by six tooth-wear stages (TWC, Figure 1), which based on dental wear on the cusps and the differentiation of the main structures. In this context, we considered as adults those specimens belonging to the TWC 4 to 6. These animals were employed in morphological qualitative assessment and ulterior statistical analyses based on 18 craniodental measurements (Appendix 4), taken with a digital caliper and expressed in millimeters. For descriptive purposes, univariate statistics for each measurement were calculated. To perform a multivariate exploration, we used a sample composed by 12 specimens of *N. bogotensis* and 21 of *N. latebricola* (sexes pooled) as input data for a principal component analysis (PCA; [Johnson and Wichern 1999](#); [Carleton and Musser 1989](#)). Raw data were standardized by transformation to their natural logarithms and the first three principal components were calculated on the resultant covariance matrix. To test the potential variation of *N. bogotensis* through its range, we added to the analysis several Venezuelan speci-

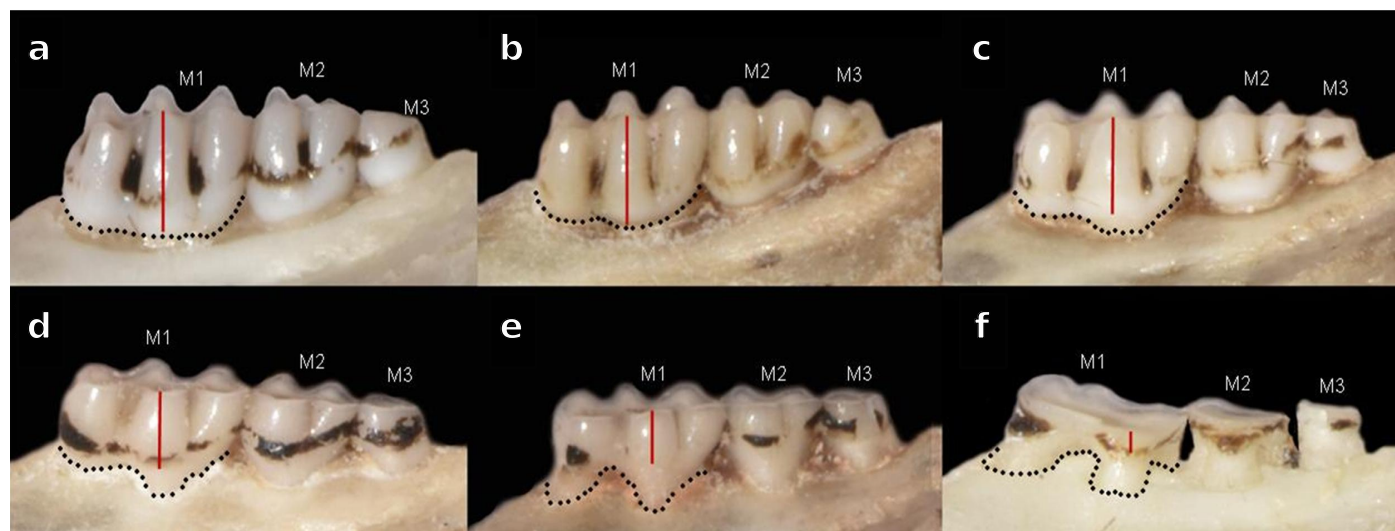


Figure 1. *Neomicroxus* age classification estimated by the dental wear on the cusps and the differentiation of the main structures. a) TWC1: M1-M2 cusps pronounced with flexus and fosses visible. Features associated with the procingulum are notorious. M3 erupted, no wear, b) TWC2: M1-M2 similar to TWC1, but M3 shows slight wear worn although still complex in morphology, c) TWC3: M1 has a vestige of posteroloph, roots still are not very visible. M2 retaining some structures, but possesses some fosses and vestige of the anteroloph. M3 structures are less distinguishable, d) TWC4: Smaller flexus and posteroloph in M1, with noticeable roots. M3 is almost flat with anteroloph and posteroloph barely visible or not distinguishable, e) TWC5: Molar surfaces with scarce occlusal structures, M1 anteromedian flexus not differentiated, M2 flexus slightly evident, and M3 fully flattened, and f) TWC6: Molar surfaces without occlusal structures, roots very visible. M3 is totally worn, clearly exposing the dentin.

mens (Mérida and Táchira states) with incomplete measurements because they were assessed with a different goal by the senior author. For this reason and to avoid calculations with missing data, we reduced the number of variables considered to eight (ONL, BZP, LD, LIF, LM1-3, BB, CIL, IML), and worked on a matrix composed by 12 individuals. For *N. latebricola*, the PCA was executed with 21 individuals and 18 variables (Appendix 3). Additionally, to assess the differentiation between the molecular recovered groups, we perform a Discriminant Analysis (DA) employing the same log-transformed data removing missing values (25 individuals, 16 variables). Group assignments were validated by a jackknife resampling. For all morphometrical analyses, we used the free software Past version 4.0 (Hammer *et al.* 2001).

Results

Phylogenetic relationships and genetic divergence. Phylogenetic analyses recovered well-resolved topologies within Oryzomyia (*sensu* Steppan *et al.* 2004), with tribal relationships mostly concordant with previous studies (*e. g.*, Alvarado-Serrano and D'Elía 2013; Salazar-Bravo *et al.* 2016; Gonçalves *et al.* 2018). The genus *Neomicroxus* was found to be monophyletic with high support values (Figure 2a; BT1/BT2/PP = 99/99/1.0), but without affiliation to any recognized tribe in the MP and BI topologies, and sister to Abrotrichini + Wiedomyini in the ML analysis but weakly supported. In all approaches (MP, ML, and BI), two major clades strongly supported were retrieved within the genus. One clade is formed by individuals from Colombia (100/96/0.9) and can be referred to what is currently understood as *N. bogotensis*; another clade is represented by sequences from

Ecuadorian Cordillera Oriental and Occidental (100/74/0.9), and can be confidently associated to *N. latebricola*. The overall mean divergence at the *cytb* gene for *Neomicroxus* reaches 6.3 %, meanwhile, the genetic distance between the two main clades is 11 % (see Appendix 3). In the *bogotensis* clade, the phyletic relationships show a profound divergence between individuals from Santander and Cundinamarca departments (> 6 %). Our sampling is insufficient to evaluate the demography of the species, however, the analyzed localities are geographically close, so we can affirm that the divergence observed between northern and central (Cundinamarca) Colombia is not due to a phenomenon of isolation by distance. This deep divergence (also reflected in the branch lengths), suggests that the populations of *N. bogotensis* here analyzed are older, possibly demographically stable, with a strong barrier (geographical or ecological) that interrupts gene flow.

On the other hand, within the *latebricola* clade, we recovered a shallow genealogy with two minor groups or subclades which diverge by 1.4 %. One subclade is composed of the same haplotype shared by QCAZ4160 and QCAZ4167 individuals, both from the Ecuadorian Napo province. Meanwhile the other subclade groups three different haplotypes, slightly divergent, from Carchi (MECN3727/MECN3734, QCAZ9801) and Napo (QCAZ4121) provinces (Appendix 3). Conversely to the observed variation in *N. bogotensis*, the genealogical relationships and the divergence values between and within *N. latebricola* subclades reveal the existence of current genetic flow between populations, reflected by the lack of reciprocal monophyly between the provinces, which also is a sign of populations in the process of expansion.

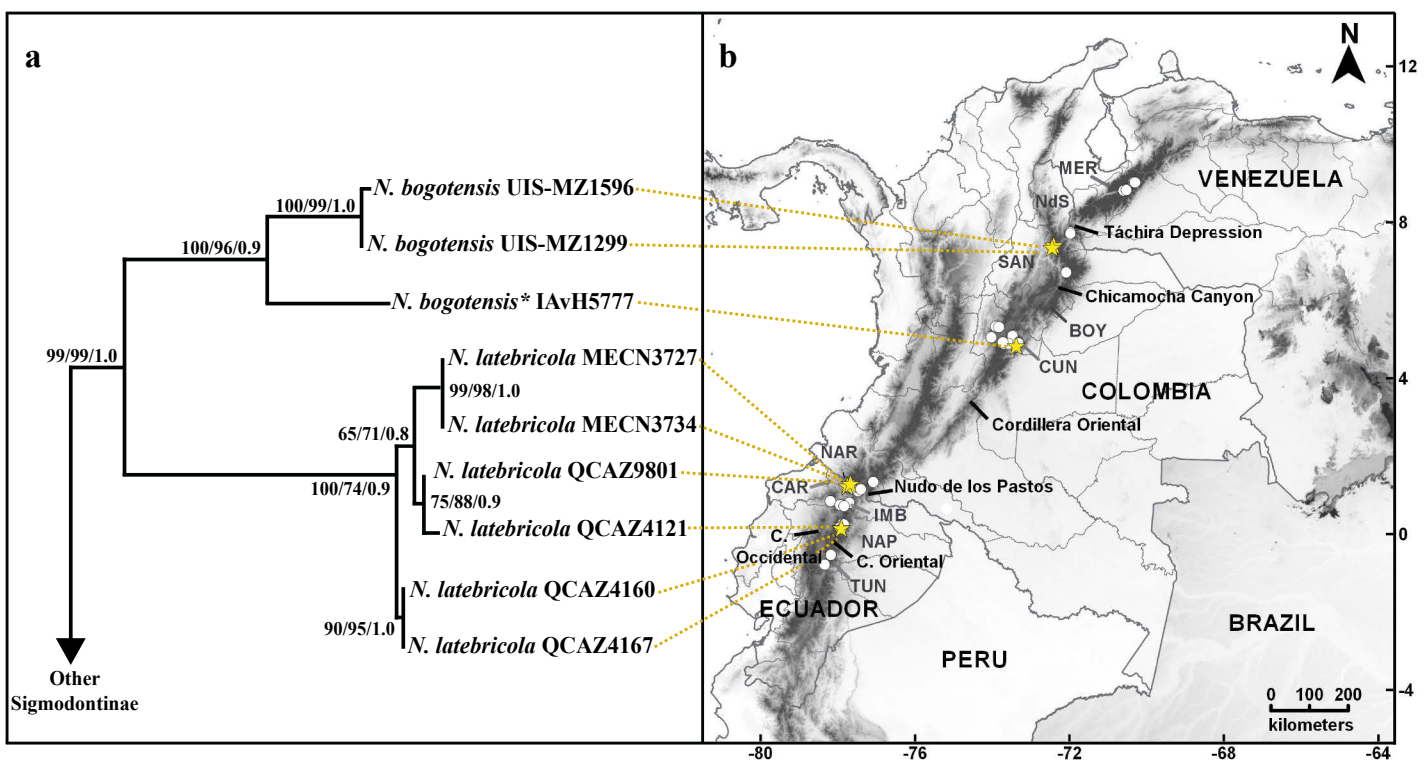


Figure 2. a) Phylogenetic tree of concatenated matrix related to the b) geographical distribution of *Neomicroxus* specimens from the Andes of Ecuador, Colombia and Venezuela. Support values (MP/ML/BI) are indicate next to each node. Yellow stars indicate specimens used in the phylogenetic analyses.

Morphometric analyses. The univariate morphometric analysis reveals little differences among the samples, being *N. bogotensis* who possesses lower values to several of the craniodental variables here recorded (Table 1). The PCA for *N. bogotensis* showed a clear separation between specimens from north of Colombia (Santander and Norte de Santander departments), Cundinamarca, and Venezuela (Figure 3). The 88.6 % of the total variation is summarized in the first two principal components, none of which can be interpreted as a size factor because they include positive and negative coefficients for some variables (Table 2). The largest contribution of the first component is attributed to the follow-

ing variables: breadth of zygomatic plate, length of incisive foramina, length of upper diastema, occipitonasal length, while for the PC2 are the lengths of incisive foramina and the upper diastema. The *N. latebricola* PCA retrieves two partially overlapping groups from the Cordillera Oriental (Napo province) and Occidental (Carchi province; Figure 3). These results are congruent with the molecular results (see above); 77.2 % of the variation is explained by the PC1-2. The craniodental variables with the greatest contribution are the breadth of incisive foramina and breadth of the bony palate on the PC1, and breadth of zygomatic plate and length of incisive foramina on the PC2 (Table 2).

Table 1. Univariate statistics for selected craniodental measurements in *Neomicroxus*. Values provided are mean \pm standard deviation and [minimum–maximum] range. All measurements are expressed in millimeters.

	<i>N. latebricola</i> Occidente	<i>N. latebricola</i> Oriente	<i>N. bogotensis</i> North Colombia	<i>N. bogotensis</i> Cundinamarca	<i>N. bogotensis</i> Venezuela
	<i>n</i> = 13	<i>n</i> = 9	<i>n</i> = 3	<i>n</i> = 1	<i>n</i> = 9
Occipitonasal length - ONL	25.53 \pm 0.4 [24.95 - 26.21]	25.18 \pm 0.22 [24.89 - 25.65]	23.52 \pm 0.71 [22.75 - 24.14]	24.33	23.18 \pm 0.39 [22.49 - 23.74]
Condyllo-incisive length - CIL	23.18 \pm 0.49 [22.49 - 23.91]	22.62 \pm 0.24 [22.15 - 22.93]	20.57 \pm 0.67 [19.9 - 21.24]	21.45	20.43 \pm 0.31 [20.03 - 21.14]
Greatest zygomatic breadth - ZB	11.97 \pm 0.15 [11.73 - 12.34]	12.04 \pm 0.12 [11.82 - 12.21]	---	11.67	11.25 \pm 0.21 [11.01 - 11.56]
Interorbital breadth - IB	4.70 \pm 0.1 [4.41 - 4.87]	4.82 \pm 0.12 [4.69 - 5.06]	4.45 \pm 0.19 [4.25 - 4.63]	4.75	---
Breadth of zygomatic plate - BZP	1.39 \pm 0.06 [1.3 - 1.5]	1.38 \pm 0.1 [1.26 - 1.52]	1.33 \pm 0.04 [1.29 - 1.37]	1.67	1.36 \pm 0.1 [1.23 - 1.54]
Length of upper diastema - LD	6.26 \pm 0.19 [6 - 6.68]	6.38 \pm 0.2 [6.09 - 6.74]	5.75 \pm 0.16 [5.58 - 5.9]	6.01	5.6 \pm 0.13 [5.39 - 5.83]
Breadth of bony palate - BBP	5.39 \pm 0.1 [5.24 - 5.6]	5.36 \pm 0.09 [5.26 - 5.51]	5.24 \pm 0.35 [4.99 - 5.64]	5.59	---
Length of incisive foramina - LIF	4.75 \pm 0.18 [4.44 - 5]	4.73 \pm 0.25 [4.46 - 5.15]	4.12 \pm 0.71 [3.3 - 4.56]	4.5	3.97 \pm 0.14 [3.76 - 4.17]
Breadth of incisive foramina - BIF	1.66 \pm 0.1 [1.55 - 1.84]	2.02 \pm 0.14 [1.83 - 2.2]	1.76 \pm 0.13 [1.62 - 1.85]	1.87	---
Length of maxillary tooththrow - LM1-3	3.63 \pm 0.1 [3.41 - 3.83]	3.5 \pm 0.13 [3.26 - 3.69]	3.46 \pm 0.06 [3.42 - 3.53]	3.73	3.57 \pm 0.09 [3.43 - 3.69]
Breadth of first upper molar - BM	1.17 \pm 0.04 [1.08 - 1.25]	1.12 \pm 0.04 [1.03 - 1.17]	1.14 \pm 0.09 [1.04 - 1.2]	1.15	---
Breadth of palatal bridge - BPB	2.65 \pm 0.16 [2.46 - 3.1]	2.99 \pm 0.17 [2.75 - 3.31]	2.68 \pm 0.49 [2.29 - 3.23]	3.13	---
Length of nasals - LN	10.11 \pm 0.16 [9.66 - 10.27]	10.1 \pm 0.12 [9.87 - 10.24]	9.24 \pm 0.37 [8.84 - 9.58]	9.52	---
Breadth of braincase - BB	11.65 \pm 0.20 [11.21 - 11.96]	11.65 \pm 0.15 [11.28 - 11.79]	10.93 \pm 0.37 [10.53 - 11.25]	11.26	11.11 \pm 0.21 [10.72 - 11.38]
Breadth of the occipital condyles - BOC	6.14 \pm 0.12 [5.92 - 6.39]	6.14 \pm 0.09 [6.04 - 6.3]	5.82 \pm 0.24 [5.55 - 5.98]	5.77	---
Zygomatic internal length - ZIL	7.03 \pm 0.17 [6.75 - 7.36]	7.08 \pm 0.1 [6.85 - 7.18]	---	6.61	---
Mandibular length - ML	12.76 \pm 0.33 [11.98 - 13.25]	13.04 \pm 0.37 [12.6 - 13.59]	11.41 \pm 0.29 [11.19 - 11.74]	12.15	---
Mandibular molar tooththrow length - IML	3.8 \pm 0.08 [3.63 - 3.94]	3.65 \pm 0.13 [3.43 - 3.78]	3.77 \pm 0.03 [3.74 - 3.79]	3.87	3.77 \pm 0.11 [3.63 - 3.9]

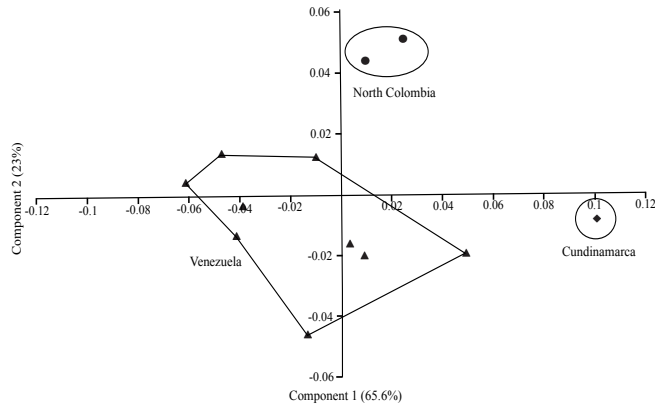
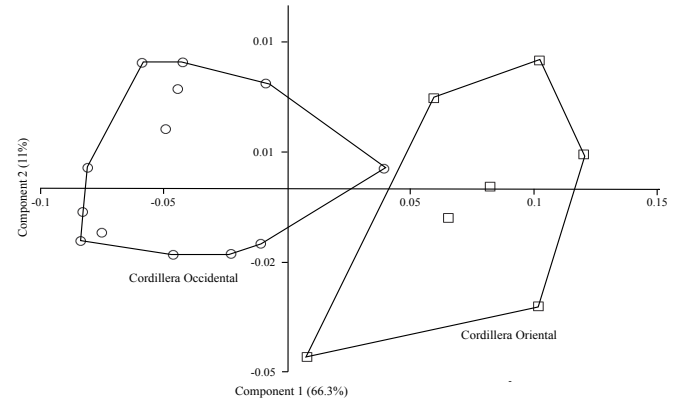
a) *Neomicroxus bogotensis*b) *Neomicroxus latebricola*

Figure 3. Principal component analysis, components 1 and 2, of the 8 log-transformed craniodental measurements for in *N. bogotensis* ($n=12$), and 18 for *N. latebricola* ($n=21$). ◆: *N. bogotensis* Cundinamarca, ●: *N. bogotensis* North Colombia (Norte de Santander and Santander), ▲: *N. bogotensis* Venezuela, ○: *N. latebricola* Ecuadorian Cordillera Occidental, and □: *N. latebricola* Ecuadorian Cordillera Oriental.

The Discriminant Analysis confirms the separation of *N. bogotensis* from the north of Colombia (*i.e.* Norte de Santander and Santander departments) and the specimen of Cundinamarca department. Similarly, the samples of *N. latebricola* from the Oriental and Occidental cordilleras of Ecuador are clearly differentiated (Figure 4). For both species, the recovered groups are completely concordant with the molecular arrangements. According to jack-knife resampling, the predefined groups (*i.e.* *N. bogotensis*: North Colombia [Norte de Santander and Santander departments], Cundinamarca, and Venezuela [Mérida], *N. latebricola*: Ecuadorian Cordillera Oriental and Occidental) are correctly classified in a 72 % when Venezuela is excluded, and a 70 % when it is included (Appendix 5). The variables which most contributed to the discrimination among these groups were the interorbital breadth, breadth of bony palate, breadth of incisive foramina, and breadth of first upper molar.

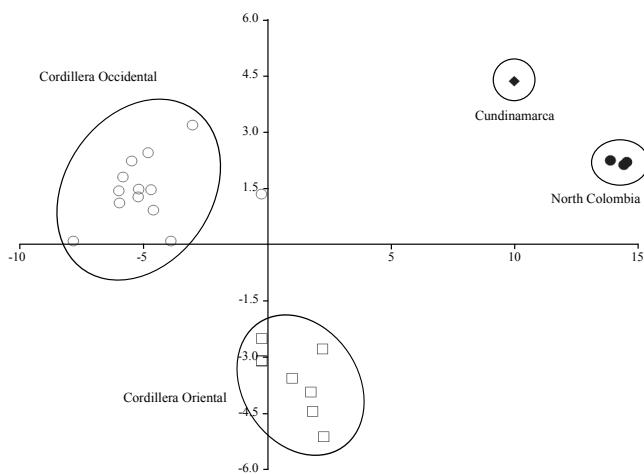


Figure 4. P Plot of canonical discriminant analysis based on 16 craniodental measurements from Colombian and Ecuadorian specimens of *Neomicroxus*. ◆: *N. bogotensis* Cundinamarca, ●: *N. bogotensis* North Colombia (Norte de Santander and Santander), ○: *N. latebricola* Ecuadorian Cordillera Occidental, and □: *N. latebricola* Ecuadorian Cordillera Oriental.

Discussion

Neomicroxus uniqueness and phylogeny. The distinction of *Neomicroxus* as a new entity was based on molecular data from a few specimens of *N. latebricola*, cemented with a shallow morphological review at generic level, mostly pointed to disconnect *Neomicroxus* from *Akodon* (Alvarado-Serrano and D'Elía 2013). Since then, only Curay (2019) ventured to evaluate the variability of *N. latebricola* studying several population samples in Ecuador. This approach highlighted the occurrence of *N. latebricola* in western locations from the cordillera Occidental, a finding previously reported by Brito (2013; overlooked in Alvarado-Serrano and D'Elía 2015) and revealed unsuspected geographical variation.

Despite these findings, the non-inclusion of *N. bogotensis* in a formal phylogenetic analysis has limited the confirmation of hypothesis advanced by Voss (2003) and Alvarado-Serrano and D'Elía (2013) about the generic status of *Neomicroxus*. The monophyly of *Neomicroxus* is not an unsuspected result since both species have been traditionally considered very close due to morphological similarity (Voss 2003). In turn, the novelty molecular data for *N. bogotensis*, added to those of *N. latebricola*, strengthens the consideration that the genus does not appear closely related to any other lineage, placing *Neomicroxus* as a Sigmodontinae *incertae sedis* (Alvarado-Serrano and D'Elía 2013). This finding invites to the recognition of a new clade on Andean rodents with tribal rank.

An additional issue is to explain the differential genealogical structure detected in each species of *Neomicroxus*, suggesting contrasting evolutionary histories. Probably, it could be linked with differential environmental conditions in the northern Andes along the Neogene that could promote the spatial structuring. Judged as a whole, the range of *Neomicroxus* shows an important gap in southern Colombia (Figure 2b). If this "lagoon," which turns sharply allopatric both species, is artefactual or real is debatable. Colombian southernmost portions to the Ecuadorian bor-

Table 2. Results of the principal component analysis based on measurements of *Neomicroxus* specimens. Scheme and names of taken measurements are illustrated in the Supporting information S3.

<i>N. bogotensis</i> (n=12)		
	PC 1	PC 2
ONL	0.18529	0.12481
BZP	0.79866	-0.51397
LD	0.23801	0.22664
LIF	0.46159	0.76969
LM1-3	0.1036	-0.25169
BB	0.004621	0.023879
CIL	0.19013	0.07015
IML	0.10575	-0.087326
Eigenvalue	0.0019788	0.0006965
% variance	65.571	23.081
<i>N. latebricola</i> (n=21)		
	PC 1	PC 2
ONL	-0.010971	0.11015
ZB	-0.006378	-0.025584
IB	0.09867	0.063224
BZP	0.041397	0.66519
LD	0.15393	0.24007
BBP	0.0086206	0.071494
LIF	0.067016	0.50184
BIF	0.78061	-0.11472
LM1-3	-0.096618	0.21955
BM1	-0.12144	0.16342
BPB	0.5329	0.031021
LN	0.024229	0.089939
BB	-0.018767	-0.077084
BOC	0.041391	-0.034099
CIL	-0.026062	0.19255
ZIL	0.074836	0.088529
MH	0.13971	0.20511
IML	-0.11945	0.18693
Eigenvalue	0.00417	0.00069
% variance	66.307	10.977

der have been largely controlled by armed forces, turning mammalogical surveys an almost impossible task. Since *N. latebricola* is recorded in Ecuador very close to this border, and taking into account the habitat continuity (Curay 2019), its occurrence in Colombia is highly expected. The Andean geography in southern Colombia is very complex involving, towards north of Nudo de los Pastos, the occurrence of three main chains (cordilleras) instead of the two branches characterizing the Ecuadorian Andes. We could assume that contact between populations of *N. latebricola* and *N. bogotensis* has been limited by factors associated with this complexity. However, the finding of a single specimen from Nariño, Pasto Municipality, (Ramírez-Chaves and

Noguera-Urbano 2010), which was erroneously identified as *N. latebricola* (Appendix 6), evidences that the distribution of *bogotensis* extends to the south of Colombia, and supports our hypothesis of reduced sampling in the region.

Neomicroxus bogotensis spatial structure and taxonomic implications. Of the two species currently considered in *Neomicroxus*, *N. bogotensis*, the smallest in body size, is the most poorly known. Almost a century after its shallow original description (Thomas 1895), *N. bogotensis* received some attention. Reig (1987:360) concluded, after the inspection of its holotype, that *bogotensis* belongs "... neither to *Akodon* nor to *Abrothrix* and that is a distinctive genus of *Akodontini*." In addition, provided an informal diagnosis of *Microxus*, the genus where he placed this form, and distinguished *bogotensis* by their unique diploid complement ($2n = 35-37$, $FN = 48$; Barros and Reig 1979), and the lacking of paired ventral prostates (shared with *Thaptomys*, a finding conducted by Voss and Linzey 1981). The most recent descriptions of the species (Alvarado-Serrano and D'Elía 2015:98; Pardiñas and Brito 2017:409) considered this taxon as monotypic, despite previous indications in opposite way (see below).

Although stated as "rare" (see Linares 1998:272; Alvarado-Serrano and D'Elía 2015:98), *N. bogotensis* is an abundant cricetid in Andean highlands, at elevations between 2,400 and 3,900 masl, which corresponds to the cloud forest and páramo ecosystems (Cuatrecasas 1958; López-Arévalo et al. 1993; Rangel 2001). Ecological and systematic studies report it as an easy species to found in evergreen ombrophile montane forest and shrubby upland meadows (e. g., Reig 1986; López-Arévalo et al. 1993; Soriano et al. 1999; Ventura et al. 2000; Viachá et al. 2012).

Originally described for the "Plains of Bogota" (Thomas 1895:369), Cundinamarca, it has also been collected in others departments associated with the Cordillera Oriental in Colombia as Boyacá, Santander, and Norte de Santander (Saénz-Jiménez 2010; Viachá et al. 2012). Some databases of mammalian collections also list specimens, not reviewed in this contribution, from the departments of César, Tolima, and Huila (*i. e.*, American Museum of Natural History, The Field Museum of Natural History). The record of Ramírez-Chaves and Noguera-Urbano (2010) from the Nariño department is a significant data about the extension of the *N. bogotensis* geographic range towards southern Colombia. The range for the species is completed by its occurrence in the Cordillera de Mérida and Páramo de Tamá, in the Venezuelan states of Táchira and Mérida (Alvarado-Serrano 2005), plus an unconfirmed mention from Trujillo (Soriano et al. 1999).

Our analyses revealed a clear geographic structure in *N. bogotensis*, separating with strong support the specimens of Norte de Santander and Santander from that of Cundinamarca. Although our study has only a sequence of Cundinamarca, the high genetic distance values ($> 6\%$) suggest the specific distinction of the populations from northern Colombia. This also warns about the restricted gene flow between northern departments and Cundinamarca.

It is interesting to note that so far, no studies have evaluated populations in northern Colombia and Venezuela as a whole. [Soriano et al. \(1999\)](#) highlight the need to examine the taxonomic identity of the populations of *N. bogotensis* in Venezuelan Andes. According to these authors, "it is convenient to examine the taxonomic identity of the populations of the latter [*Neomicroxus bogotensis*], in the light of the parapatric or gradient speciation model, as has been referred to by Patton et al. (1990). Thus, given its high Andean distribution pattern, we expect that the morphotype of the Cordillera de Mérida, by virtue of its possible geographical isolation, could be distinguishable from the rest of the Andean populations. In the same way, we think that the identity of the Venezuelan populations of *T. [Thomasomys] laniger* and *Chilomys instans* would have to be examined" ([Soriano et al. 1999:22](#)).

The Andes in northern Colombia and Venezuela have great geographical complexity characterized by some depressions (e. g., Táchira and Barquisimeto Depression) that separate the mountains and generate significant breaks that lead to isolation and formation of so-called "montane sky islands" ([Reig 1986; Anderson et al. 2012](#)). In this sense, the Táchira Depression, characterized by a dry subtropical climate, has been regarded as a biogeographical barrier to the dispersal of Andean species from both cordilleras (Cordillera Oriental de Colombia and Cordillera de Mérida, [Soriano et al. 1999; Soriano et al. 2005](#)). Species with lower vagility and strictly restricted to the cloud forest and páramo, would be virtually absent today, but probably had a wider and continuous distribution during glacial periods as suggested for *Heteromys australis* ([Anderson and Soriano 1999](#)) and *Marmosa waterhousei* ([Gutiérrez et al. 2011](#)), both species distributed in a lower altitudinal range than *Neomicroxus*. Based on the morphometrical results, the individuals from Venezuela are smaller (Figure 3, Table 1), clearly distinguishable from the Colombian specimens. It seems unlikely that the absence of *N. bogotensis* in the Táchira Depression is just an artifact of inadequate sampling. Probably, the current climatic conditions of this geographical barrier are too dry and would be an inadequate habitat for a typical species of cloud forest and páramo environments, which would restrict gene flow between Colombian and Venezuelan populations. In this way, a study with greater geographical coverage could favor the predictions of [Soriano et al. \(1999\)](#).

Our preliminary data from populations of the Norte de Santander and Santander add diversity to the current concept of *N. bogotensis* in Colombia. The high divergence level suggests a deep break between specimens from northern Colombia and Cundinamarca (the department where the type locality is placed; [Thomas 1895](#)). An important geographic barrier of this area is the Chicamocha canyon produced by the erosion of the tributary of Chicamocha river through the Boyacá and Santander departments, and it has been referred to as responsible for the allopatric speciation in some small vertebrates (e. g., [Guarnizo et al. 2015; Cárdenas 2017](#)). Unpublished data from one of the authors (JCP) also

suggests a high divergence degree on *cytb* sequences in *Cryptotis thomasi*, *Thomasomys niveipes* and *Notosciurus granatensis* from both sides of this barrier.

Although *N. bogotensis* has only been formally mentioned for Cundinamarca, Boyacá and Santander departments ([Saéñz-Jiménez 2010; Vianchá et al. 2012](#)), is very probably that the species occurs in the Cordillera Oriental and extends its distribution southward. In this sense, the record of [Ramírez-Chaves and Noguera-Urbano \(2010\)](#) from Nariño, support this assumption and suggest that the museum specimens from Tolima, Huila and Cauca would correspond to *N. bogotensis*. So, the gap that we observe in the distribution of this species is probably due to insufficient sampling and both *Neomicroxus* species would not be allopatric.

Our findings expose key points to consider in future studies: i) the diversity of *N. bogotensis* seems greater than that reflected in its current concept, ii) topographic and climatic complexity are playing an important role in the diversification of small Andean mammals being probably responsible for the observed genetic discontinuities, especially in the northern Andes of Colombia, iii) as a way of clarifying the gap observed towards southern Colombia and bordering Ecuador, is necessary to focus the sampling efforts towards regions still unexplored, iv) the review of specimens deposited in collections that were not evaluated in this work is imperative, and v) the importance of future studies that evaluate the Colombian and Venezuelan populations as a whole.

Neomicroxus latebricola spatial structure and taxonomic implications. *N. latebricola* was originally described from a single specimen from Tungurahua province in central Ecuador ([Anthony 1924](#)). A few additional studies have extended its distribution to include Napo, Pichincha, Imbabura, and Carchi provinces as well as revealed findings like a shallow geographical structure ([Curay 2019; Voss 2003; Alvarado-Serrano 2005; Brito 2013](#)). Additionally, [Muñoz et al. \(2018\)](#) determined a chromosomal number of $2n = 44$, $FN = 42$, for specimens from Pirámides de Cochasqui, Cantón Pedro Moncayo, Pichincha province. Similar to *N. bogotensis*, *N. latebricola* is a common and abundant species easy to capture in *Polylepis* forests and páramo between 2,420 and 3,950 masl ([Brito 2013; Curay 2019](#)).

Our molecular phylogenetic analysis confirms the structure observed with the morphometric dataset, which shows a partial overlapping between specimens from along both cordilleras in Ecuador. This overlapping is reflected in the genealogical relationships between individuals from Carchi and a specimen from Napo province, which could be evidence of an area of primary or secondary contact. A primary contact zone implies the differentiation of the population in situ, while the secondary is produced by the contact of previously allopatric populations (e. g., [Schneider 1996; Bertl et al. 2018](#)). For now, our data are insufficient to distinguish between these two scenarios.

The variation observed within *N. latebricola* allows to highlight two important points: i) the measurements of the specimens from Cordillera Oriental fit into the metric variation recorded by [Anthony \(1924\)](#) and later authors ([Moreno and Albuja 2005](#); [Alvarado-Serrano and D'Elía 2013](#)), and ii) the potential distinction of a new subspecies for the Cordillera Occidental populations, distinguished from the nominotypic form by a summatory of craniodental traits and coloration. In fact, [Curay \(2019\)](#) notes variations in the dorsoventral coloration of the body and the forefoot and hindfoot, which could be related to the habitats characteristics (e. g., topography, climate, vegetation) in both cordilleras. Our geographic coverage allows us to state that *N. latebricola* in the Cordillera Occidental is a frequent species, strictly associated to forests with shrubs and trees where *Polylepis incana* is the dominant plant ([Brito 2013](#)). By the contrary, *N. latebricola* in the Cordillera Oriental occurs in the ecotonal zone between the páramo and forest whose typical vegetation is the wiry bunch grass to 1 m high and other larger species frequent of wooded environments ([Voss 2003](#)). The intraspecific color variation in rodents has been associated with the sex, age, seasonality, and habitat (e. g., [Camargo et al. 2016](#); [Ríos and Álvarez-Castañeda 2012](#); [Sandoval et al. 2016](#)). In this regard, the coloration pattern in *N. latebricola* seems linked with the soil and vegetation color and the exposure to be detected by predators. It varies from darker in the open habitat from the Cordillera Oriental to light brownish in the habitat with more vegetation coverage in the Cordillera Occidental.

Related to the molecular data, the shallow topology (Figure 2a), shared haplotypes, and low genetic distance values reveal the existence of current genetic flow among its populations suggesting there are no apparent geographical barriers that limit it. Contrary to what we have inferred for *N. bogotensis* populations, *N. latebricola* has experienced recent demographic expansion. These results imply that the geographic complexity of the Ecuadorian Andes is not a determining factor in the differentiation of these populations.

The presumptive existence of a new infraspecific taxon within *N. latebricola* implies raising the wide debate over the importance and utility of the subspecies (e. g., [Wilson and Brown 1953](#); [Endler 1977](#); [Fitzpatrick 2010](#)). The traditional concept involves geographic discontinuities on some morphological traits within a species as the result of ecological and historical factors, but the constant search for agreement between morphological and molecular data has led to an incorrect interpretation of what subspecies would be. Based mainly on DNA data, many authors have equated obtaining geographic structure and reciprocal monophyly, used to delineate species, as useful and appropriate ways to identify or to reject subspecies. However, this goes against the gene flow that exists between the populations of a species and that maintains them as a clear taxonomic unit. The geographic variation recovered in *N. latebricola* reminds us of the statement of [Patton and Conroy \(2019:1019\)](#) about

the subspecies "... are genealogical networks of populations, often without cladistics structure..." instead the species are considered "... hierarchical units with a dichotomous branching history." This conceptual distinction is key to improve the understanding that species and subspecies are not equivalent, and that this misunderstanding has caused us to ignore or obscure the infraspecific diversity of taxa. In this case, our data clearly support the existence of a new subspecies for *N. latebricola* such a typical inhabitant of the forests of *Polylepis*.

Conflicts between molecular data and morphological evidence, especially the necessity to find data congruence and monophyly, and the attempt to delineate molecular clades with phenotypical features, triggered the progressive discard of infraspecific treatments and its biological value. Paradigmatic examples are abundant among Patagonian sigmodontines with prolific nominal contents (e. g., *Abrothrix*, *Loxodontomys*, *Oligoryzomys*, *Paynomys*; see [Palma et al. 2010](#); [Cañón et al. 2010](#); [Alarcón et al. 2011](#); [Palma and Rodríguez-Serrano 2017](#)). Clearly, we need to reevaluate large series of specimens, looking for diagnosable patterns of size and color in accordance with geography, in a refoundational effort to recover the value of geographic races among South American cricetids.

Finally, despite the verifiable progress during last decades there is a remarkable lack of basic knowledge affecting many Andean sigmodontines (e. g., *Aepeomys lugens*, *Chilomys instans*, several *Thomasomys*). *Neomicroxus* is a crystal example for which many aspects of its natural history, ecology, biogeography and alpha taxonomy still remain unknown. Our contribution set a preliminary base for future studies evaluating the variation within the genus, as well as that of other small non-volant mammals with shared distributions. On the other hand, it exposes the importance of the subspecies concept such as nonhierarchical, nonreciprocal monophyletic, closely interbreed, and geographically structured groups.

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Appendix 1

Specimens examined in the morphologic and genetic analyses. Genbank access numbers of the five sequenced specimens in this study are indicated in bold. * Cytb, ** IRBP

N. bogotensis: COLOMBIA: 1) Boyacá, Municipio Guacamayas, vereda Alfaro, sitio Piedras Blancas 6.416, -72.505 (ICN 14722). 2) Cundinamarca, Junín, Reserva Biológica Carpanta 4.563, -73.683 (ICN 11027, ICN 11028, ICN 11029). 3) Cundinamarca, PNN Chingaza (IAvH 5777 - **MT240521***). 4) Nariño, Pasto, aproximadamente 15 km carretera Pasto-Mocoa, páramo, cabaña La Pastora 0.866, -77.316 (ICN13284). 5) Norte de Santander, Cucutilla, Sisavita, Romeral, Predio Greystar [no coordinates] (UIS-MZ 907). 6) Santander, Santa Bárbara, Páramo del Almorzadero, Vereda Volcanes 7.076, -72.848 (UIS-MZ 1596 - **MT240520* MT249798****). 7) Santander, Santa Bárbara, Vereda Esparta 7.019, -72.892 (UIS-MZ 1299 - **MT240522* MT249797****), VENEZUELA: 8) Mérida, Tabay, 7 Km SE Tabay, La Coromoto 8.6, -71.02 (USNM 374611, USNM 374612, USNM 374613).

N. latebricola: ECUADOR: 1) Carchi, Espejo, La Libertad, Sector Bosque de *Polylepis* 0.712202, -77.981639, 3650 (MECN 3717-19, 3727 - **MT240523* MT249799****, 3734 - **MT240524* MT249800****, 3735-36, 3739-40, 3748, 4376-77; QCAZ 11142, 11158, 11145, 12504, 12503, 9814; MEPN 10869, 10870, 10887, 10886, 12716, 10644, 12718, 12715B, 10485, 12712, 12715). 2) Carchi, Tulfán, Tufiño, Páramo del Artesón, Comuna La Esperanza (QCAZ 9801). 3) Imbabura, Pimampiro, Mariano Acosta, Laguna Blanca 0.22367, -77.97867, 3400 msnm (MECN 4763). 4) Imbabura, Zuleta, Faldas del Imbabura 0.248372, -78.15425, 3610 msnm (MECN 6134-36). 5) Napo, Quijo, bosque administrado por la fundación TERRA -0.33422, -78.1433, 3400 msnm (QCAZ 4090, 4121, 4160, 4167, 5230, 5236, 5239). 6) Tunguragua, Pisayambo, km. Parque Nacional Llanganates -1.044686, -78.345828, 3102 msnm (CNP 6396 - MECN 1739).

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Appendix 2

List of taxa for which DNA sequences were included in the phylogenetic analysis. GenBank accession numbers and vouchers for mitochondrial and nuclear genes are indicated.

Species	Cytochrome b		IRBP		Species	Accession number	Voucher	Accession number	Voucher
	Access number	Voucher	Access number	Voucher					
<i>Abrawayaomys chebezi</i>	KR069109	CG184	MN969035	CG184	<i>Neacomys spinosus</i>	EU579504	MVZ155014	AY163597	MVZ155014
<i>Abrawayaomys ruschii</i>	JX949189	MN67557	JX949185	MN67557	<i>Necomys amoenus</i>	AY273911	MVZ171563	AY277458	MVZ171569
<i>Abrothrix hirta</i>	U03530	MVZ154494	KC953347	MVZ154494	<i>Nectomys squamipes</i>	GU126522	FMNH141632	EU273419	TK63841
<i>Aegialomys xantheolus</i>	EU074632	TK135790	EU273420	TK135790	<i>Neomicroxus bogotensis</i>	MT240520	UIS-MZ 1596	MT249798	UIS-MZ 1596
<i>Aepeomys lugens</i>	---	---	DQ003722	MNHN4350	<i>Neomicroxus bogotensis</i>	MT240521	IaVH5777	---	---
<i>Akodon boliviensis</i>	M35691	MVZ171607	KC953351	FMNH162747	<i>Neomicroxus bogotensis</i>	MT240522	UIS-MZ 1299	MT249797	UIS-MZ 1299
<i>Amphinctomys savamis</i>	EU579480	MV97005	AY163579	MV970045	<i>Neomicroxus latebricola</i>	HQ731489	QCAZ4121	---	---
<i>Andalgalomys pearsoni</i>	JQ434418	MSB80512	JQ434398	MSB80512	<i>Neomicroxus latebricola</i>	HQ731488	QCAZ9801	---	---
<i>Andinomys edax</i>	JQ434419	MSB70545	JQ434399	MSB70545	<i>Neomicroxus latebricola</i>	HQ731490	QCAZ4167	KF437367	QCAZ4167
<i>Arvicola terrestris</i>	AY275106	MVZ155884	AY277407	MVZ155884	<i>Neomicroxus latebricola</i>	KF437365	QCAZ4160	KF437366	QCAZ4160
<i>Auliscomys sublimis</i>	JQ434421	MSB75260	JQ434402	MSB75260	<i>Neomicroxus latebricola</i>	MT240523	MECN3727	MT249799	MECN3727
<i>Baiomys musculus</i>	EF989933	ROM97641	KC953360	ROM JM48	<i>Neomicroxus latebricola</i>	MT240524	MECN3734	MT249800	MECN3734
<i>Bibimys labiosus</i>	DQ444329	MN62062	AY277436	MN62062	<i>Neotoma floridana</i>	AF294344	TK52115	KC953411	OSU OK 107
<i>Blarinomys breviceps</i>	AY275112	CIT1391	AY277437	CIT1391	<i>Neotomys ebriosus</i>	JQ434424	MSB87134	JQ434413	MSB87134
<i>Brucepattersonius soricinus</i>	AY277486	MVZ183036	AY277438	MVZ183250	<i>Nephelomys albicularis</i>	EU579505	AMNH268125	AY163614	AMNH268125
<i>Calassomys apicalis</i>	JQ434425	GDE2012	KX431561	?	<i>Nesomys rufus</i>	AF160592	Nruf508	AY326099	FMNH151915
<i>Calomys laucha</i>	AY033190	NK72376	JQ434404	MSB80539	<i>Nesoryzomys swarthi</i>	EU340014	ASNHC10003	AY163601	ASNHC10003
<i>Castoria angustidens</i>	EF622508	?	KF815411	MN78921	<i>Neusticomys monticolus</i>	KF359515	ACUNHC900	KR105605	QCAZ6531
<i>Cerradomys subflavus</i>	EU579481	MNRJ61885	AY163626	MNRJ61665	<i>Nyctomys sumichrasti</i>	AY195801	TK101875	KC953421	MSB45815
<i>Chelemys megalonyx</i>	DQ309559	NK109208	EU091259	NK109253	<i>Oecomys concolor</i>	JF693876	MVZ155005	KC953424	MVZ192947
<i>Chilomys instans</i>	AF108679	JLP16693	---	---	<i>Oligoryzomys fulvescens</i>	GU126529	AMNH257262	AY163611	AMNH257262
<i>Chinchillula sahamae</i>	JQ434422	MSB75154	JQ434409	MSB75254	<i>Onychomys leucogaster</i>	EF989959	ROM114892	EF989860	ROM114892
<i>Cricetionomys gapperi</i>	AY309431	?	AY326080	UMMZ162467	<i>Oreoryzomys balearator</i>	EU579510	AMNH268144	AY163617	AMNH268144
<i>Cricetulus longicaudatus</i>	KM067270	?	AY326082	USNM449102	<i>Oryzomys palustris</i>	GU126539	TTU75311	AY163623	TTU75311
<i>Cricetus cricetus</i>	AJ490302	?	AY277410	MVZ155880	<i>Oxotylomys phyllotis</i>	AY009789	FN32783	KC953429	ROM35529
<i>Delomys dorsalis</i>	KF317031	JFV226	KC953369	MVZ182789	<i>Oxymycterus nasutus</i>	EF661854	?	AY277468	ROM182701
<i>Deltamys kempii</i>	AY195862	MNHN4151	AY277444	MNHN4151	<i>Paynomys macronyx</i>	U03533	MVZ155800	AY277441	MVZ155800
<i>Drymoreomys albimaculatus</i>	EU579487	MVZ182088	EU649042	MVZ182088	<i>Pennatomys nivalis</i>	LN810055	B5 534	---	---
<i>Eligmodontia typus</i>	AF108692	MVZ182681	AY277445	MVZ182681	<i>Peromyscus leucopus</i>	EF989979	ROM101861	EF989880	ROM101861
<i>Eremoryzomys poliois</i>	EU579483	FMNH129243	AY163624	FMNH129243	<i>Phaeomys ferrugineus</i>	KM065876	MZUFV3400	KM065877	MZUFV3400
<i>Euneomys chinilloides</i>	AY275115	UP LB018	AY277446	UPLB018	<i>Phodopus sungorus</i>	AJ973390	?	KC953439	?
<i>Euryoryzomys macconnelli</i>	GU126538	AMNH272669	AY163620	AMNH272678	<i>Phyllotis xanthopygus</i>	U86833	MFS1324	AY163632	MVZ182703
<i>Galenomys garleppi</i>	JQ434423	AMNH262814	JQ434410	AMNH262814	<i>Podoxymys roraimae</i>	KM816650	PK3335	KM816651	PK3335
<i>Geoxus valdivianus</i>	AY275116	CAV001	AY277448	CAV001	<i>Pseudoryzomys simplex</i>	GU126547	GD065	AY163633	GD065
<i>Graomys griseoflavus</i>	AY275117	UP278	AY277449	UP278	<i>Punomys kofordi</i>	JQ434426	VPT 1890	JQ434414	VPT1890
<i>Handleyomys alfaroi</i>	EU579489	TK93700	EU649044	TK93700	<i>Reithrodontomys auritus</i>	EU579474	MVZ182704	AY163634	MVZ182704
<i>Handleyomys intectus</i>	EU579490	CADV088	AY163584	ICN16093	<i>Reithrodontomys fulvescens</i>	EF990003	ROM114901	EF989904	ROM114901
<i>Holochilus brasiliensis</i>	GU126517	GD081	AY163585	GD081	<i>Rhagomys longilingua</i>	KY754141	?	DQ003723	FMNH175218
<i>Hylaeomys megacephalus</i>	EU579499	MHNL8061	AY163621	MHNL8061	<i>Rheomys raptor</i>	KJ921706	KU159017	KC953451	ROM101294
<i>Irenomys tarsalis</i>	U03534	MVZ155839	AY277450	MVZ155839	<i>Rhipidomys macconnelli</i>	AY275130	MVZ 160082	AY277474	MVZ160082
<i>Isthmomyomys pirrensis</i>	DQ836298	?	EF989847	ROM116309	<i>Salinomys delicatus</i>	EU377608	OMNH23602	JQ434415	OMNH23602
<i>Juliomys pictipes</i>	FJ026733	TK145073	KC953385	MVZ182079	<i>Scapteromys tumidus</i>	AY275133	MVZ183269	AY277477	MVZ193269
<i>Juscelinomys huanchacae</i>	AY275119	LHE1617	AY277452	LHE1616	<i>Scolomys ucayalensis</i>	EU579518	AMNH272721	AY163638	AMNH272721
<i>Kunsia tomentosus</i>	AY275121	LHE1620	KC953386	USNM584516	<i>Scotinomys teguina</i>	AF108705	UMMZ3373	AY277415	MVZ191230
<i>Lenoxus apicalis</i>	U03541	MVZ171512	KC953388	MVZ171512	<i>Sigmodon hispidus</i>	AF425227	TK90616	AY277479	NK27055
<i>Loxodontomys micropus</i>	AY275122	EPU001	AY277457	EPU001	<i>Sigmodontomys alfari</i>	EU074635	USNM449895	AY163641	USNM449895
<i>Lundomys molitor</i>	JQ966241	MCNU2302	JQ966805	MCNU2302	<i>Sooretamys angouya</i>	GU126534	MNRJ50234	KC953456	MVZ192961
<i>Megalomys desmarestii</i>	LN810053	NHMUK1850	---	---	<i>Tanyuromys aphrastus</i>	JF693877	KU161003	JF693878	KU161003
<i>Melanomys caliginosus</i>	EU340020	TK135894	KC953397	USNM464387	<i>Tapacomys wolffsohni</i>	U86834	MSB67270	KC953460	MSB63364
<i>Mesocricetus auratus</i>	AM904612	MauCytb06	AY163591	?	<i>Thalpomys ceradensis</i>	AY273916	MZUSP30397	AY277480	MZUSP30400
<i>Microakodontomys transitorius</i>	---	---	EU649054	MN25969	<i>Thaptomys nigrita</i>	AF108666	MVZ183044	AY277482	MVZ183044
<i>Microrozomys minutus</i>	AF108698	MVZ173975	AY163592	MVZ166666	<i>Thomasomys aureus</i>	U03540	MVZ170076 & 166714	AY277483	MVZ170076
<i>Microtus californicus</i>	EF506105	MVZ216595	KC953401	MVZ207423	<i>Transandinomys talamancae</i>	GU126544	USNM449894	KC953465	MSB91815
<i>Myospalax aspalax</i>	AF326272	?	AY326097	MSB100576	<i>Tylomys nudicaudus</i>	DQ179812	TK41551	AY163643	ROM103590
					<i>Wiedomys pyrhorhinos</i>	EU579477	MVZ197566	AY277485	MVZ197567
					<i>Wilfredomys oenax</i>	KJ663726	UFSM619	KJ663727	MCNU2025
					<i>Zygodontomys brevicauda</i>	GU126549	AMNH257321	AY163645	AMNH257321

Appendix 3

Genetic divergence values (*p* distance) among cytochrome b sequences of *Neomicroxus*.

	<i>Neomicroxus</i> genus	
Overall mean	<i>p</i> dist	%
<i>Neomicroxus</i> genus	0.063	6.3

<i>Neomicroxus p distance</i>								
Pairwise differences	UIS-MZ 1596	IAvh5777	UIS-MZ 1299	QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
UIS-MZ 1596 Nbogotensis								
IAvh5777 Nbogotensis		0.065						
UIS-MZ 1299 Nbogotensis		0.001	0.061					
KF437365 Nlatebricola QCAZ4160		0.107	0.113	0.107				
HQ731490 Nlatebricola QCAZ4167		0.107	0.112	0.106	0.000			
HQ731489 Nlatebricola QCAZ4121		0.109	0.112	0.109	0.014	0.014		
HQ731488 Nlatebricola QCAZ9801		0.109	0.110	0.109	0.010	0.010	0.004	
MECN3727 Nlatebricola		0.113	0.114	0.113	0.016	0.016	0.015	0.011
MECN3734 Nlatebricola		0.113	0.114	0.113	0.016	0.016	0.015	0.011

<i>Neomicroxus percentage</i>								
Pairwise differences	UIS-MZ 1596	IAvh5777	UIS-MZ 1299	QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
UIS-MZ 1596 Nbogotensis		6.522						
IAvh5777 Nbogotensis		0.127	6.089					
UIS-MZ 1299 Nbogotensis		10.673	11.268	10.652				
KF437365 Nlatebricola QCAZ4160		10.673	11.215	10.625	0.000			
HQ731490 Nlatebricola QCAZ4167		10.928	11.215	10.875	1.377	1.373		
HQ731489 Nlatebricola QCAZ4121		10.928	10.981	10.875	1.001	0.999	0.375	
HQ731488 Nlatebricola QCAZ9801		11.309	11.449	11.250	1.627	1.623	1.498	1.124
MECN3727 Nlatebricola		11.309	11.449	11.250	1.627	1.623	1.498	1.124
MECN3734 Nlatebricola								0.000

<i>p</i> dist			%		
Between species	<i>N. bogotensis</i>	<i>N. bogotensis</i>	<i>N. bogotensis</i>	<i>N. bogotensis</i>	<i>N. bogotensis</i>
<i>N. bogotensis</i>					
<i>N. latebricola</i>		0.111		11.051	

<i>p</i> dist			%		
Overall mean	<i>N. bogotensis</i>	<i>N. bogotensis</i>	<i>N. bogotensis</i>	<i>N. bogotensis</i>	<i>N. bogotensis</i>
<i>N. bogotensis</i>		0.042		4.2	

<i>N. bogotensis p distance</i>		
Pairwise differences	UIS-MZ 1596	IAvh5777
UIS-MZ 1596 Nbogotensis		0.065
IAvh5777 Nbogotensis		0.001
UIS-MZ 1299 Nbogotensis		0.061

<i>N. bogotensis percentage</i>		
Pairwise differences	UIS-MZ 1596	IAvh5777
UIS-MZ 1596 Nbogotensis		6.522
IAvh5777 Nbogotensis		0.127
UIS-MZ 1299 Nbogotensis		6.089

<i>p</i> dist			%		
Overall mean	<i>N. latebricola</i>	<i>N. latebricola</i>	<i>N. latebricola</i>	<i>N. latebricola</i>	<i>N. latebricola</i>
<i>N. latebricola</i>		0.011		1.1	

<i>N. latebricola p distance</i>					
Pairwise differences	QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
KF437365 Nlatebricola QCAZ4160					
HQ731490 Nlatebricola QCAZ4167		0.000			
HQ731489 Nlatebricola QCAZ4121		0.014	0.014		
HQ731488 Nlatebricola QCAZ9801		0.010	0.010	0.004	
MECN3727 Nlatebricola		0.016	0.016	0.015	0.011
MECN3734 Nlatebricola		0.016	0.016	0.015	0.011

<i>N. latebricola percentage</i>					
Pairwise differences	QCAZ4160	QCAZ4167	QCAZ4121	QCAZ9801	MECN3727
KF437365 Nlatebricola QCAZ4160					
HQ731490 Nlatebricola QCAZ4167		0.000			
HQ731489 Nlatebricola QCAZ4121		1.377	1.373		
HQ731488 Nlatebricola QCAZ9801		1.001	0.999	0.375	
MECN3727 Nlatebricola		1.627	1.623	1.498	1.124
MECN3734 Nlatebricola		1.627	1.623	1.498	1.124

<i>N. latebricola p distance</i>			%		
Between clades <i>N. latebricola</i>	<i>p</i> distance	<i>N. latebricola</i>	<i>p</i> distance	<i>N. latebricola</i>	<i>N. latebricola</i>
<i>N. latebricola</i> clade 1 [Napó]					
<i>N. latebricola</i> clade 2 [Carchi & Napó]		0.014		1.406	

<i>N. latebricola p distance</i>			%		
Within clades <i>N. latebricola</i>	<i>p</i> distance	<i>N. latebricola</i>	<i>p</i> distance	<i>N. latebricola</i>	<i>N. latebricola</i>
<i>N. latebricola</i> clade 1 [Napó]		0		0	
<i>N. latebricola</i> clade 2 [Carchi & Napó]		0.009		0.936	

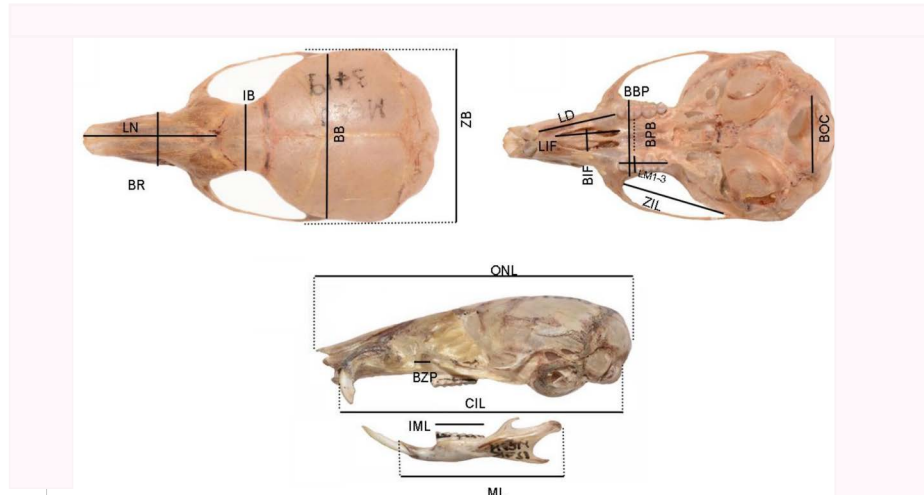
<i>N. latebricola p distance</i>			%		
Between subcl - clade 2 <i>N. latebricola</i>	subcl. 1	subcl. 1	subcl. 1	subcl. 1	subcl. 1
latebricola clado 2 subclado 1					
latebricola clado 2 subclado 2		0.013		1.311	

<i>N. latebricola p distance</i>			%		
Whitin subcl - clade 2 <i>N. latebricola</i>	<i>p</i> distance	<i>N. latebricola</i>	<i>p</i> distance	<i>N. latebricola</i>	<i>N. latebricola</i>
latebricola clade 2 subclado 1		0.004		0.375	
latebricola clade 2 subclado 2		0.000		0.000	

<i>N. latebricola</i>		Locality	
Clade 1	QCAZ4160	Ecuador, Napo, Papallacta, bosque administrado por la fundación TERRA	
	QCAZ4167	Ecuador, Napo, Papallacta, bosque administrado por la fundación TERRA	
Clade 2	subclado 1	QCAZ4121	Ecuador, Napo, Papallacta, bosque administrado por la fundación TERRA
	subclado 2	QCAZ9801	Ecuador, Carchi, Tulfán, Tufiño, Páramo del Artesón, Comuna La Esperanza
		MECN3727	Ecuador, Carchi, Espejo, La Libertad, Sector Bosque de Polylepis
		MECN3734	Ecuador, Carchi, Espejo, La Libertad, Sector Bosque de Polylepis

Appendix 4

Linear measurements used in descriptive, univariate, and multivariate analyses.



BB Breadth of braincase, **BIF** Breadth of incisive foramina, **BM** Breadth of first upper molar, **BBP** Breadth of bony palate, **BPB** Breadth of palate bridge, **BOC** Breadth of the occipital condyles, **BZP** Breadth of zygomatic plate, **CIL** Condylar-incisive length, **IB** Interorbital breadth, **IML** Mandibular molar tooththrow length, **LD** Length of upper diastema, **LIF** Length of incisive foramina, **LMI-3** Length of maxillary tooththrow, **LN** Length of nasals, **ML** Mandibular length, **ONL** Occipitonasal length, **ZB** Greatest zygomatic breadth, **ZIL** Zygomatic internal length.

Appendix 5

Groups classification achieved in the discriminant analysis with jackknife resampling.

	<i>N. latebricola</i>		<i>N. bogotensis</i>		Total
	Occidente	Oriente	North Colombia	Cundinamarca	
<i>N. latebricola</i>					
Occidente	11	1	1	0	13
Oriente	2	6	0	0	8
<i>N. bogotensis</i>					
North Colombia	0	0	1	2	3
Cundinamarca	0	0	1	0	1
Total	13	7	3	2	25

	<i>N. latebricola</i>		<i>N. bogotensis</i>		Venezuela	Total
	Occidente	Oriente	North Colombia	Cundinamarca		
<i>N. latebricola</i>						
Occidente	11	2	0	0	0	13
Oriente	2	6	0	0	0	8
<i>N. bogotensis</i>						
North Colombia	0	0	0	0	3	3
Cundinamarca	0	0	0	1	1	1
Venezuela	0	0	1	1	7	9
Total	13	8	1	1	11	34

Appendix 5

Craniodental anatomy in a specimen referred as *Neomicroxus bogotensis* (ICN13284; previously mentioned as *N. latebri-cola* by Ramírez-Chaves and Noguera-Urbano 2010) from Nariño department, Colombia: a, cranium in palatal view; b, right half of the cranium in dorsal view; c, lacrimal region; d, zygomatic plate region in lateral view; e, left upper molars in occlusal view; f, left lower molars in occlusal view; g, auditory region in lateral view. Abbreviations: ab: auditory bulla (ectotympanic), fr: frontal, fs: frontal sinus, if: incisive foramen, l: lacrimal, mal: malleus, man: manubrium, m: maxillary, ms: maxillary septum, n: nasal, oap: orbicular apophysis, pal: palatine, pgf: postglenoid foramen, pm: premaxillary, sf: subsquamosal fenestra, tt: tegmen tympani, zn: zygomatic notch, zp: zygomatic plate.

