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Integration of morphological, ecological, and genetic evidence suggests that the genus *Andinomys* (Rodentia, Cricetidae) is monospecific

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Two subspecies of *Andinomys edax* are currently recognized. *Andinomys e. edax* ranges from southern Perú to northernmost northwestern Argentina and *A. e. lineicaudatus* is mainly distributed in southern northwestern Argentina. However, some workers have recognized both taxa as distinct species, stating that *A. edax* is restricted to Puna and Prepuna habitats between 2,000 and 4,800 m elevation, whereas *A. lineicaudatus* occurs in Yungas forest below 2,500 m. We assessed the taxonomic status of both forms through an integrative approach including morphological (discrete skin and skull characters), morphometric (univariate and multivariate), geographic-environmental niche modeling (Mahalanobis Typicalities), and molecular (Bayesian analysis of cytochrome-*b* gene sequences) analyses. We did not find characters that consistently differentiated skins and skulls of the 2 forms. The morphometric analysis indicated that *lineicaudatus* is, on average, larger than *edax* for some measurements, but only 2 (alveolar width and occipital condyle width) differed significantly between forms. No group of specimens was clearly segregated in the PCA morphospace. Distribution models obtained separately for each taxon do not offer a better fit to the known distribution than models based on the combined data sets. We documented coincident environmental variables as relevant in the model building of *edax* and *lineicaudatus*, noting some segregation in elevation, but similar habitat suitability for the remainder of the environmental variables. The geographic continuity between niche models of *edax* and *lineicaudatus* was clear but specimens morphologically assignable to each of the nominal forms were not found in areas of overlap. The phylogenetic analyses recovered a polytomy of 4 allopatric and genetically divergent clades, which also failed to support the taxonomic hypothesis of 2 species. Based on all available evidence, we conclude that *Andinomys* consists of a single species. Nevertheless, observed genetic divergences among clades and their geographic distribution indicate that past events probably fragmented populations of *A. edax*.

Actualmente se reconocen 2 subespecies de *Andinomys edax*. *Andinomys e. edax* se extiende desde el extremo sur de Perú hasta el extremo norte del noroeste argentino y *A. e. lineicaudatus* se distribuye principalmente en el extremo sur del noroeste argentino. Sin embargo, algunos autores consideran a ambos taxones como especies diferentes, restringiendo a *A. edax* a ambientes de Puna y Prepuna entre 2000 y 4800 m de altitud, y a *A. lineicaudatus* a regiones de Yungas por debajo de 2500 m. Evaluamos el estatus taxonómico de ambas formas nominales a través de una aproximación integrativa que incluyó análisis morfológicos (caracteres discretos de piel y cráneo), morfométricos (univariados y multivariados), de modelado de nicho geográfico y ambiental (Mahalanobis Typicalities), y moleculares (análisis Bayesianos de secuencias del gen citocromo-*b*). No encontramos caracteres que permitan consistentemente diferenciar las pieles y cráneos de ambas formas. El análisis morfométrico indicó que *lineicaudatus* es, en promedio, más grande que *edax* para algunas de las medidas consideradas, pero solo 2 de ellas (ancho alveolar y ancho del cóndilo occipital) fueron significativamente diferentes entre las 2 formas. Ningún grupo de especímenes se separó claramente en el espacio morfológico del ACP. Los modelos de distribución obtenidos para cada taxón no evidenciaron un mejor ajuste a la distribución conocida que el modelo basado en los datos agrupados. Documentamos variables ambientales relevantes coincidentes en la construcción de los modelos de *edax* y *lineicaudatus*, observando alguna segregación en altitud, pero similar idoneidad de hábitat para el resto de las variables ambientales. La continuidad geográfica entre los modelos de distribución de *edax* y *lineicaudatus* fue clara pero no observamos especímenes morfológicamente asignables a cada una de las formas nominales en la zona de solapamiento. El análisis filogenético recuperó una politomía de 4 clados alopátridos genéticamente divergentes, lo cual no apoya la hipótesis taxonómica de 2 especies válidas. Sobre la base de toda la evidencia, concluimos que *Andinomys* consiste de una sola especie. Sin embargo, las divergencias genéticas observadas entre clados y su distribución geográfica indican que eventos del pasado probablemente fragmentaron las poblaciones de *A. edax*.

Key words: Andean rat, central Andes, Muridae, Sigmodontinae, South America, species limits, type locality

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The monotypic genus *Andinomys* (Andean mouse) ranges between 14°S and 28.5°S, from southeastern Peru and northernmost Chile through southwestern Bolivia and northwestern Argentina (Salazar-Bravo and Jayat 2015). Individuals have been trapped from 650 to 4,500 m elevation, with most records occurring above 1,500 m. Across this wide geographic distribution, the genus occupies multiple types of habitats, from subtropical montane forests and humid high-elevation grasslands to semiarid grasslands of the Puna and Prepuna (Jayat et al. 2009).

Traditionally, only a single species (*Andinomys edax*) with 2 subspecies are recognized (Yepes 1935; Salazar-Bravo and Jayat 2015). *Andinomys e. edax* (type locality in El Cabrado, 3,700 m, between Potosi and Sucre, [Potosí] Bolivia) ranges from southern Perú to northernmost northwestern Argentina and *A. e. lineicaudatus* (type locality in Cerro San Javier, Tucumán, Argentina) is mainly distributed in southernmost northwestern Argentina (Hershkovitz 1962). However, based on the supposed occurrence of both forms at a locality in the Prepuna area of Jujuy province, Argentina, Díaz (1999) recognized both taxa at the species level. Díaz and Barquez (2007) also recognized the 2 subspecies as distinct species, stating that *A. edax* was restricted to Puna and Prepuna habitats between 2,000 and 4,800 m altitude, whereas *A. lineicaudatus* occurred in Yungas forest below 2,500 m.

Here, we test the taxonomic hypothesis of Díaz (1999) and Díaz and Barquez (2007) through an integrative approach including morphological, morphometric, molecular, and geographic-environmental niche modeling analyses. In particular, we evaluate if the geographic variation observed in samples of *Andinomys* throughout its distribution allows the taxonomic recognition of *edax* and *lineicaudatus* as distinct species under diagnosable (qualitative and quantitative fixed differences), ecological (different niche or adaptive zone), and monophyletic (reciprocal monophyly) species concepts (see de Queiroz 2007 for a summary of these alternative species concepts, the properties upon which they are based, and authors who advocate each one of them). Conclusions are drawn on the basis of accumulated evidence.

MATERIALS AND METHODS

We studied specimens of *Andinomys* newly collected by us using Sherman traps (H. B. Sherman Co., Tallahassee, Florida) and those already housed in natural history collections. Newly captured specimens were deposited at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” collection (MACN, Buenos Aires, Argentina) or are temporarily housed in the collection of 1 of the authors (JPJ; these specimens will be deposited in the MACN collection). Sampling included specimens collected near the type locality of *A. edax edax* Thomas and at the type locality of *A. edax lineicaudatus* Yepes (Appendices I, II, and III). In the course of reviewing the geographic provenance of the specimens used in this study, we identified a problem with the location of the type locality of *A. e. edax*. The correct type locality for *A. edax* should be “Posta El Cabrado, 3500 m elevation,” in the Chuquisaca Department, Bolivia. We realized that “El Cabrado, 3700 m, Potosí, Bolivia” as established by Hershkovitz (1962:481) and later adopted by subsequent authors (e.g., Anderson 1997; Salazar-Bravo and Jayat 2015) is not the locality where Perry O. Simons collected the specimens deposited in the British Museum. There is robust evidence, as provided in the ornithological gazetteer of Chubb (1919), that Simons obtained the 2 specimens comprising the type series of *A. edax* from the Chuquisaca Department and not Potosí Department. All parts of the study involving live animals followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Taxonomic assignment of the samples.—Following the taxonomic hypothesis of Díaz and Barquez (2007), we used morphological characters as well as geographic and environmental provenance of the specimens to assign them to taxa, as follows: specimens from high-elevation, arid and semiarid environments (Prepuna, Puna, and Altos Andes ecoregions) of the western pre-Andean mountain slopes were regarded as representing *A. edax*; those coming from humid, eastern pre-Andean mountain slopes (Yungas ecoregion) as representing *A. lineicaudatus* (Fig. 1). We also followed original (Thomas 1902; Yepes 1935) and subsequent descriptions of both taxa (Pearson 1958; Hershkovitz 1962) for the morphological assignment of specimens. Two characters often have been used to distinguish the 2 forms: a supposedly paler coloration of the fur in *A. e. edax* and the midventral line in the tail of *A. e. lineicaudatus* (Yepes 1935; Hershkovitz 1962). We note, however, that tail coloration is unreliable, as some specimens assignable to *A. e. lineicaudatus* by pelage color and geographic or environmental provenance lacked the brown midventral line from where the trinomial derives its name (all specimens assignable to *A. e. edax* uniformly lack this line), so we did not use this character. Specimens coming from high-elevation, arid and semiarid areas agree with the morphological characterization of *A. e. edax* and specimens coming from lower altitudes of the humid eastern slopes (including humid grasslands and forests) closely agree with the description of *A. e. lineicaudatus*. Using this criterion, we assigned 37 of the specimens to the nominal form *edax* and 32 to the nominal form *lineicaudatus*. All specimens examined and their locality data are listed in Appendix I. Georeferenced localities are summarized in Appendix II.

Morphometric analyses.—Standard external measurements were recorded from specimen tags or field catalogs: TL: total length; T: tail length; HF: hind foot length (including claw); E: ear length; and W: body mass. The following skull measurements were recorded with a vernier caliper to the nearest of 0.01 mm following Myers et al. (1990): MSL: maximum skull length; CIL: condyloincisive length; BL: basal length; PL: palatal length; PB: palatal bridge; NL: nasal length; RL: rostral length; OL: orbital length; RW2: midrostral width; ZP: zygomatic plate depth; IOC: interorbital constriction; ZL: zygomatic length; ZB: zygomatic breadth; BB: braincase breadth; OCW: occipital condyle width; DL: diastema length; MTRL: maxillary toothrow length; IFL: incisive foramina length; AW1: alveolar width (across external side of both M1); AW2: alveolar width (across external side of both M3); BPL: basal-posterior length; ML: mandible length; mTRL: mandibular toothrow length; MDL: mandibular diastema length. Five age classes were defined according to tooth wear. 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 (Supplementary Data SD1). Descriptive morphometric and univariate comparisons for samples of each taxon were carried out with the software PAST (Hammer et al. 2001) for each age class separately in search of significant differences (*t*-tests with $P \leq 0.05$ and $P \leq 0.01$; Table 1).

A principal component analysis (PCA) for individuals in age classes 2 and 3, the largest pool of available specimens,

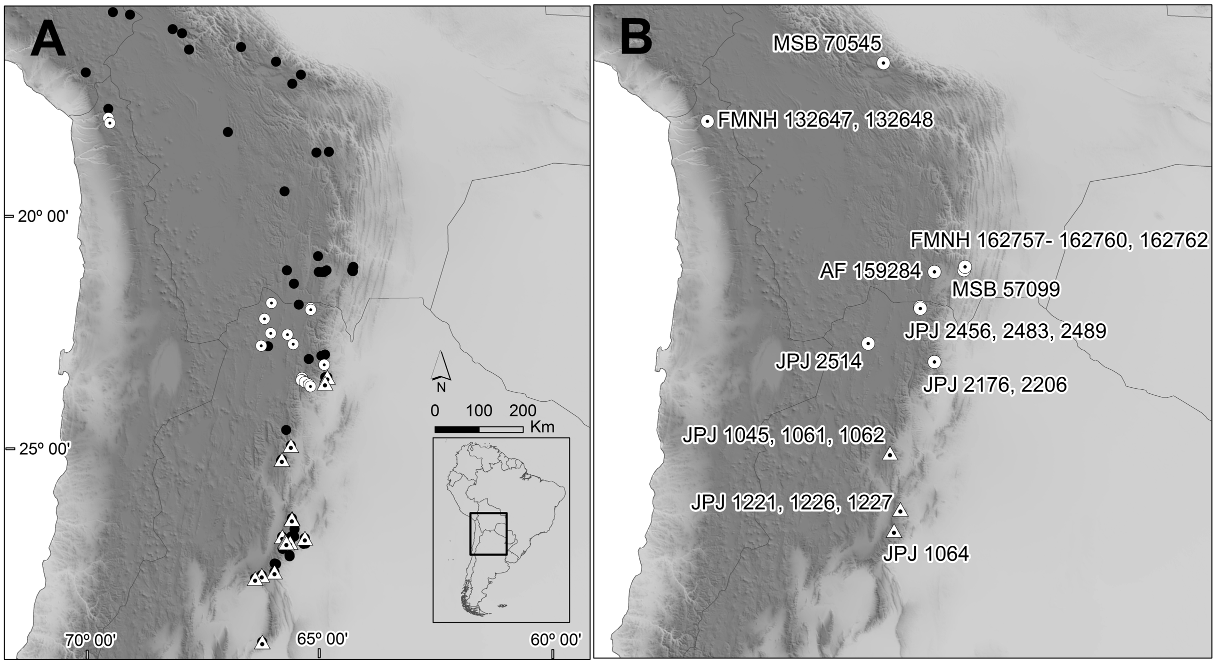

Fig. 1.—Map of the central Andes in South America, showing the geographic localities of the specimens used in this study. A) Collection localities for *Andinomys* specimens examined (see Appendix I). Circles with a midpoint indicate specimens assigned to the nominal form *edax*. Triangles with a midpoint indicate specimens assigned to the nominal form *lineicaudatus*. Black points indicate all known locality records for *Andinomys*. B) Collection localities for specimens of *Andinomys* included in the molecular analysis (see Appendix III). Gray shading corresponds to areas above 2,000 m elevation.

Table 1.—External and craniodental measurements for specimens of *Andinomys* assigned to the nominal forms *edax* and *lineicaudatus* (Appendix I) for 5 age classes. $\overline{X}$ = mean; *SD* = standard deviation; *r* = range; *n* = sample size. * and ** indicate a significant difference at $P < 0.05$ or $P < 0.01$, respectively.

		Age class 1		Age class 2		Age class 3		Age class 4		Age class 5	
		A. e. edax	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*
TL	*n*	9	9	5	11	3	6	2	3	2	1
	$\overline{X}$	242	249	286	284	286	287	295	294	297	322
	SD	21.21	27.46	18.59	20.24	9.00	26.22	49.50	3.61	12.73	
	r	(208–281)	(217–304)	(270–315)	(249–308)	(277–295)	(247–312)	(260–330)	(291–298)	(288–306)	
T		9	9	5	11	3	6	2	3	2	1
		113	115	135	132	132	133	135	136	135	146
		10.10	12.89	14.53	12.46	6.11	22.13	14.14	7.21	6.36	
		(94–128)	(99–139)	(125–160)	(109–150)	(127–139)	(102–164)	(125–145)	(130–144)	(130–139)	
HF		10	9	5	11	4	5	2	3	2	1
		28	27	27	32**	33	31	32	28	28	34
		1.87	5.27	1.48	2.22	3.10	5.13	4.95	5.69	2.83	
		(26–32)	(21–35)	(25–29)	(28–35)	(30–37)	(23–37)	(28–35)	(22–33)	(26–30)	
E		10	9	4	11	4	6	2	3	2	1
		23	24	25	24	28	26	28	28	28	26
		1.22	4.74	2.00	5.65	4.55	2.69	0.71	1.15	0.71	
		(21–25)	(15–30)	(22–26)	(11–33)	(24–34)	(24–31)	(27–28)	(27–29)	(27–28)	
W		4	5	1	6	2	2	1	2	2	
		50	67	79	83	84	83	132	108	105	
		9.95	18.59		10.79	2.83	17.68		19.09	4.24	
		(38–62)	(43–90)		(70–99)	(82–86)	(70–95)		(94–121)	(102–108)	
MSL		9	5	4	11	7	7	2	2	3	1
		31.34	32.61	34.85	35.34	34.97	36.39	36.91	37.33	36.89	38.06
		1.86	2.23	1.26	1.24	1.51	2.33	1.27	1.32	0.42	
		(28.22–33.88)	(29.07–35.12)	(33.19–36.18)	(33.04–36.98)	(32.28–36.63)	(33.10–40.12)	(36.01–37.80)	(36.40–38.26)	(36.49–37.32)	
CIL		9	5	4	11	6	7	2	2	3	1
		29.15	30.65	32.83	33.30	32.94	34.20	34.82	35.59	35.21	36.10
		1.86	2.17	1.16	1.24	1.45	2.35	1.34	1.32	0.54	
		(26.24–32.22)	(27.26–33.30)	(31.41–34.26)	(31.00–34.53)	(30.47–34.44)	(30.68–37.72)	(33.87–35.76)	(34.66–36.52)	(34.75–35.80)	
BL		9	5	4	11	6	7	2	2	3	1
		26.82	28.39	30.63	30.73	30.89	31.71	32.45	32.74	33.05	32.90
		1.92	1.79	1.18	1.23	1.51	2.43	1.24	1.24	0.54	
		(23.76–30.06)	(25.53–30.46)	(29.31–32.10)	(28.28–32.00)	(28.20–32.26)	(27.90–35.14)	(31.57–33.32)	(31.86–33.62)	(32.60–33.64)	
PL		9	9	4	12	8	8	2	3	3	1
		16.14	16.56	18.37	18.49	18.92	19.27	19.40	20.17	19.92	20.40
		1.07	1.23	0.93	0.66	0.70	1.10	1.19	0.28	0.77	
		(14.74–18.02)	(15.09–18.72)	(17.17–19.38)	(17.28–19.36)	(17.76–19.69)	(17.60–20.72)	(18.56–20.24)	(19.92–20.48)	(19.39–20.80)	
DL		11	9	5	12	8	8	2	3	3	1
		7.57	7.62	9.18	8.84	9.36	9.64	9.58	10.43	9.91	9.70
		0.68	0.78	0.62	0.50	0.49	0.71	0.15	0.53	0.41	
		(6.50–8.46)	(6.71–9.18)	(8.27–9.82)	(8.00–9.66)	(8.41–9.87)	(8.40–10.56)	(9.47–9.68)	(9.86–10.92)	(9.61–10.38)	
PB		9	9	5	12	8	8	2	3	3	1
		6.12	6.67**	6.52	7.21**	7.07	7.04	6.93	7.18	6.65	7.62
		0.36	0.46	0.23	0.36	0.60	0.46	1.10	0.14	0.42	
		(5.58–6.68)	(6.08–7.58)	(6.18–6.76)	(6.46–7.76)	(6.00–7.95)	(6.48–7.76)	(6.15–7.70)	(7.02–7.28)	(6.26–7.10)	

Table 1.—*Continued*

	Age class 1		Age class 2		Age class 3		Age class 4		Age class 5	
	A. e. edax	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*
MTRL	11	9	5	12	8	8	2	3	3	1
	6.99	7.46**	6.97	7.75**	7.30	7.48	7.83	7.57	7.10	6.76
	0.17	0.38	0.26	0.28	0.18	0.28	0.81	0.45	0.14	
	(6.74–7.23)	(6.97–8.19)	(6.64–7.34)	(7.32–8.10)	(7.00–7.58)	(7.10–7.77)	(7.25–8.40)	(7.06–7.92)	(6.96–7.24)	
IFL	9	9	5	12	8	8	2	3	3	1
	6.82	6.56	8.17	7.81	8.15	8.51	8.62	9.24	9.22	8.98
	0.74	1.07	0.38	0.54	0.47	0.59	0.51	0.79	0.16	
	(5.74–7.60)	(4.64–8.48)	(7.64–8.70)	(6.96–8.48)	(7.56–9.02)	(7.66–9.16)	(8.26–8.98)	(8.42–10.00)	(9.05–9.36)	
AW1	10	9	5	12	8	8	2	3	3	1
	5.73	6.18**	6.13	6.36	6.18	6.32	6.19	6.32	6.07	6.20
	0.14	0.24	0.37	0.27	0.22	0.33	0.07	0.24	0.42	
	(5.54–5.90)	(5.91–6.56)	(5.74–6.70)	(5.82–6.73)	(5.86–6.57)	(5.64–6.64)	(6.14–6.24)	(6.10–6.57)	(5.80–6.56)	
AW2	10	9	4	12	7	8	2	3	3	1
	6.20	6.49**	5.87	6.67**	6.32	6.69**	6.23	6.66	6.29	6.60
	0.21	0.27	0.32	0.26	0.24	0.26	0.39	0.10	0.13	
	(5.96–6.54)	(6.17–7.01)	(5.44–6.21)	(6.22–7.11)	(5.90–6.60)	(6.40–7.10)	(5.95–6.50)	(6.54–6.72)	(6.14–6.39)	
ZL	10	7	5	12	8	8	2	2	3	1
	16.19	16.34	17.59	17.47	18.37	17.64	18.83	18.53	20.05	19.26
	0.90	1.08	0.62	0.84	0.69	1.15	0.49	0.44	0.40	
	(14.58–17.22)	(14.84–17.43)	(17.00–18.54)	(16.34–19.07)	(16.98–19.17)	(15.76–19.24)	(18.48–19.18)	(18.22–18.84)	(19.64–20.43)	
ZP	11	9	5	12	8	8	2	3	3	1
	3.10	3.04	3.88	3.46*	3.81	3.54	3.94	3.92	4.45	4.90
	0.28	0.31	0.25	0.33	0.39	0.46	0.16	0.47	0.13	
	(2.56–3.62)	(2.42–3.46)	(3.48–4.12)	(2.64–3.76)	(3.30–4.46)	(2.86–4.12)	(3.82–4.05)	(3.38–4.24)	(4.30–4.54)	
ZB	9	8	4	12	7	8	2	2	2	
	16.89	17.61	18.04	19.00	19.31	19.48	20.32	20.08	20.40	
	0.87	0.99	0.84	0.53	0.56	0.97	0.74	0.11	0.24	
	(15.49–17.94)	(15.88–19.12)	(17.14–18.82)	(18.26–19.96)	(18.46–20.27)	(18.10–20.94)	(19.80–20.84)	(20.00–20.16)	(20.23–20.57)	
BB	9	6	4	12	7	7	2	2	3	1
	14.31	14.76	14.62	15.05	15.07	15.28	15.72	14.33	15.32	15.56
	0.36	0.43	0.37	0.51	0.65	0.54	0.46	0.44	0.14	
	(13.71–14.76)	(14.11–15.25)	(14.07–14.80)	(14.36–16.00)	(13.70–15.65)	(14.50–16.00)	(15.39–16.04)	(14.02–14.64)	(15.18–15.45)	
IOC	11	9	5	12	7	8	2	2	3	1
	4.28	4.60*	4.34	4.33	4.33	4.40	4.26	4.24	4.41	4.12
	0.24	0.36	0.13	0.15	0.11	0.20	0.20	0.34	0.14	
	(3.98–4.80)	(4.18–5.35)	(4.19–4.48)	(4.10–4.62)	(4.20–4.43)	(3.98–4.62)	(4.12–4.40)	(4.00–4.48)	(4.25–4.52)	
RW2	10	9	5	12	8	8	2	2	3	1
	6.32	6.25	6.96	6.76	7.09	7.14	7.29	7.35	7.51	8.00
	0.43	0.41	0.40	0.28	0.37	0.49	0.04	0.16	0.12	
	(5.50–6.92)	(5.51–6.90)	(6.38–7.35)	(6.29–7.16)	(6.55–7.46)	(6.48–7.96)	(7.26–7.32)	(7.24–7.46)	(7.42–7.56)	
NL	11	9	4	11	7	8	2	3	3	1
	12.40	12.30	14.31	14.13	14.49	14.52	15.08	15.52	15.63	16.24
	1.03	0.95	0.43	0.76	0.78	1.04	0.17	0.77	0.67	
	(10.80–13.74)	(11.08–14.10)	(13.77–14.72)	(13.00–15.31)	(13.36–15.49)	(12.96–16.22)	(14.96–15.20)	(14.80–16.34)	(14.96–16.29)	

Table 1.—*Continued*

	Age class 1		Age class 2		Age class 3		Age class 4		Age class 5	
	A. e. edax	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*	*A. e. edax*	*A. e. lineicaudatus*
RL	11	9	4	11	7	8	2	3	3	1
	11.57	12.01	13.43	13.62	13.69	13.92	14.12	14.80	14.55	14.82
	0.81	1.04	0.45	0.75	0.83	1.23	0.00	0.97	0.44	
	(9.88–12.82)	(10.65–13.84)	(12.78–13.82)	(12.46–14.83)	(12.41–14.94)	(12.30–16.20)	14.12	(13.86–15.79)	(14.18–15.04)	
OL	11	8	5	12	8	8	2	2	3	1
	10.55	10.81	11.74	11.73	11.98	12.33	12.46	12.94	12.46	12.72
	0.51	0.59	0.54	0.43	0.54	0.86	0.57	0.03	0.43	
	(9.72–11.22)	(10.15–11.78)	(11.22–12.62)	(11.22–12.58)	(10.90–12.56)	(11.18–13.64)	(12.06–12.86)	(12.92–12.96)	(12.11–12.94)	
OCW	8	5	5	11	7	7	2	2	3	1
	7.53	7.96**	7.53	8.03**	7.57	7.99**	7.79	8.00	7.86	7.86
	0.16	0,30	0,16	0,21	0,31	0,24	0,07	0,23	0,04	
	(7.30–7.74)	(7.59–8.34)	(7.38–7.75)	(7.78–8.50)	(7.10–7.88)	(7.66–8.40)	(7.74–7.84)	(7.84–8.16)	(7.83–7.90)	
ML	10	8	4	12	8	8	2	2	3	1
	17.62	18.06	19.52	19.55	19.71	20.40	21.09	21.49	21.58	20.66
	1.06	0.74	0.70	0.74	0.99	1.17	1.12	0.58	0.54	
	(15.99–19.44)	(17.18–19.22)	(18.47–19.96)	(18.30–20.70)	(18.09–21.00)	(18.40–21.78)	(20.30–21.88)	(21.08–21.90)	(21.23–22.20)	
mTRL	10	9	5	12	8	8	2	3	3	1
	6.90	7.34**	6.82	7.47**	7.15	7.22	7.45	7.60	7.04	7.16
	0.20	0.36	0.22	0.20	0.32	0.19	0.64	0.35	0.02	
	(6.64–7.38)	(6.90–7.99)	(6.48–7.05)	(7.00–7.66)	(6.64–7.58)	(6.86–7.40)	(7.00–7.90)	(7.22–7.91)	(7.02–7.05)	
MDL	10	7	5	12	8	8	2	3	3	1
	3.65	3.77	4.14	4.10	4.12	4.52	4.60	4.87	4.76	5.44
	0.29	0.33	0.35	0.31	0.37	0.37	0.57	0.43	0.31	
	(3.18–4.20)	(3.22–4.20)	(3.63–4.54)	(3.76–4.54)	(3.42–4.55)	(4.04–4.98)	(4.19–5.00)	(4.58–5.36)	(4.42–5.04)	

was conducted with the aim of reducing the dimensionality of morphometric data and exploring the variation between samples of *A. e. edax* and *A. e. lineicaudatus* (Table 2). Principal components (PCs) were extracted from the variance–covariance matrix and computed using $\log_{10}$-transformed variables. Statistical significance of the PC was evaluated following the Broken-stick test (Peres-Neto et al. 2005). All multivariate statistical analyses were conducted in PAST (Hammer et al. 2001).

Ecological niche modeling.—We developed 3 ecological niche models (ENMs): 1 for each named taxon and 1 including the pooled samples of *Andinomys*. We followed the same modeling protocol in each case. Occurrence records were obtained from museum collections and personal field catalogs (Appendices I and II). Since spatial autocorrelation (an inherent feature in data sets from museum collections and field observations) may influence the predictions of distribution models, we performed a spatial filtering of occurrence points (Kramer-Schadt et al. 2013), randomly selecting records to produce a sample without contiguous occurrence cells (minimum distance between points was 3.4 km).

We used a "presence-only" modeling approach, the Mahalanobis Typicalities, which is commonly used in classifying remotely sensed imagery (Foody et al. 1992). It involves the calculation of a similarity metric based on the Mahalanobis distance algorithm. Distances were computed using the multidimensional mean conditions of known localities described by the environmental predictors and the covariance between these predictors (Farber and Kadmon 2003). Typicality probabilities are derived by rescaling Mahalanobis distances to values from 0 to 1, where pixels with values equal to 1 show environmental conditions identical to the multivariate mean (Eastman 2012). Examples of application of Mahalanobis Typicalities to environmental suitability modeling include those of Rodríguez-Soto et al. (2011), Li and Fox (2012), and Torres et al. (2015). We implemented Mahalanobis Typicalities using the software Idrisi v17 Selva (Eastman 2012).

For modeling, we first considered all 19 bioclimatic variables available in WorldClim (Hijmans et al. 2005), downloaded at a resolution of 2.5 arc-minutes for continental South America. We also included elevation, using a layer from the SRTM database (http://srtm.usgs.gov/) downloaded at a resolution of 90 m, as well as slope and aspect variables derived from elevation. All variables were interpolated to a resolution of 2.5 arc-minutes (ca. 9 km in the study area). In all cases, spatial error associated with the geographic location of the occurrence records (an inherent error of data collections from some museum specimens) was lower than such resolution.

Given that environmental variables are frequently intercorrelated (Graham 2003), we selected fewer uncorrelated variables by means of a PCA, using the values of all environmental variables at occurrence localities of *Andinomys*. We examined variable correlations on those components accounting for at least 95% of the variation in occurrence data, and selected the variable with the highest loading on each component, provided that its correlation exceeded 0.70. Ten replicates with each modeling technique were performed with the reduced set of variables, selecting randomly 70% of occurrences for training and 30% for testing on each run.

Predictive power was assessed by the mean value of the continuous Boyce index (Boyce et al. 2002; Hirzel et al. 2006), a measure developed for models without absences or pseudo-absences. For this, the prediction is divided into a number of

Table 2.—Principal component analysis of craniodental measurements of young specimens (age classes 2 and 3, $n = 21$) of *Andinomys*: *A. e. edax* ($n = 10$), *A. e. lineicaudatus* ($n = 11$). * and ** indicate a principal component (PC) significant at $P \le 0.05$ or $P \le 0.01$, respectively, under the Broken-stick test.

Variables	Eigenvectors					
	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
MSL	−0.9533	−0.0277	0.0847	0.0571	0.0831	0.0280
PL	−0.9442	−0.1294	0.1242	0.0339	−0.1621	−0.0595
DL	−0.8896	−0.2975	0.0574	0.0804	−0.0892	−0.1148
PB	−0.6562	0.2469	0.4696	−0.0938	−0.4586	0.0432
MTRL	−0.6267	0.6504	0.0698	−0.0806	0.1437	0.1192
IFL	−0.7455	−0.3083	−0.4314	0.0949	0.1412	−0.0870
AW1	−0.6375	0.2412	−0.4049	−0.3948	0.2963	−0.1697
AW2	−0.5247	0.7289	−0.2596	−0.0475	−0.1113	0.0871
ZP	−0.4998	−0.4097	0.5864	−0.3315	0.1225	−0.1197
ZB	−0.8087	0.1960	−0.3285	−0.3251	−0.1538	0.0879
RW2	−0.6279	−0.4047	−0.3291	−0.1937	−0.4243	0.2047
NL	−0.7605	−0.3806	0.2779	−0.1574	0.2051	0.1452
RL	−0.7656	−0.1967	0.0610	0.1091	0.3289	0.4367
OL	−0.8481	−0.1717	−0.1354	−0.0568	−0.0009	−0.3417
OCW	−0.6367	0.5565	0.1709	0.4084	−0.0052	−0.1347
ML	−0.9296	−0.1464	0.1427	0.1618	0.0449	−0.0858
mTRL	−0.5079	0.7887	0.1903	0.0055	0.0951	−0.0074
MDL	−0.7246	−0.2700	−0.2582	0.5262	−0.0496	0.0418
Eigenvalue	9.887	2.884	1.481	0.956	0.775	0.497
% of variance	54.928	16.021	8.225	5.312	4.304	2.763
Broken-stick eigenvalue	3.495**	2.495*	1.995	1.662	1.412	1.212

classes (10 here) representing increasing suitability ranges, and the number of test points falling into each class is counted. Then a predicted-to-expected frequency (PE) is obtained for each point considering the total area covered by each class in the study area. The continuous Boyce index is finally obtained by computing the Spearman's rank between PE and the class rank. This index ranges from −1 to 1, with values near zero indicating an essentially random prediction (Hirzel et al. 2006; Sattler et al. 2007). In addition, we performed another model comparison, evaluating the differences in the mean values of predicted suitability for cells actually containing occurrence localities (Fitzpatrick et al. 2013). The best models should show higher values of predicted suitability in those cells associated with localities of occurrence. Differences in metrics between models were tested by means of the Wilcoxon matched-pairs test for related samples.

The spatial projections obtained were trimmed by the summed extent of ecoregions harboring 2 or more occurrence localities, which can be considered as the area that can effectively be occupied by the species (Soberón and Peterson 2005; Barve et al. 2011). Finally, we obtained a binary prediction (presence-absence) selecting the minimum suitability value of occurrence points as a threshold for habitat suitability (Pearson et al. 2007).

Spatial and environmental niche analysis.—First, we compared and evaluated the response curves of the variables contributing more for ENM building in each of the nominal forms, looking for coincident variables and similar behaviors. Second, to evaluate differentiation in the geographical space of *A. e. edax* and *A. e. lineicaudatus*, we documented the geographic overlap between niche models (as a measure of the geographical space potentially shared by the 2 forms) and computed the number of records that each ENM predicted for its own nominal form and for the other (i.e., inter-predictability sensu Martínez-Gordillo et al. 2010). Third, to determine whether the different forms can be distinguished on the basis of ecological space, we performed a nonmetric multidimensional scaling (NMDS) by extracting values for 19 ecological variables at 500 random points within the individual ENMs. We executed the "autopilot" function in PC-ord (McCune and Mefford 1997), setting the "medium" options for "speed vs. thoroughness" and the Sørensen (Bray–Curtis) option for the distance measure. The autopilot function was chosen as it allowed for the automated execution of multiple runs, the consequent identification of the best solution at each dimensionality, and tests for significance (Table 3). Then, we repeated the NMDS analyses specifying 3 dimensions and the configuration judged superior by the autopilot results; this procedure helped us to speed up the convergence on a minimum stress and avoid local minima. Last, we determined if niche models of the 2 nominal forms provided a better fit (as indicated by the Boyce index) to the known distribution as compared to models based upon the combined (lumped) data set (Raxworthy et al. 2007). All geographical analyses and value extractions were performed with the geoprocessing tools of the ArcView ver. 10.3 computer packages.

Genetic and phylogenetic analyses.—Genetic and phylogenetic analyses were based on an 801-base pair fragment of the cytochrome-*b* gene. We gathered 21 sequences following the protocol detailed below; 2 others were retrieved from GenBank (accession numbers in Fig. 2 and Appendix III). Geographic coverage was relatively broad; it included sequences from specimens of *Andinomys* collected at 12 localities in Argentina, Chile, and Bolivia (Fig. 1; Appendix III). A sequence of *Punomys*, the sister genus of *Andinomys* (Salazar-Bravo et al. 2013), was used as the outgroup. We generated partial cytochrome-*b* sequences using primers MVZ 05 and MVZ 16 (da Silva and Patton 1993) following the protocol outlined in Cañon et al. (2010). Amplicons were purified and sequenced by Macrogen Inc., Korea. New sequences were deposited in GenBank (KY608037–KY608056).

Sequence alignment was performed with Clustal as implemented in MEGA 6 (Tamura et al. 2013) using the default values for all alignment parameters. Aligned sequences were subjected to a Bayesian analysis (Rannala and Yang 1996) performed in MrBayes 3.1 (Ronquist and Huelsenbeck 2003), by means of 2 independent runs with 5 heated and 1 cold Markov chains each. The HKY + G model, selected with jModelTest (Darriba et al. 2012), was specified; 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, with trees being sampled every 1,000 generations. Log-likelihood values against generation time were plotted to check that the runs converged on a stable log-likelihood value. The 1st 25% of the trees sampled were discarded as burn-in; the remaining trees were used to compute a 50% majority rule consensus tree and to obtain posterior probability (PP) estimates for each clade.

Observed percentage of sequence divergence, between pairs of local samples and clades (see below), was calculated with MEGA 6 (Tamura et al. 2013) in the form of *p*-distances ignoring those sites with missing data. Sequence AF159284, downloaded from GenBank and obtained from voucher specimen MSB 67192, is highly divergent from all other sequences of

Table 3.—Analysis of stress relative to dimensionality (Monte Carlo test with 50 runs) using the autopilot function in PC-ord for the nonmetric multidimensional scaling. A 3-dimensional solution was recommended to rerun the best starting configuration.

Axes	Stress in real data			Stress in randomized data			*P*
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	
1	23.302	48.977	57.677	45.729	47.890	57.677	0.0196
2	11.270	16.781	42.038	21.556	23.885	42.037	0.0196
3	6.143	6.390	8.190	17.133	17.470	17.984	0.0196

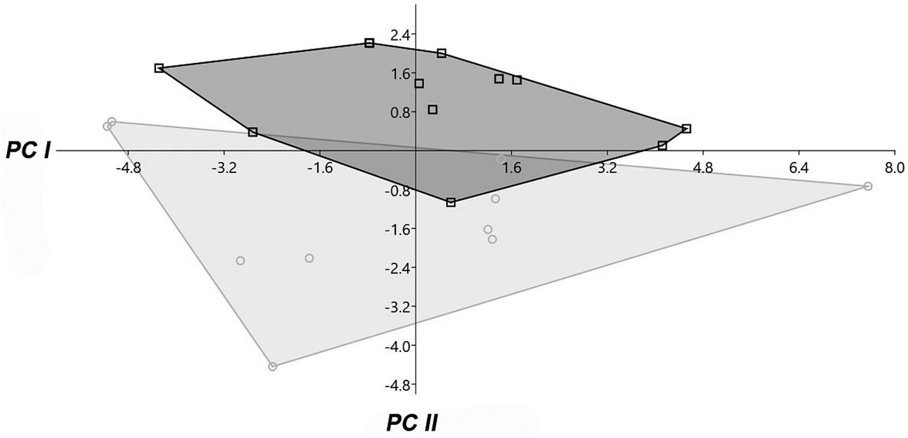

Fig. 2.—Individual specimen scores based on log-transformed values of 18 cranial measurements, projected onto the 1st and 2nd principal components extracted from analysis of young specimens (age classes 2 and 3, $n = 21$) of *Andinomys* from northwestern Argentina. Open gray circles: *A. e. edax*. Open black squares: *A. e. lineicaudatus*. Character loadings and the variance explained by each of the 1st 6 principal components appear in Table 2.

Andinomys (6.7%; while the rest of the sample diverges on average by 3.2%), despite being recovered in one of the clades. This sequence also has 15 unique nonsynonymous substitutions, so we excluded it from all estimates of sequence divergence.

RESULTS

Morphological and morphometric analyses.—We did not find qualitative external characters that consistently differentiated *edax* and *lineicaudatus*. Specimens from high-elevation, arid and semiarid environments of the study area show paler pelages, more tinged by gray, and consistently lack the midventral line on their tails. Brownish pelage and richer colors characterize specimens from more humid and lower-elevation localities of the geographic range of *Andinomys*; in these specimens a midventral line may or may not be present. In addition, specimens with intermediate pelage colorations occur in high-altitude grasslands in the watershed of pre-Andean mountain chains, which separated humid environments on eastern slopes from arid and semiarid habitats on western slopes. Qualitative skull characters differentiating both forms were not evident, nor did we find morphological differences between similar-aged samples.

The univariate morphometric analysis indicated that *lineicaudatus* averaged larger than *edax* for some of the measurements analyzed (Table 1). This trend can be seen in some cases for all, or most, age classes (TL, MSL, CIL, BL, PL, PB, AW1, AW2, BB, RL, OL, OCW, ML, mTRL, and MDL). Notwithstanding, only AW2 and OCW differed significantly between forms in at least 3 of the 5 defined age classes (Table 1).

The PCA corroborated the univariate analysis (Fig. 2; Table 2); no group of *Andinomys* specimens was clearly segregated in the morphospace. The 1st 3 PCs summarized 79.17% of the total variation but only PC I (54.92% of the variance) and PC II (16.02%) were judged statistically significant by the Broken-stick test (Table 2). PC I was mostly a size component, as the variables representing cranial lengths (e.g., MSL, PL, DL, and OL) had equal sign and loaded heavily on this axis. Specimens of both forms widely overlapped on this component. PC II better separated individuals of both nominal forms (mainly owing to the variables MTRL, AW2, OCW, and mTRL), but some overlap was also evident (Fig. 2). This PC indicated that *lineicaudatus* had proportionally larger molar series, occipital condyle width, and posterior alveolar width, whereas *edax* had a comparatively broader zygomatic plate and rostral width.

Ecological niche modeling.—Models obtained separately for each subspecies mostly showed north–south and high elevation–low elevation segregation (Fig. 3). The nominal form *edax* has a larger and more continuous area of potential distribution, which extends from southern Perú to northwestern Argentina, and occupies mostly high-elevation, arid and semiarid environments. In contrast, *lineicaudatus* potentially occupies southern areas from southern Bolivia to southernmost northwestern Argentina, mainly in humid and lower-elevation areas. This potential distribution is smaller than that of *edax* and shows a patchier configuration. Both models overlap in a narrow strip, at intermediate elevations, mostly in northwestern Argentina (Fig. 3).

The model obtained with the pooled samples mostly coincided with that of the 2 separate forms, but appeared less continuous and more extensive in Chile compared with the model for *edax*; and more extensive to the south and failing to reach the lower belts of Yungas forest, compared with the model of *lineicaudatus* (Fig. 3). The model for the pooled data set showed higher values of the Boyce index than models fitted separately for *edax* and *lineicaudatus* ($Z = 2.8$ and $P < 0.005$ for lumped data set versus *lineicaudatus*; $Z = 2.40$ and $P < 0.05$ for lumped data set versus *edax*, Wilcoxon matched-pairs test; Fig. 4). In contrast, no differences between groups were observed for the mean values of habitat suitability (Fig. 4).

Spatial and environmental niche analysis.—The PCA conducted on the occurrence localities of *Andinomys* (Supplementary Data SD2) revealed 3 and 4 uncorrelated variables as relevant in the model building of the forms *edax* and *lineicaudatus*, respectively. Seasonality in temperature (ST), elevation (E), and annual precipitation (AP) were important in models for both nominal forms, whereas exposure of the slopes was also relevant in the *lineicaudatus* model (Fig. 5). We observed a segregation of habitat suitability for both nominal forms along E, with optimal habitats for *edax* mainly located in higher areas and for *lineicaudatus* mainly distributed in lower-elevation localities; however, there was a broad overlap of habitat suitability between 2,500 and 4,000 m. For AP and ST the overlap was even more pronounced, with habitat suitability for both forms quickly declining at values above 800 mm of AP, and with the suitability for the form *edax* indicating a broader tolerance to ST values (Fig. 5). Four variables were also relevant in model building when considering the entire data set. In this case, only ST was coincident with models for both nominal forms and exposure of the slope (ES) with the *lineicaudatus* model. The steepness of the slope (SS) and the temperature of the coldest month (TCM) were important variables only in this model.

The geographic continuity between niche models of *edax* and *lineicaudatus* was clear, but the geographic overlap between them was minimal (less than 6%), indicating practically no shared geographic areas (see also Fig. 3). This lack of overlap was also indicated by the inter-predictability percentages, with just 26% of the records of *edax* being recovered by the model for *lineicaudatus*, and only 11.7% for the opposite comparison.

The ecological space, as characterized by the NMDS on the 19 environmental variables, did not clearly separate the 500 random points within individual ENMs of both nominal forms (Fig. 6). The 3-dimensional solution (final stress: 6.13495; final instability: 0.00001; number of iterations: 68) accounted for 98% of the represented variance (r^2 Axis 1 = 36.2%, Axis 2 = 39.9%, Axis 3 = 22.1%).

Genetic and phylogenetic analyses.—The phylogenetic analyses recovered 4 main genetically divergent clades (Fig. 7): 1 highly supported (PP = 1) clade corresponding to haplotypes recovered from specimens from Bolivia, northern Chile, and northernmost northwestern Argentina (here referred to as northern clade 1 [NC1]; sequence AF159284 falls in this clade), a 2nd clade (here labeled as NC2) formed by a single haplotype recovered from specimen MACN 26443, which was collected at the same locality (Quebrada Alumbriojo) as specimen CNP 2364 whose haplotype falls in NC1, and 2 clades from central–southern northwestern Argentina (here southern clade 1 [SC1; PP = 1] and southern clade 2 [SC2; PP = 0.99]). Relationships among these 4 clades were unresolved; NC1 and NC2 were sister to each other, but this relationship lacks significant support (PP = 0.54; Fig. 7). NC1 and NC2 included specimens morphologically assignable to *A. e. edax*, whereas SC1 and SC2 included specimens morphologically referable to *A. e. lineicaudatus*. As such, neither nominal form was recovered as monophyletic with statistical support. NC1 is more variable than the other 2 clades, which each include multiple haplotypes; observed *p*-distance average values are: 1.6% for NC1, 0.1% for SC1, and 0.3% for SC2. The observed genetic distances between clades are moderately high: comparisons involving NC1 are 4.5%, 4.8%, and 4.5% with NC2, SC1, and SC2, respectively; between NC2 and SC1 is 3.3%; between

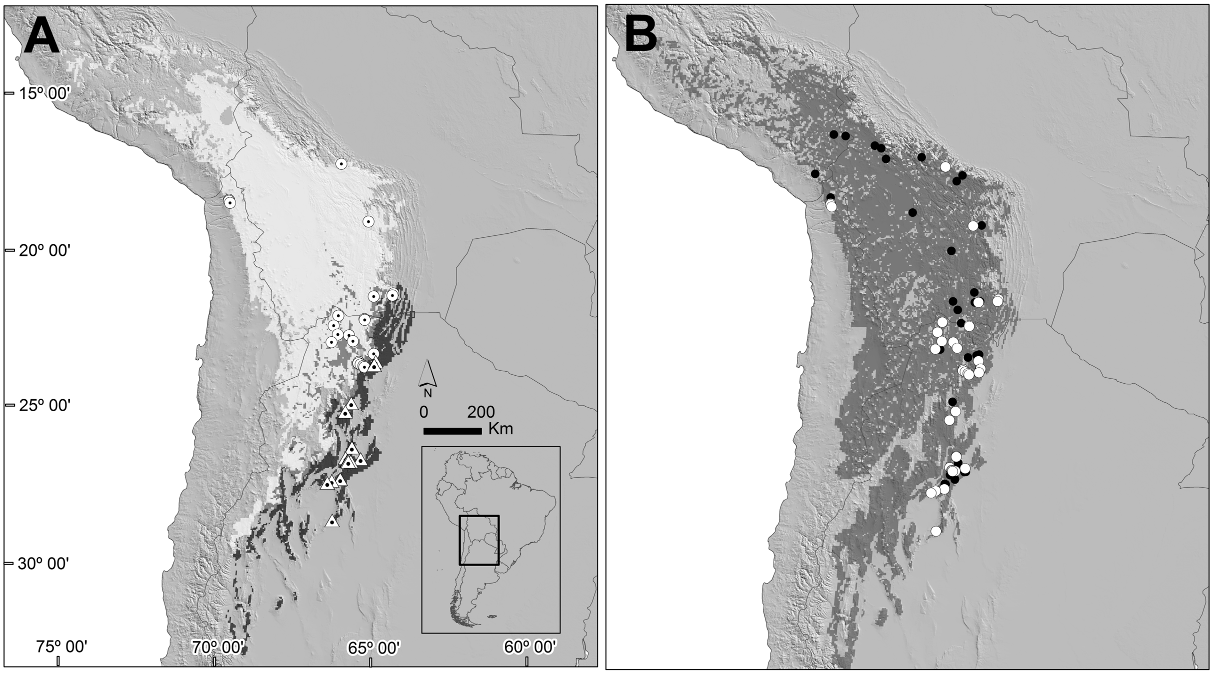

Fig. 3.—Map of the central Andes in South America showing the geographic projections of niche models for *Andinomys*. A) Models obtained for the 2 subspecies separately. Circles with a midpoint indicate locality records used to model *edax*. Triangles with a midpoint indicate locality records used to model *lineicaudatus*. Light gray-shaded areas represent the distribution model of *edax*. Black-shaded areas represent the distribution model of *lineicaudatus*. Dark gray areas represent areas of overlap for both models. B) Model obtained with the pooled data set. White circles show locality records used to model *Andinomys* as a single species. Black points indicate all the known locality records for *Andinomys*. The dark gray tone corresponds to the distribution model.

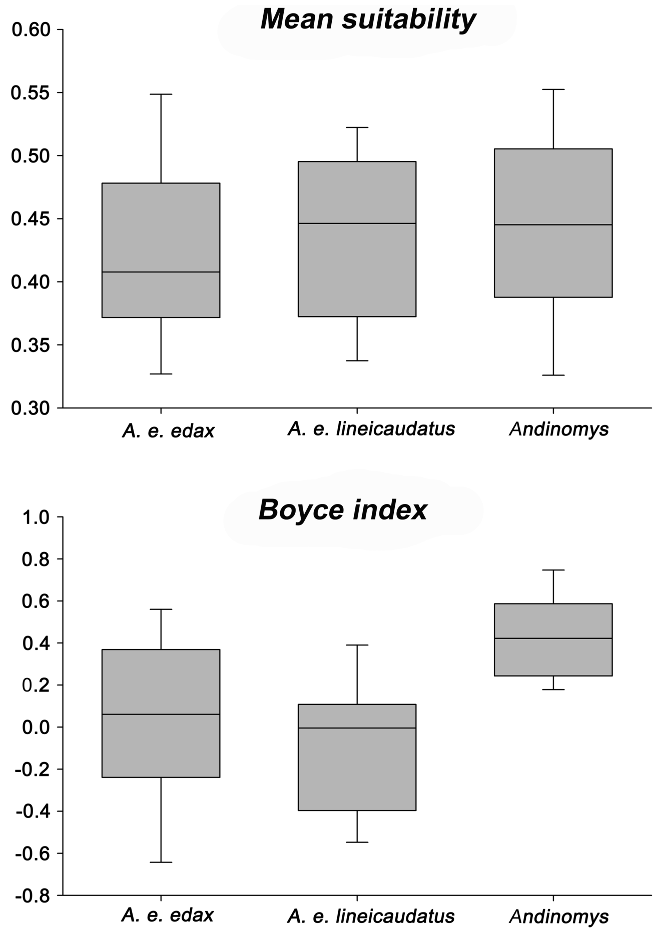

Fig. 4.—Boxplot of 2 performance measures of niche models, minimum suitability (top) and the Boyce index (bottom) for the nominal forms of *Andinomys* (*edax* and *lineicaudatus*) and for the pooled data set. Significant differences (as judged by the Wilcoxon matched-pairs test) were observed only for the *Andinomys* pooled data set model on the Boyce index.

NC2 and SC2 is 3.1%; and the comparison between the 2 southern clades SC1 and SC2 is 3.2%.

DISCUSSION

Traditionally considered to be monospecific, *Andinomys* was regarded as a highly distinct lineage within the sigmodontine radiation and provisionally treated as Sigmodontinae incertae sedis by several authors (e.g., D'Elía et al. 2007; Martínez et al. 2012). Recent analyses, including both mitochondrial and nuclear DNA sequences and a broader taxonomic sampling, recovered a clade formed by *Andinomys* and *Punomys* (Parada et al. 2013; Salazar-Bravo et al. 2013; Schenk et al. 2013). This clade is 1 of the main lineages of the sigmodontine radiation and has been recently ranked at the tribal level (Salazar-Bravo et al. 2016). The distinctiveness of *Andinomys* was also highlighted by its peculiar cranial and dental characters (Hershkovitz 1962; Steppan 1995), being only superficially similar with *Punomys* (Salazar-Bravo et al. 2013).

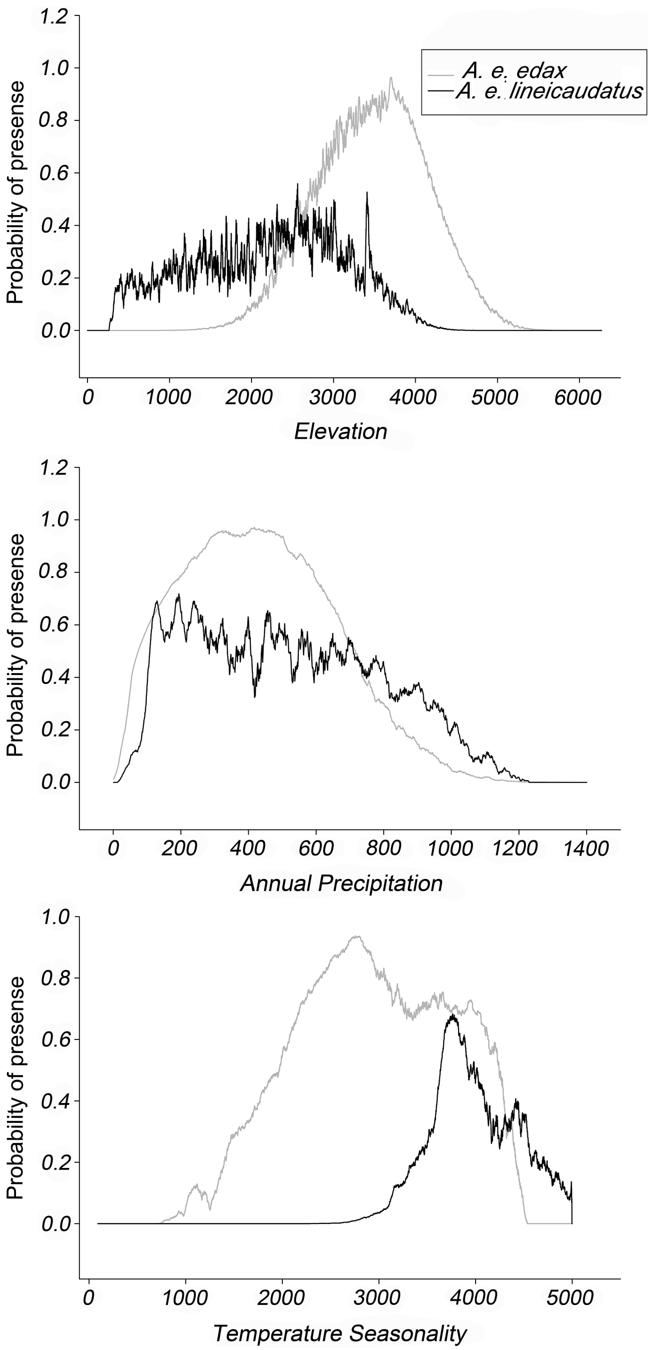

Fig. 5.—Graphical representation of habitat suitability of the nominal forms of *Andinomys* (*edax* and *lineicaudatus*) considering the 3 coincident variables selected as most relevant for model construction by the principal component analysis.

Since the revisionary works of Pearson (1958) and Hershkovitz (1962), who both viewed this genus as monospecific, only Díaz (1999) and Díaz and Barquez (2007) have suggested the recognition of 2 species, *A. edax* and *A. lineicaudatus*. These latter authors proposed this taxonomic scenario on the basis of 2 characters, namely the midventral line on the tail and a foot length > 30 mm in *lineicaudatus*, and their supposed sympatry in Maimará, Jujuy province, Argentina (Díaz and Barquez 2007).

In this study, we evaluated the status of the nominal forms *edax* and *lineicaudatus*, as delimited by Díaz (1999) and

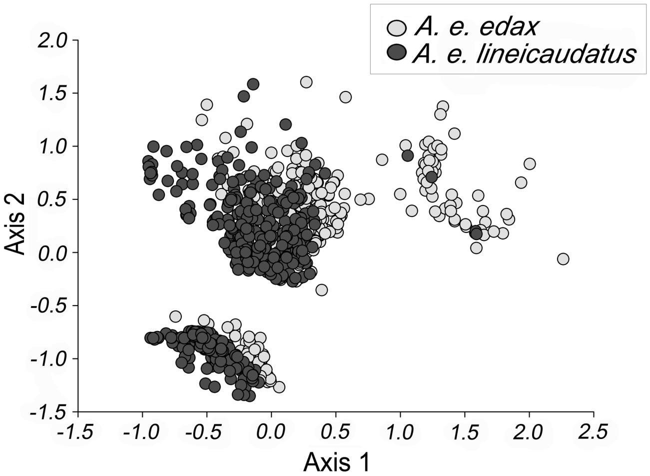

Fig. 6.—Scores for 500 random points based on log-transformed values of 19 environmental variables, projected onto the 1st and 2nd axis of the nonmetric multidimensional scaling for each of the nominal forms of *Andinomys* (*edax*—light gray circles, and *lineicaudatus*—dark gray circles). Percentage of variance explained by each of the 1st 2 axes was 36.2% and 39.9%, respectively.

Díaz and Barquez (2007), on the basis of morphological and genetic variation, as well as environmental niche preferences. We followed de Queiroz (2007) in conceptualizing species as separately evolving metapopulation lineages, and using distinct operational criteria to discover and delimit species lineages. With this approach we tested the status of these 2 nominal forms integrating diagnosable, ecological, and genealogical operational criteria.

We were unable to find discrete skin and skull characters to differentiate these nominal forms (e.g., spots on the skin or cranial character states present in 1 form and absent in the other). Observed coloration patterns (e.g., paler fur in *edax*) mentioned in the literature as diagnostic or characteristic for both nominal forms, showed clinal variation that may result from distinct selective pressures along the environmental gradient (as observed for many other species: e.g., Kaufman 1974; Stoner et al. 2003; Bedford and Hoekstra 2015), with specimens from humid areas of the eastern pre-Andean slopes (those traditionally assigned to *A. e. lineicaudatus*) having darker tinges; intermediate coloration patterns were observed in specimens from geographic and environmental transitional areas. The presence of a midventral line on the tail did not seem to be a useful character state in recognizing *A. e. lineicaudatus*. We observed specimens assignable to this subspecies (by pelage coloration, geographic and environmental distribution, and genetic characteristics) with or without this line, even at the same collecting locality. Notwithstanding, the midventral line on the tail appears to be mostly absent in *A. e. edax*. Other putative differences between nominal forms, such as hind foot length, which Yepes (1935) asserted was larger in *lineicaudatus*, were not confirmed by our studies. We examined at least 5 specimens (CNP 2364, CML 372, MACN 25193, 26443, 26444) from Puna and Altos Andes ecoregions of Salta and Jujuy provinces assignable to the nominal form *edax* that show a hind foot length greater than the 30 mm threshold mentioned by Díaz and Barquez (2007) as diagnostic for *A. e. lineicaudatus*. We found hind foot length in *lineicaudatus* significantly larger only for specimens of age class 2; however, this difference pattern can even be inverted in other age classes, with *edax* having larger values than *lineicaudatus* (Table 1). We also examined specimen MACN 31.24 from Maimará assigned to *lineicaudatus* by Díaz and Barquez (2007); the hind foot length measurement on the specimen tag is 28.1 mm, below the 30 mm threshold; in addition, this specimen has pale pelage and lacks the midventral line on its tail.

Although we documented some minor morphometric differences among samples assigned to both nominal forms, differences were neither evident for most of the morphometric variables nor constant among age classes or population samples. The PCA showed some separation of *edax* and *lineicaudatus* on the 2nd PC, which was explained mainly by variation in lengths of the upper and lower molar tooth rows (significantly different only in young age classes), the alveolar width across M3, and the width of occipital condyle (both significantly different in at least 3 age classes; Table 1). However, some overlap was also evident and this component only explained 16% of the total phenotypic variation (Table 2).

The projections of niche models obtained for *edax* and *lineicaudatus* indicate some geographic segregation but also show an area of overlap in northwestern Argentina. This overlap mainly occurs in transition zones between arid and semiarid high-elevation environments on western pre-Andean slopes and the more humid and lower-elevation habitats on the eastern side of these pre-Andean ranges. This could be interpreted as indicating 2 valid species having somewhat separate geographic distributions. However, according to the Boyce index, these models do not offer a better fit to the known distribution than models based on the combined data sets. Raxworthy et al. (2007) reasoned that, in cases of divergent ecological niches for a pair of distinct species, these models should produce a better fit to their distributions when each of the candidate species is modeled separately compared to models obtained with a pooled data set.

The geographic continuity obtained for the distribution models for *edax* and *lineicaudatus* give us a "test of sympatry" over which we can evaluate their taxonomic status. Under the taxonomic hypothesis of 2 species, we should observe specimens morphologically assignable to each of the nominal forms in areas of overlap and evidence of niche differentiation, which may interrupt gene flow; neither prediction appears to be met. On the contrary, specimens from zones of overlap have intermediate morphologies, at least in pelage coloration pattern. In addition, our study failed to find environmental niche segregation between *edax* and *lineicaudatus*, with niche models of both forms showing coincidence in the most relevant environmental variables and similar behavior of the curves representing the response of the habitat suitability of the 2 forms to changing values of these variables. The NMDS also failed to segregate random samples from the niche models of both nominal forms considering 19 environmental variables (Fig. 6).

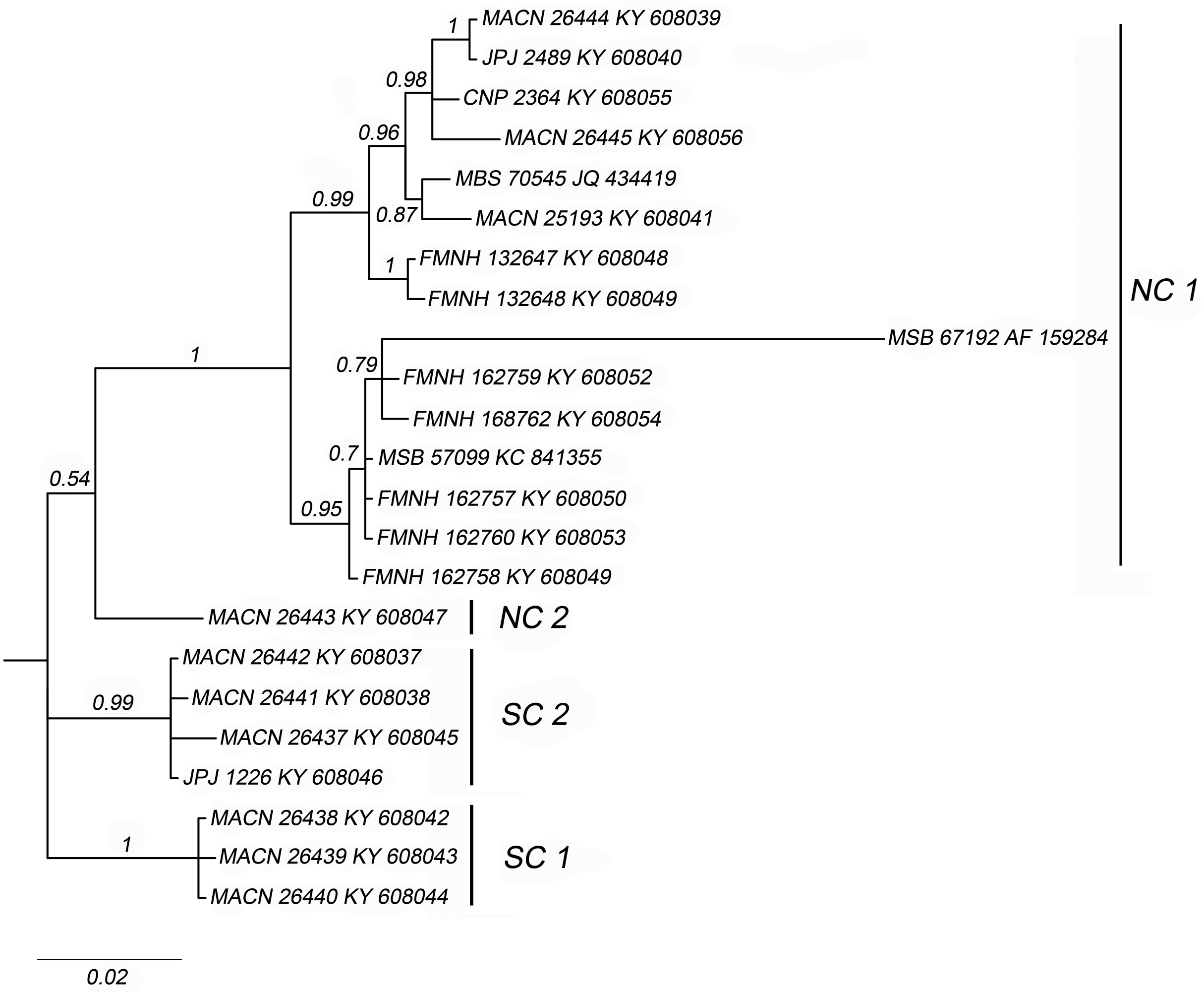

Fig. 7.—Majority rule consensus tree obtained from the Bayesian analysis of 23 *Andinomys* cytochrome-*b* gene sequences and using *Punomys* as the outgroup taxon. Numbers indicate posterior probability values of adjacent nodes. Terminal designations are the museum catalog and GenBank accession numbers, respectively. Locality data are provided in Appendix III.

Previous workers have argued for the existence of climatic niche conservatism between many sister-species pairs of plants and animals (e.g., Ricklefs and Latham 1992; Peterson et al. 1999; Prinzig et al. 2001), and this could be the case in our study system. However, such evolutionary scenarios are usually associated with allopatric speciation. A geographic barrier that consists of suboptimal environmental conditions for the species generally causes allopatry, and niche conservatism may occur in this context. Current data cannot refute that the 2 forms of *Andinomys* differentiated in allopatry and have secondarily come back into contact but evidence of environmental barriers that separated populations of *edax* and *lineicaudatus* in the past is lacking. Wiens and Graham (2005) stated that such patterns do not support the hypothesis of 2 distinct species. By this view, when 2 sets of populations share a similar climatic niche envelope, and this niche envelope also includes the intervening areas, the forms would lack spatial isolation and therefore be candidates for ongoing gene flow between them.

In addition, our genetic-based analyses failed to support the recognition of 2 species. In fact, we found evidence for 4 main clades of *Andinomys* (1 of which is genetically diverse, whereas another is formed by a single haplotype; Fig. 7). The 4 clades are somewhat divergent; values of observed *p*-distance genetic divergence between clade pairs ranged from 3.1% to 4.8%. Clades replace each other mostly along a north–south axis, and not an elevational or environmental one as predicted by the hypothesis of 2 species. This pattern of latitudinal structure characterizes several biological systems at many organization levels (communities, species, and populations) in northwestern Argentina (e.g., Navarro et al. 2009; Sandoval et al. 2010; Sandoval and Ferro 2014; Coll Aráoz et al. 2016). A similar pattern of phylogeographic structure has been noted for other species and some species groups of sigmodontine rodents in northwestern Argentina (D'Elía et al. 2008; Jayat et al. 2016).

Based on integration of morphological, ecological, and genetic analyses, we conclude that there is not convincing evidence for the recognition of 2 separately evolving metapopulation lineages within *Andinomys*. The morphological and ecological differences observed between nominal forms are subtle and inconsistent. Likewise, the pattern of variation of the mitochondrial genome fails to support 2 main groups. In this context, we think that the recognition of a single species is the taxonomic scheme that best matches the data. Under this scenario, observed patterns of variation are seen as resulting from having old populations distributed across a large and environmentally heterogeneous region.

It remains unclear how historic events have influenced populations of *A. edax*. All known fossil localities for *A. edax* are located in areas where the species occurs today, despite the dramatic environmental fluctuations that occurred during the Late Quaternary (Ortiz and Jayat 2007). This suggests that Late Pleistocene glacial cycles, with recurring displacements of vegetation belts on mountain slopes, would have had a relatively minor influence on its geographic distribution (Ortiz and Jayat 2007; Ortiz et al. 2011). Nevertheless, the pattern of cytochrome-*b* variation, with distinct and mostly allopatric clades showing relatively high divergence, indicates that past events probably fragmented populations of *A. edax*. Additional surveys in areas of elevational and latitudinal overlap of both taxa, coupled with a broader phylogeographic study based on additional genetic markers, surely will expand our understanding of these processes, their influence on the evolutionary and biogeographic history of *Andinomys*, and the taxonomic status of its populations.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Toothwear age classes of *Andinomys*.

Supplementary Data SD2.—Relevant environmental variables used in construction of distributional models for the 2 nominal forms of *Andinomys* (*edax* and *lineicaudatus*).

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Appendix I

List of *Andinomys* specimens examined. Acronyms for Argentinian institutions and personal catalogs are as follows: Colección Mamíferos Lillo (CML), Tucumán; Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires. JPJ: field number of J. Pablo Jayat to be deposited at MACN. Localities are listed in alphabetical order. Asterisks (*) indicate specimens used in the principal component analysis.

Andinomys edax edax (*N* = 37)—ARGENTINA. Jujuy Province: Abra Pampa (CML 1220); "Cuesta del Hurón," 29 km W of Cieneguillas, on Hwy Nº 64 (CML 7364, 7365, 7367*); Guairazul, 4,107 m (MACN 26445); km N of Rinconada, on the road to Timón Cruz (CML 7366, 7368); La Laguna, 4,500 m. Sierra de Zenta, E of Maimará (MACN 27.125); La Laguna, Sierra de Zenta, 4,500 m (MACN 27.85); Maimará (CML 109, 111, MACN 31.38); Maimará, 2,230 m (MACN 27-83, 27-84); Maimará, 2,300 m (CML 372, 373); Maimará, 2,500 m (MACN 31-24, 31-25, 31-26, 31-27*); Maimará, 3,000 m (CML 279); Mina Pan de Azúcar (CML 8162); Quebrada Alumbriojo, app. 8 km NE of Santa Ana, 2,900 m (CNP 2364; MACN 26443*); Sierra de Tilcara, El Hueco, 21 km SE Tilcara, 3,100 m (CML 8462*, 8463*); Sierra de Tilcara, El Matadero, 26.2 km SE Tilcara (CML 8464*); Sierra de Zenta, 4,500 m (MACN 31-114); Sierra de Zenta, 4,500 m (MACN 32-58*, 17822); Tilcara, 2,400 m (MACN 17562, 17563*, 17564*); Tres Cruces, 4,000 m (CML 380); Salta Province: 9 km NW Lizoite, 3,959 m (JPJ 2489; MACN 26444*); 13 km NW Lizoite, 4,246 m (MACN 25193). CHILE: Putre, Belén (UACH 7022); Putre, Chapiquiña (UACH 3623).

Andinomys edax lineicaudatus (*N* = 32)—ARGENTINA. Catamarca Province: Andalgalá, junction of the rivers Minas and Candado, 2,600 m (CML 4814); km 33 of the Hwy Nº 47, S of Capillitas, 2,500 m (JPJ 718*); Otro Cerro, 3,000 m (MACN 20261); Río Vallecito, 1,500 m (MACN 50-422); Jujuy Province: Abra de Cañas, El Monolito, 1,700 m (CML 1805); Abra de Cañas, Parque Nacional Calilegua, 1,710 m (MACN 19542*, 19543); Cerro Hermoso (MACN 19.554); Salta Province: app. 15 km W Escoipe, on Hwy Nº 33, 2,680 m (MACN 26438*, 26439*, 26440); Campo Quijano (MACN 17.565); Tucumán Province: 17 km W of Tafí (CML 9371); 20.6 km W of Tafí (CML 9372); 20.6 km W of Tafí, 3,024 m (CML 9373); Aconquija, 3,000 m (MACN 29.250*, 29.251*); app. 10 km S of Hualinchay, on the road to Lara, 2,300 m (JPJ 752, 1226*; MACN 26441, 26442); on the road to Amaicha, km 83 (CML 670*); on the road to Amaicha, km 98, Hwy Nº 307 (CML 2221, 2406); Carapunco, km 81 of the Hwy Nº 307, 2,960 m (MACN 26437); Cerro San Javier, 2,000 m (MACN 26.147*, 26.148); El Infiernillo (MACN 17.566*); Infiernillo, 3,000 m (CML 688, 689); Hualinchay, on the road to Cafayate, 1,861 m (JPJ 254); km 98 Hwy 307 (CML 2222); La Ciénaga, 2,600 m (CML 10015*); Sierra de Tafí Viejo, Tucumán, 2,000 m (MACN 33.85).

Appendix II

List of locality records used to model distributions of *Andinomys*.

Andinomys edax edax

1.- 16.5 km NW Colomi, 3,500 m (Cochabamba, Bolivia) 17.23330º S, 65.9500' W.
2.- Arica, ca 72 km E & Chapiquina, 10 km S & Putre, 22 km S, 3,650 m (Tarapaca, Chile) 18.41670º S, 69.55000 W.
3.- El Cabrado, 3,700 m (Chuquisaca, Bolivia) 19.08330º S, 65.08330 W.
.- La Cabrada [type locality].
4.- Narvaez, ca 10 km by rd W, 2,200 m (Tarija, Bolivia) 21.38333º S, 64.29167º W.
5.- 61 km E Tarija (by road), Rancho Tambo, 2,100 m (Tarija, Bolivia) 21.45000º S, 64.31667º W.
.- Rancho Tambo, 61 km by rd E Tarija, 2,100 m.
6.- 4.3 km E Iscayachi, 3,750 m (Tarija, Bolivia) 21.48333º S,

64.91667º W.
.- 4.5 km E of Iscayachi, 3,750 m.
7.- "Cuesta del Hurón", 29 km al W de Cieneguillas, sobre ruta prov. 64. 3,835 m (Jujuy, Argentina) 22.10000º S, 66.05000º W.
.- Cuesta del Hurón, 29 km al O de Cienegüillas, sobre ruta provincial Nº 64, 3,835 m.
.- Cuesta del Hurón, 29 km O Cieneguillas sobre ruta provincial 64, 3,835 m.
.- Cuesta del Hurón, 29 km W Cienegüillas on highway 64, 3,835 m.
8.- 13 km al NW de Lizoite, 4,246 m (Salta, Argentina) 22.20225ºS, 65.21113º W.
9.- 9 km al NW de Lizoite, 3,959 m (Salta, Argentina) 22.23298º S, 65.20606º W.
10.- 6 km N Rinconada, camino a Timón Cruz, 4,286 m (Jujuy, Argentina) 22.41600º S, 66.20000º W.
.- km al N de Rinconada, camino a Timón Cruz.
.- Rinconada, 6 km al N, camino a Timón Cruz, 4,286 m.
11.- Mina Pan de Azúcar (Jujuy, Argentina) 22.70000º S, 66.06600º W.
.- Mina Pan de Azúcar, 13 km al S, sobre Río Cincel.
.- Pan de Azúcar Mine, 13 km S, on Río Cincel.
12.- Abra Pampa (Jujuy, Argentina) 22.72828º S, 65.70702º W.
13.- Tres Cruces (Jujuy, Argentina) 22.91600º S, 65.58300º W.
.- Tres Cruces, 4,000 m.
14.- Guairazul, 4,107 m (Jujuy, Argentina) 22.94658º S, 66.26902º W.
15.- Quebrada Alumbriojo, approximately 8 km to the northeast of Santa Ana, 2,900 m (Salta, Argentina) 23.32113º S, 64.91772º W.
16.- Tilcara (Jujuy, Argentina) 23.57677º S, 65.39359º W.
.- Tilcara, 2,400 m.
17.- Maimará, 3,000 m (Jujuy, Argentina) 23.62355º S, 65.38483º W.
18.- Maimará (Jujuy, Argentina) 23.62477º S, 65.40868º W.
.- Maimará, 2,000 m.
.- Maimará, 2,200 m.
.- Maimará, 2,230 m.
.- Maimará, 2,300 m.
.- Maimará, 2,328 m.
.- Maimará, 2,500 m.
19.- Cerro de La Lagunita (Jujuy, Argentina) 23.66280º S, 65.33547º W.
.- Cerro de Lagunita, E de Maimará, 4,500 m.
.- Cerro de Lagunita, Maimará, 4,500 m.
.- Cerro La Lagunita, Maimará, 4,500 m.
.- Cerro Lagunita, Maimará, 4,500 m.
.- La Laguna 4,500 m, Sierra de Tilcara, E de Maimará.
.- La Laguna 4,500 m, Sierra de Zenta, E de Maimará.
.- La Laguna, Sierra de Zenta (=Tilcara), 4,500 m.
.- La Laguna, Sierra de Zenta, 4,500 m.
.- Sierra de Zenta, 4,500 m.s.n.m.
.- Sierra de Tilcara, 4,500 m.
.- Sierra de Zenta.
.- Sierra de Zenta (=Tilcara).
.- Sierra de Zenta, 4,500 m.
.- Sierra de Zenta, a 4,500 m.
20.- El Hueco, 21 km SE de Tilcara (Jujuy, Argentina) 23.70750º S, 65.24555º W.
.- Sierra de Tilcara, El Hueco, 21 km SE de Tilcara, 3,100 m.
21.- El Matadero, 26 km SE de Tilcara (Jujuy, Argentina) 23.74666º S, 65.21333º W.
.- Sierra de Tilcara, El Matadero, 26,2 km al SE de Tilcara.

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1.- Cerro Hermoso (Jujuy, Argentina) 23.56666º S, 64.85000º W.
.- Cerro Hermoso (cercanías), 2,800 m.
.- Cerro Hermoso (surroundings), 2,800 m.
.- Parque Nacional Calilegua, Cerro Hermoso.
2.- Abra de Cañas (Jujuy, Argentina) 23.68213º S, 64.90149º W.
.- Abra de Cañas, 1,700 m.
.- Abra de Cañas, app. 30 km NW of Calilegua on Valle Grande Rd, 1700 m.
.- Abra de Cañas, approx. 30 km NW of Calilegua on Valle Grande Rd, 1,700 m.
.- Abra de Cañas, El Monolito, 1,700 m.
.- Abra de Cañas, Parque Nacional Calilegua, 1,710 m.
3.- Campo Quijano (Salta, Argentina) 24.90000º S, 65.63333º W.
4.- App. 15 km W Escoipe, on highway 33, 2,680 m (Salta, Argentina) 25.17410º S, 65.82536º W.
.- Aprox. 15 km al W de Escoipe, sobre Ruta Provincial Nº 33, 2,680 m.
.- Aproximadamente 15 km al W de Escoipe, sobre Ruta Provincial Nº 33, 2,680 m.
5.- Hualinchay, on road to Cafayate, 1,861 m (Tucumán, Argentina) 26.30591º S, 65.61021º W.
.- Hualinchay, sobre el camino a Cafayate, 1,861 m.
.- 10 km by road south of Hualinchay on the trail to Lara.
.- App. 10 km S Hualinchay, on road to Lara, 2,300 m.
.- Aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2,316 m.
.- Aproximadamente 10 km al S de Hualinchay, sobre el camino a Lara, 2,300 m.
6.- Amaicha del Valle, km 98, Ruta 307 (Tucumán, Argentina) 26.65958º S, 65.81791º W.
.- camino a Amaicha, km 98, ruta provincial 307.
.- km 98 Ruta Prov. 307 (Tafí-Amaicha).
.- On road to Amaicha, km 98, highway 307.
7.- Cerro San Javier, 2,000 m (Tucumán, Argentina) 26.68705º S, 65.33233º W.
.- Sierra de Tafí Viejo, 2,000 m.
.- Sierra de Tafí Viejo, Tucumán, 2,000 m.
.- Taficillo.
8.- 20 km O Tafí, 3,024 m (Tucumán, Argentina) 26.74283º S, 65.75473º W.
.- 20,6 km W of Tafí.
.- 20,6 km W of Tafí, 3,024 m.
.- Tafí del Valle, 20 km W Tafí, 3,024 m.
9.- Camino a Amaicha, km 83 (Tucumán, Argentina) 26.74375º S, 65.75541º W.
.- Camino a Amaicha, km 83, sobre ruta 307.
.- El Infiernillo.
.- El Infiernillo, 3,000 m.
.- El Infiernillo, 79 km on Route 307, at 3,000 m.
.-Infiernillo, 3,000 m.
.- on highway to Amaicha, km 83.
10.- Carapunco, km 81 de la Ruta Provincial N° 307, 2,960 m (Tucumán, Argentina) 26.75526º S, 65.74408º W.
.-Carapunco, km 81 of highway 307, 2960 m.
11.- La Ciénaga, 2,600 m (Tucumán, Argentina) 26.77138º S, 65.64916º W.
12.- 17 km O Tafí, 2,844 m (Tucumán, Argentina) 26.77708º S,

65.72875º W.
.- 17 km W of Tafí.
.- Tafí del Valle, 17 km W Tafí, 2,844 m.
13.- Río Vallecito (Catamarca, Argentina) 27.33229º S, 65.98576º W.
.- Río Vallecito, 1,500 m.
14.- Andalgalá, confluence of the rivers Minas and Candado, 2,600m (Catamarca, Argentina) 27.39403º S, 66.25963º W.
.- Andalgalá, confluencia de los ríos Minas y Candado, 2,600 m.
.- Confluencia de los Ríos Mina y Candado.
.- Confluencia de los ríos Minas y Candado, 2,600 m.
.- Confluencia ríos Mina y Candado.
15.- km 33 de la Ruta Provincial Nº 47, al S de Capillitas, 2,500 m (Catamarca, Argentina) 27.45718º S, 66.40041º W.
.- km 33 of highway 47, S Capillitas, 2,500 m.
16.- 45 km west of Chumbicha, about 3,000 m (Catamarca, Argentina) 28.65541º S, 66.24708º W.
.- Otro Cerro, 3,000 m.

APPENDIX III

List of specimens used in our phylogenetic analysis. Acronyms for institutions and personal catalogs are as follows. Argentina: Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires. United States: Field Museum of Natural History (FMNH), Chicago; Museum of Southwestern Biology (MSB), New Mexico. JPJ: field number of J. Pablo Jayat to be deposited at MACN. Localities are listed in alphabetical order. GenBank accession numbers for cytochrome-*b* sequences are provided between [] next to the collection numbers of their vouchers (i.e., specimens from which haplotypes were generated).

Andinomys edax edax (16): ARGENTINA: Jujuy Province: Guairazul, 4,107 m (MACN 26445 [KY608056]); Quebrada Alumbriojo, app. 8 km NE of Santa Ana, 2,900 m (CNP 2364 [KY608055]; MACN 26443 [KY608047]). Salta Province: 9 km NW Lizoite, 3,959 m (JPJ 2489 [KY608040]; MACN 26444 [KY608039]); 13 km NW Lizoite, 4,246 m (MACN 25193 [KY608041]). BOLIVIA: 4.3 km E Iscayachi, 3,750 m (MSB 67192, Anderson and Yates, 2000 [AF159284]); 16.5 km NW of Colomi, 3,500 m (MSB 70545 [JQ434419]); Narvaez, ca. 10 km by rd W, 2,200 m (FMNH 162757 [KY608050], FMNH 162758 [KY608051], FMNH 162759 [KY608052], FMNH 162760 [KY608053], FMNH 168762 [KY608054]); Rancho Tambo, 61 km by rd E Tarija, 2,100 m (MSB 57099; Coyner et al. 2013 [KC841355]). CHILE: Arica, ca. 72 km E & Chapiquina, 10 km S & Putre, 22 km S, 3,650 m (FMNH 132647 [KY608048], FMNH 132648 [KY608049]).

Andinomys edax lineicaudatus (7): ARGENTINA: Salta Province: app. 15 km W Escoipe, on Hwy Nº 33, 2,680 m (MACN 26438 [KY608042], MACN 26439 [KY608043], MACN 26440 [KY608044]). Tucumán Province: app. 10 km S Hualinchay, on the road to Lara, 2,300 m (JPJ 752, JPJ 1226 [KY608046]; MACN 26441 [KY608038], MACN 26442 [KY608037]); Carapunco, km 81 of the Hwy Nº 307, 2,960 m (MACN 26437 [KY608045]).