Taxonomic status of the nominal forms assigned to *Necromys lactens* (Rodentia, Cricetidae) as revealed by molecular and morphometric evidence

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*Necromys* is a genus of sigmodontine rodent that inhabits grasslands and scrublands in South America. Eight extant species are recognized in the genus; one of these is *Necromys lactens*, which inhabits high-elevation grasslands in the Yungas from south-central Bolivia to northwestern Argentina. Morphological variation in *N. lactens* has been recognized by the description of three nominal forms. Geographically structured genetic diversity also has been observed, but a thorough revision of these nominal forms within an integrative framework has yet to be performed. We conducted a phylogeographic assessment based on an 801 base-pair fragment of the cytochrome-*b* gene that guided morphometric analyses (univariate and multivariate comparisons) of patterns of geographic variation in the species, and the distinction of its nominal forms. Haplotypes of *N. lactens* form a well-supported and geographically structured clade. Within it, there are two main clades; haplotypes from the northern range form a well-supported clade, sister and allopatric to a weakly supported southern clade, which includes variants collected at or near the type localities of three nominal forms. In turn, both main clades are composed by two allopatric subclades. Morphometric analyses indicated no differences in shape of the skull among the three nominal forms or between the recovered clades and subclades. Taking together all the available evidence, we consider *N. lactens* to be a monotypic species.

*Necromys* es un género de roedor sigmodontino que habita los pastizales y arbustales de América del Sur. Se reconocen ocho especies actualmente en existencia en el género; una de ellas, *Necromys lactens*, habita pastizales de altura en las Yungas, desde el centro-sur de Bolivia hasta el noroeste de Argentina. Se ha reconocido variación morfológica en *N. lactens* con base en descripciones de tres formas nominales; también se ha observado diversidad genética geográficamente estructurada, pero una revisión exhaustiva de esas formas nominales dentro de un esquema integrativo aún no se ha llevado a cabo. Realizamos una evaluación filogeográfica basada en un fragmento de 801 pares de bases del gen citocromo *b* que orientó análisis morfométricos (comparaciones univariadas y multivariadas) respecto al patrón geográfico de variación de la especie y la distinción de sus formas nominales. Los haplotipos de *N. lactens* forman un clado bien apoyado y geográficamente estructurado. Dentro de este clado, los haplotipos del norte de su área de distribución forman un clado bien apoyado que es hermano y alopatrino con respecto de un clado austral débilmente apoyado, el cual incluye variantes colectadas en las localidades tipo de las tres formas nominales o sus cercanías. A su vez, ambos clados principales están compuestos por dos sub-clados alopatrinos. Los análisis morfométricos no revelaron diferencias en la forma del cráneo entre las tres formas nominales ni entre los clados y sub-clados recuperados. Teniendo en cuenta toda la evidencia disponible, consideramos que *N. lactens* es una especie monotípica.

Key words: *Akodon orbus*, Akodontini, *Bolomys negrito*, central Andes, Sigmodontinae, South America

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Necromys is a polytypic sigmodontine genus with a distribution encompassing more than 5,400 km from northern South America to southern Uruguay and central Argentina, and extending from the Atlantic coast to the Andean elevations, up to about 5,000 m (D’Elía et al. 2008; Pardiñas et al. 2015). Across this extensive distribution, different species of Necromys inhabit distinct environments, mostly characterized by open grassland–shrubland vegetation structure.

Seven extant species of Necromys were recognized in the last compilation of South American rodents (Pardiñas et al. 2015; but see Pardiñas et al. 2017 for the treatment of N. lenguarum as junior synonym of N. lasiurus); an additional species was subsequently described (Jayat et al. 2016). Five species of Necromys occur on the eastern slopes of the southern-central Andes, of which Necromys lactens has the broadest distribution (Pardiñas et al., 2015, 2017). This species primarily inhabits high-elevation grasslands between 1,500 and 4,000 m in the highest vegetation belts of the Yungas, spanning this relatively narrow altitudinal belt over ca. 12° of latitude: from Cochañamba Department in south-central Bolivia to Catamarca province in northwestern Argentina (Jayat and Pacheco 2006; Pardiñas et al. 2015). Despite its extended latitudinal distribution, the preference of N. lactens for high-elevation environments restricted to mountain tops has resulted in a fragmented distribution of its populations.

Necromys lactens constitutes one of the three main lineages of the genus as recovered in phylogenetic analysis of mitochondrial DNA sequences (D’Elía et al. 2008). Morphological variation among populations of N. lactens has been underscored by the description of three nominal forms: Akodon lactens Thomas, 1918, with type locality at Léon, 1,500 m, in Jujuy province; A. orbis Thomas, 1919, with type locality at “Otro Cerro,” Catamarca province; and Bolomys negrito Thomas, 1926, from “Las Parás [= Las Pavas], about 4000 m,” Tucumnán province. At present, A. orbis and B. negrito are considered junior synonyms of N. lactens (see Pardiñas et al., 2015), as suggested by the topology of the phylogenetic trees, and percent sequence divergence of the mitochondrial cytochrome-b (Cytb) sequences of specimens assigned to these forms (D’Elía et al. 2008). However, despite limited sampling, the genetic diversity of N. lactens appears geographically structured (D’Elía et al. 2008). The seven sequences analyzed in that study were gathered from specimens collected at seven localities and formed two clades. One clade was distributed in northernmost Argentina (Salta province) on the eastern slopes of the Sierra de Santa Victoria, near the Bolivian border, and Sierra de Zenta, while the other clade was distributed in more southern localities (southern Jujuy, Catamarca, and Tucumán provinces) in the Chañi, Centinela, Cumbres Calchaquíes, Ambato, and Ancasti mountain systems; the clades themselves displayed sequence divergence of 3.0% to 3.8% in Cytb sequences. D’Elía et al. (2008) suggested that this geographically structured genetic diversity may have resulted from Pleistocene dynamics (glaciation induced upwards and downwards movements of the patchily distributed high-altitude grasslands, which alternatively separated and came into contact). However, given their limited sampling (e.g., omitting Bolivian variants), those authors called for a broader phylogeographic analysis of this and other allied grassland specialist species. Moreover, a thorough revision of the nominal forms associated to N. lactens, including representative series of specimens analyzed within the framework of an integrative approach (including molecular and morphometric data), has yet to be performed.

In the present work, additional newly collected specimens of N. lactens from southern Bolivia and northwestern Argentina allowed us to undertake a range-wide phylogenetic reconstruction and an associated analysis of morphometric variation. These analyses allowed us to test the taxonomic status of its three nominal forms in an integrative framework (Padial et al. 2010; Schlick-Steiner et al. 2010).

**Materials and Methods**

**Materials examined.**—Specimens of N. lactens used in this study were newly collected by us using Sherman folding traps of 8 × 9 × 23 cm (H. B. Sherman Co., Tallahassee, Florida) or already housed at natural history collections (Fig. 1; Appendix I). Newly captured specimens (Appendix I) were deposited in the mammal collections of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-Ma; Ciudad Autónoma, Buenos Aires, Argentina); in the Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut, Argentina); and in the Instituto Miguel Lillo (CML; San Miguel de Tucumán, Tucumán, Argentina). Sampling included specimens collected near the type locality of A. lactens Thomas, 1918, A. orbis Thomas, 1919, and B. negrito Thomas, 1926. All aspects of the study involving live animals followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

**Genetic and phylogenetic analyses.**—Genetic and phylogenetic analyses were based on an 801 base-pair fragment of the Cytb gene following the general protocol delineated in D’Elía et al. (2008; see also Jayat et al. 2016). Our sample of N. lactens is more complete than the earlier study: we analyzed sequences of 31 specimens of N. lactens, of which 23 were newly generated in this study and eight were retrieved from GenBank (accession numbers in Appendix II). Geographic coverage was relatively broad; we included sequences from specimens of Necromys collected in 15 localities in Argentina and Bolivia, including sites located in the vicinity of the type localities of the three nominal forms allocated to N. lactens (Fig. 1A). A homologous sequence from one individual of each of the six available species of Necromys (N. amoenus, N. lasiurus, N. lenguarum, N. liloi, N. obscurus, and N. urichi) was used to form the outgroup. Sequences gathered here were generated using primers MVZ 05 and MVZ 16 (da Silva and Patton 1993) following the protocol outlined in Cañón et al. (2010). Amplicons were purified and sequenced by Macrogen Inc., Korea, or Macrogen USA. Sequences were edited and proofread (e.g., checked for the existence of internal stop codons and reading frame shifts) with Codon Code (Codon Code Aligner, Dedham, Massachusetts). Newly generated sequences were deposited in GenBank (MN102727–MN102749).
Fig. 1.—Map of southern Bolivia and northwestern Argentina, showing the geographic localities of specimens used in this study. A) Collection localities of the sequenced specimens of *Necromys* (white circles) and the type localities (white stars) of *Akodon lactens* (León), *A. orbus* (Otro Cerro), and *Bolomys negrito* (Las Pavas). B) Collection localities for specimens of *Necromys* used in morphometric analyses assigned to *Akodon lactens* (white triangles), *A. orbus* (white squares), and *Bolomys negrito* (white circles). C) Collection localities for specimens of *Necromys* used in morphometric analyses assigned to the two main clades: northern clade (NC, white circles) and southern clade (SC, white squares). D) Collection localities for specimens of *Necromys* used in morphometric analyses assigned to the four subclades: northernmost clade (NNC, white circles), central-northern clade (CNC, white circles with a midpoint), central-southern clade (CSC, white squares with a midpoint), and southernmost clade (SSC, white squares). Gray shading corresponds to areas above 2,000 m elevation.
Sequences were aligned with Clustal X (Thompson et al. 1997) as implemented in MEGA7 (Kumar et al. 2016), using the default values for all alignment parameters; after a visual inspection in search of internal stop codons and reading frame shifts, no adjustment was needed. Genetic distances ($p$-distances) were calculated using MEGA7. A gene tree was constructed by Bayesian inference (reviewed in Huelsenbeck et al. 2001) conducted in MrBayes 3.1 (Ronquist and Huelsenbeck 2003). The best-fit model of nucleotide substitution, HKY+G (Hasegawa et al. 1985), was determined based on the Bayesian Information Criterion (BIC) using jModeltest2 (Darriba et al. 2012). Two independent runs, each with five heated and one cold Markov chains, were performed. All model parameters were estimated in MrBayes. Uniform interval priors were assumed for all parameters except base composition and HKY parameters, which assumed a Dirichlet process prior. Runs were allowed to proceed for 20 million generations; trees were sampled every 1,000 generations for each chain. To check that each run converged on a stable log-likelihood value, we plotted the log-likelihood values against generation time for each. The first 25% of the trees were discarded as burn-in and the remaining trees (all sampled at the convergence zone) used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade.

**Taxonomic assignment of the samples.**—To conduct quantitative morphological analyses, we followed two different criteria for grouping examined specimens. First, we tested the existence of quantitative morphological differences among the three described nominal forms, grouping the individuals nearby type localities (Fig. 1B). Second, the same sets of individuals were assigned to one of the mitochondrial lineages documented in our phylogenetic analysis (Figs. 1C and 1D) following a criterion of geographic proximity among localities (with respect to those of the sequenced specimens). For both groupings, we took into account the absence of discontinuities in size and shape within groups.

**Morphometric analyses.**—Standard external measurements were recorded from specimen labels or field catalogs: total length, TL; tail length, T; hind foot length (including claw), HF; ear length, E; and body mass, W. The following skull measurements were recorded with digital calipers to the nearest of 0.01 mm following definitions provided by Hershkovitz (1962), Myers (1989), and Myers et al. (1990): condyloincisive length, CIL; palatal length, PL; diastema length, DL; palatal bridge, PB; maxillary toothrow length, MTRL; incisive foramina length, IFL; alveolar width (across external side of both M1), AW; zygomatic length, ZL; zygomatic plate depth, ZP; zygomatic breadth, ZB; braincase breadth, BB; interorbital constriction, IOC; mid-rostral width, RW2; nasal length, NL; rostral length, RL; orbital length, OL; occipital condyle width, OCW. In addition, we recorded the following mandible measurements: mandible length, ML; mandibular toothrow length, mTRL; mandibular diastema length, MDL.

Specimens were assigned to age classes based on tooth wear following the model shown in the Fig. 2. Five age classes were defined: age class 1, M3 is incompletely erupted or unworn; age class 2, M3 is fully erupted and exhibits moderate wear, M1–2 unworn; age class 3, M3 is well worn, its occlusal surface is flat or concave, M1–2 exhibit moderate wear; age class 4, M3 heavily worn, being generally concave, M1–2 have worn and flattened cusps, M2 with no trace of the paraflexus; age class 5, M1–3 are all worn and concave; most details of the occlusal topography are obliterated.

![Age class 1](image1.png) ![Age class 2](image2.png) ![Age class 3](image3.png) ![Age class 4](image4.png) ![Age class 5](image5.png)

**Fig. 2.**—Toothwear age classes of *Necromys*. Age class 1: M3 incompletely erupted or unworn; age class 2: M3 fully erupted and exhibits moderate wear, M1–2 unworn; age class 3: M3 well worn, its occlusal surface is flat or concave, M1–2 exhibit moderate wear; age class 4: M3 heavily worn, being generally concave, M1–2 have worn and flattened cusps, M2 with no trace of the paraflexus; age class 5: M1–3 are all worn and concave; most details of the occlusal topography are obliterated.
Descriptive morphometric and univariate comparisons for samples of each of the three nominal forms (Tukey’s pairwise comparison) and for the specimens recovered for the two main clades (t-tests) recovered via phylogenetic analysis (NC and SC; see below) were carried out with the software PAST (Hammer et al. 2001). Specimens of age classes 2 and 3 were pooled in tests of significant size differences (for both, \( P \leq 0.05 \) and \( P \leq 0.01 \)).

In order to reduce the dimensionality of morphometric data and explore the differences in the form of the skull among samples of Necromys we used a “size-free” Principal Component Analysis (sfPCA) including individuals of the five age classes. To reduce the effect of size, Mosimann shape variables were calculated through geometric mean transformation of data prior to statistical analyses (as developed by Meachen-Samuels and Van Valkenburgh 2009). The geometric mean is a size variable derived from the \( n \)th root of the product of \( n \) measurements (each species measurement is divided by the \( n \)th root of the product of values of a species vector of \( n \) variables), and the ratio of any particular measurement to the overall geometric mean is a Mosimann shape variable. Statistical significance of the PCs was evaluated following the Broken-stick test (Frontier 1976; Jackson 1993). We developed three sfPCA (using individuals of all age classes to obtain sample sizes sufficiently large): one was designed to test morphometric differences among the three nominal forms (as represented by samples coming from the environs of each of the three type localities), and two others sought to test morphometric differences among the main clades obtained in the phylogenetic analysis. All multivariate statistical analyses were performed with the software PAST (Hammer et al. 2001).

**Results**

*Genetic and phylogenetic analyses.*—Average observed \( p \)-distance of all haplotype pairs of the *N. lactens* sample is 2.1%. Haplotypes of *N. lactens* form a well-supported clade (PP = 1.0), which is geographically structured, although with variable support (Fig. 3; Table 1). Haplotypes from the northern range (NC) form a well-supported clade (PP = 0.96), which is

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**Fig. 3.**—Majority rule consensus tree obtained in the Bayesian analysis of 31 cytochrome-\( b \) gene sequences of specimens of *Necromys lactens* (plus sequences of other species of the genus used as outgroup). Numbers indicate posterior probability values of the adjacent nodes. Each terminal is labeled with the institution and catalog number (see acronyms in “Materials and Methods”) of the specimen, GenBank accession number (of previously published sequences), and locality data (see complete details in Appendix II). Arg = Argentina; Bo = Bolivia.
sister and allopatric to a weakly supported (PP = 0.54) clade (SC) formed by haplotypes of the southern part of the species distributional range. The NC is divided into two allopatric subclades; a moderately supported (PP = 0.86) northernmost clade (NNC) is formed by all Bolivian haplotypes and those from northern Salta province (localities of Los Toldos and Rodeo Pampa). The NNC is sister to a highly supported (PP = 1.0) central-northern clade (CNC) formed by haplotypes from Jujuy province and one locality (Abra Ciénaga Negra) in Salta province. Clade SC also shows geographic structure. Haplotypes recovered from the southernmost localities, in Catamarca and Tucumán provinces, form a strongly supported (PP = 1.0) clade (SSC), which is sister to a weakly supported (PP = 0.52) central-southern clade (CSC) formed by haplotypes recovered from specimens collected at Jujuy and Tucumán provinces.

Internally, NC and SC clades show low levels of genetic variation (0.008 and 0.011, respectively); similarly, the four subclades are genetically homogenous (range: 0–0.006; Table 1). However, p-distances between the NC and SC clade is 0.033, while the differentiation between NNC and CNC is 0.013 and between CSC and SSC is 0.017.

**Morphometric characterizations.**—The univariate morphometric analysis did not reveal differences among the three nominal forms assigned to *N. lactens*. Two of the 25 measurements evaluated (ZP and RW2) differed significantly among samples assigned to *A. lactens* and *B. negrito*, and one (NL) differed significantly among samples of the three forms (Table 2). Four (MTRL, ZB, IOC, and MDL) of the 25 measurements differed significantly among samples assigned to the northern (NC) and southern (SC) clades (Table 2).

The first sfPCA also failed to differentiate the three nominal forms assigned to *N. lactens*. Representative specimens of these forms widely overlapped on the morphospace (Fig. 4A). The first three PCs summarized 68.97% of the total variation but only PCI (36.61% of the variance) and PCI (21.43%) were assessed as statistically significant by the Broken-stick test (Table 3). Mandibular diastema length was the most influential variable along these two axes, but do not appear to separate any of the three nominal forms.

The second and third sfPCA also failed to differentiate the two main clades (NC and SC) as well as the four subclades (NNC, CNC, CSC, SSC) resulting from the phylogeographic analysis. Samples of specimens of all these clades almost completely overlap in morphospace (Figs. 4B and 4C). Both analyses included the same specimens, so the numerical results of the two sfPCAs were coincident. The first three PCs summarized 64.94% of the total variation but only PCI (30.31% of the variance) and PCI (25.64%) were judged statistically significant by the Broken-stick test (Supplementary Data SD1). The zygomatic plate depth (ZP) and the molar series (MTRL and mTRL) were the most influential variable along these two axes, but do not appear to separate any of the clades.

**Discussion**

**Taxonomy.**—As for many other species of sigmodontine rodents described in the first half of the XX century, the three nominal forms associated to *N. lactens* were characterized and diagnosed on the basis of small series of specimens, and assessing only a limited number of morphological characters. In fact, Oldfield Thomas named and diagnosed these three nominal forms using a single specimen each; females for *A. lactens* and *A. orbus*, and a male for *B. negrito*.

Thomas (1919) recognized the overall similarity between *A. lactens* and *A. orbus* when stating in the original description of the latter: “General characters very much as in *A. lactens*.” He differentiated both forms by the putative absence of a white patch on the chin, the tone of the fur “slightly duller and more drabby” (although he recognized the scant difference in this character when he said “…but the difference amounts to little.”), the ears slightly shorter, the skull of lighter build, with markedly narrower muzzle and more bowed in outline, and the thinner incisors, in *A. orbus*. In our samples of specimens from the vicinity of the type localities, most of these characters varied, but not in association with these nominal forms. In fact, we observed specimens from the environs of the type localities of *A. orbus* and *A. lactens* with poorly expressed (almost absent) white patches on the chin; other specimens from the same localities display great variation in patch size (small, medium, or large, in size). The size of the ear (E) and the midrostral width (RW2) of specimens of both nominal forms do not show significant differences (Table 2). As such, both forms have been traditionally considered synonyms (e.g., Musser and Carleton 2005). As far as we are aware, Capllonch et al. (1997) have been the only recent authors to recognize *orbus* (as Bolomys orbus) as a valid species (but see also Galliari and Pardiñas 2000:226 who considered the synonymy of *orbus* as dubious). They referred to this species a single specimen (CML 5989) collected in the extreme north of the Sierra de San Javier in Tucumán province (northwestern Argentina). We studied this specimen and concluded that it is not morphologically similar to *A. orbus* or allied to *N. lactens*, but is more similar in external and skull characters to the lowland species of the genus—e.g., *N. lenguarum* (Thomas, 1898)—and the recently described *N. lilloi* Jayat, D’Elía, Ortiz and Teta, 2016.

Thomas (1926) was even briefer in comparisons of *B. negrito*, highlighting only the dark color of the fur and the “fossorial characters of its feet and teeth.” In the sample examined by us, we observed several specimens with very dark tones.
Table 2.—External and craniodental measurements for specimens of the nominal forms assigned to *Necromys lactens* and for those recovered for the two main clades (NC and SC) obtained with the phylogenetic analysis for the age classes 2 and 3. $\bar{X}$ = mean; $SD$ = standard deviation; $r$ = range; $n$ = sample size. Measurement abbreviations listed in “Materials and Methods.” One and two asterisks indicate a significant difference at $P < 0.05$ and $P < 0.01$, respectively.

|                | Akodon lactens | Bolomys negrito | Akodon orbis | Northern clade | Southern clade |
|----------------|----------------|------------------|-------------|----------------|----------------|
| **TL** $n$     | 17             | 6                | 9           | 10             | 39             |
| $\bar{X}$      | 176            | 166              | 172         | 172            | 173            |
| $SD$           | 7.50           | 13.10            | 11.44       | 10.23          |                |
| $r$            | 150–190        | 157–193          | 162–196     | 150–193        |                |
| **T**          | 17             | 6                | 9           | 10             | 40             |
| 67             | 64             | 66               | 68          | 67             |                |
| 5.13           | 6.01           | 5.59             | 4.16        | 5.14           |                |
| 57–75          | 56–74          | 59–75            | 63–77       | 56–75          |                |
| **HF**         | 17             | 6                | 9           | 10             | 40             |
| 26             | 26             | 26               | 26          | 26             |                |
| 0.97           | 1.05           | 1.05             | 0.92        | 1.03           |                |
| 24–27          | 24–27          | 25–28            | 24–27       | 23–28          |                |
| **E**          | 17             | 6                | 9           | 10             | 39             |
| 16             | 15             | 15               | 16          | 15             |                |
| 1.28           | 0.52           | 0.73             | 0.70        | 0.94           |                |
| 11–17          | 15–16          | 15–17            | 15–17       | 11–17          |                |
| **W**          | 17             | 6                | 9           | 10             | 39             |
| 34.9           | 32.6           | 36.7             | 31.6        | 36.4           |                |
| 5.71           | 3.32           | 8.96             | 7.67        | 6.90           |                |
| 20.0–44.0      | 29.0–38.0      | 27.5–51.0        | 26.0–49.0   | 20.0–51.0      |                |
| **CIL**        | 17             | 5                | 9           | 10             | 42             |
| 26.22          | 25.23          | 25.91            | 25.80       | 25.95          |                |
| 0.05           | 0.80           | 1.31             | 0.95        | 1.02           |                |
| 23.76–27.66    | 24.42–26.48    | 24.26–27.60      | 24.66–27.44 | 23.76–27.66    |                |
| **PL**         | 17             | 6                | 9           | 10             | 43             |
| 14.09          | 13.47          | 13.89            | 13.72       | 13.92          |                |
| 0.65           | 0.52           | 0.74             | 0.54        | 0.84           |                |
| 12.56–15.00    | 12.94–14.14    | 13.04–15.00      | 13.04–14.60 | 12.56–15.00    |                |
| **DL**         | 17             | 6                | 9           | 10             | 43             |
| 8.25           | 7.73           | 8.15             | 8.01        | 8.06           |                |
| 0.42           | 0.41           | 0.54             | 0.38        | 0.46           |                |
| 7.30–8.82      | 7.20–8.26      | 7.46–8.94        | 7.40–8.64   | 7.20–8.94      |                |
| **PB**         | 17             | 6                | 9           | 10             | 43             |
| 3.84           | 3.79           | 3.83             | 3.67        | 3.84           |                |
| 0.28           | 0.24           | 0.31             | 0.21        | 0.25           |                |
| 3.34–4.34      | 3.48–4.20      | 3.44–4.26        | 3.33–3.99   | 3.34–4.34      |                |
| **MTRL**       | 17             | 6                | 9           | 10             | 43             |
| 4.69           | 4.85           | 4.76             | 4.63        | 4.75*          |                |
| 0.18           | 0.15           | 0.15             | 0.18        | 0.16           |                |
| 4.34–4.94      | 4.70–5.10      | 4.54–5.02        | 4.36–4.90   | 4.34–5.10      |                |
| **IFL**        | 17             | 6                | 9           | 10             | 43             |
| 6.45           | 6.17           | 6.40             | 6.40        | 6.38           |                |
| 0.31           | 0.24           | 0.37             | 0.43        | 0.31           |                |
| 5.90–7.10      | 5.90–6.48      | 5.98–7.00        | 5.68–7.00   | 5.90–7.10      |                |
| **AW**         | 17             | 6                | 9           | 10             | 43             |
| 5.63           | 5.33           | 5.55             | 5.33        | 5.51           |                |
| 0.23           | 0.29           | 0.32             | 0.11        | 0.27           |                |
| 5.18–6.12      | 4.98–5.68      | 5.06–6.00        | 5.10–5.50   | 4.98–6.12      |                |
| **ZL**         | 17             | 6                | 9           | 10             | 43             |
| 14.25          | 13.43          | 14.08            | 14.41       | 14.12          |                |
| 0.87           | 0.36           | 0.68             | 0.58        | 0.74           |                |
| 12.74–15.96    | 13.08–14.10    | 13.14–14.92      | 13.54–15.44 | 12.74–15.96    |                |
| **ZP**         | 17             | 6                | 9           | 10             | 43             |
| 2.95           | 2.66*          | 2.87             | 2.87        | 2.91           |                |
| 0.20           | 0.22           | 0.22             | 0.19        | 0.22           |                |
| 2.56–3.36      | 2.30–2.94      | 2.61–3.14        | 2.63–3.16   | 2.30–3.40      |                |
| **ZB**         | 16             | 6                | 9           | 10             | 41             |
| 15.21          | 14.76          | 15.12            | 14.70       | 15.13*         |                |
| 0.69           | 0.40           | 0.86             | 0.43        | 0.64           |                |
| 13.68–16.36    | 14.40–15.50    | 14.10–16.34      | 14.16–15.40 | 13.68–16.36    |                |
| **BB**         | 17             | 5                | 9           | 10             | 42             |
| 12.52          | 12.51          | 12.55            | 12.44       | 12.55          |                |
| 0.32           | 0.28           | 0.36             | 0.17        | 0.31           |                |
| 11.90–13.14    | 12.08–12.78    | 11.83–13.00      | 12.16–12.73 | 11.81–13.14    |                |
from different populations across northwestern Argentina (including the environs of all three type localities). Striking variations in the tinge of the skins have been recognized for other species of sigmodontine rodents in northwestern Argentina (e.g., Jayat et al. 2010, 2017) as well as other species from elsewhere (e.g., Kaufman 1974; Stoner et al. 2003; Bedford and Hoekstra 2015). In general, most of the specimens we examined showed comparatively well-developed claws, although we observed variation in this regard. We also observed variation in the procumbency of the incisors across the specimens examined, but the type specimen of *B. negrito* seems extreme in this character state (Supplementary Data SD2B).

Phylogenetic studies conducted by D’Elía et al. (2008) based on Cytb gene data recovered *N. lactens* as representing a highly differentiated lineage within the radiation of Necromys. Analyzing a sample of seven specimens from seven Argentinean localities, those authors documented that the genetic variation was geographically structured and suggested that *lactens*, *negrito*, and *orbus* were conspecific. Our results, based on a larger sample of specimens, including some collected in Bolivia, corroborate the conclusion of D’Elía et al. (2008). Neither set of results supports the recognition of these three taxa as representing distinct lineages, either at the species or subspecies level. Haplotypes assigned by locality to the three nominal forms all fall into a single clade (the SC); haplotypes of the form *lactens* fall in the CSC, while those of *orbus* and *negrito* are all included in the SSC. Given the low level of genetic divergence between both clades (1.7%), that clade CSC lacks significant support (PP = 0.52), and specimens of clades CSC and SSC are not morphologically differentiated (a Discriminant Analysis performed to verify this result misclassified a large proportion of cases; Supplementary Data SD3), we corroborate the hypothesis advanced by D’Elía et al. (2008) and conclude that the best taxonomic decision is to consider *orbus* and *negrito* as junior synonyms of *lactens*.

Genetic divergence between the two main clades is appreciable, reaching 3.3%, a value distinguishing some other akodontine species (e.g., Coyner et al. 2013). By this measure, the recognition of two (*lactens* and one new form for the NC) or three (*lactens* and two new forms for NNC and CNC) taxa would be an option. Notwithstanding, the southern clade lacks significant support (PP = 0.54) and the morphometric analyses of skull shape failed to separate any of the groups emerging from these arrangements, with samples representing each of the groups highly overlapped in the morphospace (a Discriminant Analyses applied to these groups also performed poorly in classification; Supplementary Data SD3). Examined specimens, although numerous enough to allow testing for shape differences...
among groups, were insufficient to evaluate size differences for any of the five age classes (no age class has adequate series across all groups). Nevertheless, our quantitative morphometric analysis of specimens of age classes 2 and 3 fails to show the existence of distinctive size-based classes, either among populations of the three recognized nominal forms or between the two main clades (NC and SC). As such, taking together all the available evidence, we treat all studied specimens as belonging to a single and monotypic species, *N. lactens*.

**Biogeography.**—Beyond the taxonomic assignments of the clades of *N. lactens* as here understood, the pattern of variation of the mitochondrial genome, showing a deep, geographically structured genealogy, suggests a history of population differentiation in isolation. *Necromys lactens* occur in high-altitude grasslands that develop on pre-Andean mountain ranges (Jayat and Pacheco 2006). These mountain systems are a complex of parallel ridges of different heights and extensions that replace themselves from east to west and that mostly run north to south, parallel to the Andes. Their mountaintop grasslands are separated from each other by relatively large river valleys covered by arid or semiarid habitats (e.g., Chaco, Monte, and Prepuna) and the humid Yungas forest. Our results suggest that the phylogeography of *N. lactens* was shaped by the history of these high-altitude grasslands in the central pre-Andean and associated mountain systems. Today, glaciers occupy some of the mountain ridges in the area (e.g., Nevados del Aconcagua, Nevados del Chañi, and Nevados de Cachi) above 5,000 m; however, during the ice ages, glaciers in these areas extended far lower (Martini et al. 2017), reaching between 4,200 m and even to 4,000 m in some places (Halloy 1978; Haselton et al. 2002). This would have lowered the vegetation belts on mountain slopes and caused some montane vegetative zones to extend beyond the mountains. Under these conditions, patches of high-altitude grasslands inhabited by *N. lactens* may have come into two main clades (NC and SC). As such, taking together all the available evidence, we treat all studied specimens as belonging to a single and monotypic species, *N. lactens*.

**Table 3.**—Size-free Principal Component Analysis of craniodental measurements of specimens (all age classes, *n* = 49) of the three nominal forms assigned to *Necromys lactens*: *Akodon lactens* (*n* = 24), *A. orbus* (*n* = 14), and *Bolomys nigrito* (*n* = 11). Asterisks indicate statistically significant principal components under the Broken-stick method to assess the significance of the eigenvalue of each principal component.

| Variables | PCI* | PCII* | PCIII* |
|-----------|------|-------|--------|
| CIL       | 0.11597 | 0.01266 | −0.01977 |
| PL        | 0.15318 | −0.00494 | 0.02955 |
| DL        | 0.24920 | 0.10654 | −0.10085 |
| PB        | 0.02526 | 0.09680 | 0.12158 |
| MTRL      | −0.28677 | −0.21922 | 0.19562 |
| IFL       | 0.12190 | 0.08168 | −0.05152 |
| AW        | −0.12990 | −0.04210 | 0.00936 |
| ZL        | 0.23447 | −0.14722 | −0.01512 |
| ZP        | 0.40012 | 0.15243 | −0.06954 |
| ZB        | 0.02549 | −0.02694 | 0.01713 |
| BB        | −0.29261 | −0.21058 | 0.20181 |
| IOC       | −0.28383 | −0.07971 | 0.17638 |
| RW2       | 0.05038 | 0.05052 | 0.14418 |
| NL        | 0.31799 | 0.05834 | 0.01853 |
| RL        | 0.10821 | −0.02910 | 0.03114 |
| OL        | 0.00383 | −0.09775 | 0.01679 |
| OCW       | −0.22672 | −0.17280 | 0.26301 |
| ML        | 0.06949 | −0.03040 | 0.04114 |
| mLTRL     | −0.23322 | −0.32059 | −0.86028 |
| MDL       | −0.42246 | 0.82240 | −0.14915 |
| Eigenvalue | 0.0025 | 0.0015 | 0.0008 |
| % variance | 36.61 | 21.44 | 10.94 |

Fig. 4.—Individual specimen scores based on log-transformed values of 20 cranial measurements (Mosimann shape variables), projected onto the first and second principal components of the “size-free” Principal Component Analysis (PCA) extracted from A) analysis of specimens (all age classes, *n* = 49) of the three nominal forms assigned to *Necromys lactens*: *Akodon lactens* (black circles, *n* = 24), *A. orbus* (dark gray triangles, *n* = 14), and *Bolomys nigrito* (light gray squares, *n* = 11); B) analysis of specimens (all age classes, *n* = 88) of the two main clades recovered for *N. lactens*: northern clade (NC, black circles, *n* = 20) and southern clade (SC, light gray triangles, *n* = 68); C) analysis of specimens (all age classes, *n* = 88) of the four subclades recovered for *N. lactens*: northernmost clade (NNC, closed black circles, *n* = 4), southernmost clade (SSC, open light gray squared, *n* = 25), central-northern clade (CNC, open black circles, *n* = 16), and central-southern clade (CSC, open dark gray triangles, *n* = 43). Character loadings and the variance explained by each of the first two principal components appear in Table 3 and Supplementary Data SD1.
contact and allowed dispersal of the species among the different mountain ranges. This hypothesis is supported by the similar patterns of genetic variation observed in other taxa strikingly associated to high-altitude grasslands (e.g., Jayat et al. 2016, 2017) and by the discovery of several late Pleistocene to lower Holocene small mammal assemblages, in which several rodent species that currently live in high-altitude areas occurred at lower altitude (e.g., Ortiz and Pardiñas 2001; Ortiz et al. 2011a, 2011b, 2019). Future phylogeographic studies, based on larger series of specimens and on more loci (e.g., Lessa et al. 2014), could potentially answer the question of whether the differentiation scenario suggested here is corroborated or falsified.

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Supplementary Data

Supplementary data are available at Journal of Mammalogy online.

Supplementary Data S1.—Size-free Principal Component Analysis of the two main clades and the four subclades.

Supplementary Data S2.—Holotype specimens of Akodon orbis (A), and Bolomys negrito (B), and type specimen of Akodon lactens (C).

Supplementary Data S3.—Classification matrix and percentage of correct classifications of the Discriminant Analysis for the three nominal forms, the two main clades, and the four subclades.

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APPENDIX I

Specimens examined.—Acronyms for institutions are as follows. Argentina: Centro Nacional Patagónico (CNP), Puerto Madryn; Colección Mamíferos Lillo (CML), Tucumán; Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-Ma), Ciudad Autónoma de Buenos Aires; Museo Municipal de Ciencias Naturales “Lorenzo Scaglia” (MMPMa), Mar del Plata. United Kingdom: Natural History Museum (NHM), London. United States of America: Sam Noble Oklahoma Museum of Natural History (SNOMNH), Oklahoma. Asterisks (*) indicate specimens not used in the morphometric analyses.

Necromys lacteus (n = 102).—ARGENTINA: Catamarca: ca. 2 km SE of Huaco Hondo, on hwy. Nº 42, E of Portezuelo, 1,992 m, 28°25′9″S, 65°47′3″W (CML 13234, 13235; MACN-Ma 23484, 26446, 28274, 28285); jct. hwy. Nº 9 and 18, 3.4 km S, on hwy. Nº 18, 1,529 m, 27°49′48.3″S, 65°47′53.3″W (CML 7220, 13232, 13233;
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LIST OF SPECIMENS USED IN OUR PHYLOGENETIC ANALYSIS

| Acronym                        | Location                          | Data Source                                                                 |
|-------------------------------|-----------------------------------|----------------------------------------------------------------------------|
| MACN-Ma 23481                 | SNOMNH 34512                      | Las Chacritas, ca. 28 km NNW Singuil, on hwy. N° 1, 1,888 m, 27°42'24.2°W, 65°54'40.6°W (MACN-Ma 23475, 26449, 28275); Otro Cerro (NHM 19.2.7.45* [photograph of the holotype of Akodon orbis Thomas, 1919]). Jujuy: Barcena, ca. 9 km NW, 2,655 m, 23°57'5.9°S, 65°30'1.2°W (CML 7221); Bárcena, ca. 3 km S, on hwy. N° 9, 1,808 m, 24°0'2°S, 65°26'51.6°W (CML 13237; CNP 1486; MACN-Ma 26453, 26454, 28276 to 28283); Bárcena, behind the cemetery, 2,100 m, 23°58'8°S, 65°27'45.5°W (MACN-Ma 26467, 26468, 26469, 28288); ca. 3.5 km of Jaire, on hwy. 29, road to Tiraxi, 1,715 m, 24°13'6.7°S, 65°23'35.4°W (MACN-Ma 26470); Cerro Hermoso (MACN-Ma 19.5.17*); El Duraznillio, Cerro Calilegua, 2,600 m (CML 1736*, 1737); Chicuyc, 23°56'30°S, 65°28'33°W (CML 8312*, 9376); La Antena, Sierra del Centinela, S of El Fuerte, 2,350 m, 24°17'56.46°S, 64°23'9.3°W (MACN-Ma 23492, 26450, 26451, 26452); León (MMPMa 2158*, 2161*, 2169, 2185*, 2190*); topotypes of 26450, 26451, 26452); ca. 15 km N, on hwy. Provincial N° 4, 24°7'4.5°S, 65°29'19.5°W (CML 13236; MACN-Ma 28270, 28271). Salta: 1 km ENE Rodeo Pampa, km 59 of the hwy. N° 7, 3,080 m, 22°14'47.7°S, 65°3'4.3°W (MACN-Ma 28286); Abra de Ciénaga Negra, ca. 3 km SE, 3,090 m, 23°19'49°S, 64°53'32°W (CML 13241; CNP 1487; MACN-Ma 23501, 26458, 28284); ca. 5 km (on road) S of Los Toldos, on the road to Vallecito, 1,705 m, 22°19'5.7°S, 64°43'8.36°W (MACN-Ma 26459, 28287); ca. 15 km W Escoipe, on hwy. N° 33, 2,680 m, 25°10'26.76°S, 65°49'31.3°W (CML 9378, 9379, 9388*, 13240; MACN-Ma 26455, 26456, 26457, 28264 to 28269); El Corralito, ca. 23 km SW Campo Quijano, on hwy. N° 51, 24°58'S, 65°48'W (CML 13242, 13243); Pampa Verde, ca. 8 km WSW Los Toldos and S of Cerro Bravo, 2,400 m, 22°17'S, 64°48'W (MACN-Ma 28273). Tucumán: above Hualinchay (MACN-Ma 28876*); above Hualinchay, 3,000 m (MACN-Ma 28875*); ca. 10 km S of Hualinchay, on the road to Lara, 2,300 m, 26°19'20.2°S, 65°36'45.5°W (CML 13244; MACN-Ma 26448); ca. 16 km from Hualinchay, on the road to Lara, 2,750 m, 26°19'31.92°S, 65°38'51.18°W (CML 13245, 13246); Ciénaga Grande, San José de Chasquivil (CML 8453*); Hualinchay, on the road to Cafayate, 1,861 m, 26°18'21.3°S, 65°36'45.8°W (CML 13247, 13248, 13249; MACN-Ma 23514*, 26447, 28272); Las Paras [= Las Pavas], about 4,000 m (NHM 25.12.13.39* [photograph of the holotype of Bolomys negrito Thomas, 1926]); Parque Nacional Campo de Los Alisos, El Kenqueo, 3,200 m (CML 8454); Tafi del Valle, 2,800 m (CML 2062); Tafi del Valle, km 78, 2,700 m (CML 1836*); hwy. 307, km 72 (MMPMa 2985*). |