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A new living species of the genus *Ctenomys* (Rodentia: Ctenomyidae) from central-western Argentina

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Abstract

The genus *Ctenomys* Blainville, 1826 includes 68 living species of small to medium-sized (100–1200 g) caviomorph rodents of subterranean habits. During the last decade, this genus has been the subject of numerous taxonomic studies, including the description of new species and the proposal of novel synonyms. Based on phylogenetic analysis of mitochondrial DNA sequences and qualitative and quantitative morphological traits, here we review the species boundaries of the tuco-tucos of the species group of *C. mendocinus* and describe a new species. The new species is morphologically distinct from other phylogenetically and geographically close species of *Ctenomys* (e.g., *C. fochi*, *C. mendocinus*), showing several differences in their craniodental traits (e.g., proportionally longer nasals and less globose tympanic bullae). The new species occurs in montane grasslands and shrublands of northwestern Mendoza (ca. 2710 m a.s.l.) and in lowlands (ca. 1000 m a.s.l.) of the Monte Desert ecoregion in an area highly impacted by accelerated processes associated with the wine industry.

Keywords

Caviomorpha, *Ctenomys fochi*, Mendoza, Monte, Octodontoidea, Southern Andean steppe, tuco-tucos

Introduction

The genus *Ctenomys* Blainville, 1826, with 68 living species, is one of the most speciose genera of the order Rodentia. It is restricted to southern South America, ranging from southern Peru to southernmost Argentina and Chile (Bidau 2015; D'Elia et al. 2021). Based on phylogenetic analysis of mitochondrial DNA sequences and morphologic characters, different authors found that *Ctenomys* includes eight well-supported species groups and several species without clear phylogenetic relationships (e.g., Parada et al. 2011; Buschiazzo et al. 2022). During the last decade, the taxonomy of this genus received a renewed impulse, with the description of 11 species (e.g., Gardner et al. 2014; Teta and D'Elía 2020; Mapelli et al. 2022), and the redefinition of several others, including the proposition of numerous synonymies (e.g., *C. azarae* Thomas, 1903, *C. porteousi* Thomas, 1916 and *C. validus* Contreras, Roig & Suzarte, 1977 under *C. mendocinus* Philippi, 1869; *C. famosus* Thomas, 1820 under *C. coludo* Thomas, 1920; see D'Elía et al. 2021; Teta et al. 2023; Sánchez et al. 2023).

One of the groups that receive more attention (e.g., Mapelli et al. 2017; Sánchez et al. 2023; Teta et al. 2023) is the group of *C. mendocinus*, a clade containing eleven species (i.e., *C. australis* Rusconi, 1934; *C. bergi* Thomas, 1902; *C. bonettoi* Contreras & Rossi, 1982; *C. coludo* Thomas, 1920; *C. eileenae* Teta et al., 2023; *C. flamarioni* Travi, 1981; *C. fochi* Thomas, 1919; *C. johannis* Thomas, 1921; *C. mendocinus* Philippi, 1869; *C. rionegrensis* Langguth & Abella, 1970; and *C. verzi* Teta et al., 2023), and widely distributed from the Andes through central Argentina to eastern Uruguay and southernmost Brazil (D'Elía et al. 1999). As result of the revisionary work made with the species group of *C. mendocinus* new species were described (e.g., Teta et al. 2023), while others were synonymized (e.g., D'Elía et al. 2021); finally, several lineages were identified as candidate species, for which no Linnean names are available (e.g., Mapelli et al. 2017; Tammone et al. 2021; Teta et al. 2023). One of these candidate species corresponds to a lineage found in northwestern Mendoza province; first collected at a locality called Tupungato, and more recently in the nearby Valley of Arenales, Tunuyán (Slamovits et al. 2001; Parada et al. 2012; Mapelli et al. 2017; Teta et al. 2023). In previous contributions, this lineage was alternatively considered as part of *C. mendocinus* (e.g., Slamovits et al. 2001; Tammone et al. 2021) or informally referred as "Arenales" or "Arenales-Tupungato." The morphologic distinction of this lineage has not been so far assessed; as such, as it is so far identified only based on the variation of a single gene, remaining up to the current time as a candidate species.

Here, based on sequences of the cytochrome *b* gene of the mitochondrial genome, and qualitative and quantitative morphological characters of skins and skulls, we show that the individual tuco-tucos from the "Arenales-Tupungato" lineage correspond in fact to an undescribed species for which no name is available. As such, we name and describe this taxon as a new species of the *C. mendocinus* group that is sister to *C. fochi*. In addition, we discuss and consider distinctiveness and geographic distribution of two other nominal forms, including *C. fochi* and *C. johannis*, of the *C. mendocinus* species group.

Materials and methods

Species concept

As an ontological (i.e., primary) species concept, we follow the General Lineage Species Concept; under this approach, species are considered as metapopulational lineages recognized by their emergent properties (e.g., monophyly, morphological diagnosability; de Queiroz 1998, 2007). As an operational (i.e., secondary) species concept, we framed our work under the Phylogenetic Species Concept (sensu Cracraft 1983), considering that species are unique evolutionary lineages characterized by unique combinations of morphological (qualitative and quantitative) traits.

Sampling for genetic and phylogenetic analyses

Phylogenetic analyses were based on 801 bp DNA sequences of the mitochondrial cytochrome *b* gene (cyt *b*). We expanded the large matrix of DNA sequences of *Ctenomys* used by Teta et al. (2023), which includes all available sequences of specimens of the species of the *C. mendocinus* species group, representatives of all other well-established species groups of *Ctenomys* and the species without clear phylogenetic affinities, and sequences of a representative of each of the genera of Octodontidae, the sister family of Ctenomyidae, that form the outgroup. To this matrix we added several new sequences from specimens of *C. coludo* and *C. johannis* recently made available by Sánchez et al. (2023) as well as new sequences generated by us for 6 specimens of *C. fochi* and 3 specimens of the new species described here. As such, the analyzed matrix has a total of 186 sequences. Primers MVZ05 and MVZ16 (Smith and Patton 1993) were used to amplify and sequence the first 801 bp of the cyt *b* gene. Amplifications and sequences from dry skin (e.g., CFA 11621) were obtained using the combinations of primers reported in the protocol outlined in Cadenillas and D'Elía (2021). PCR products were purified and sequenced by Macrogen Inc., Korea. Genbank accession numbers and locality data for all analyzed sequences are given in Table S1.

Genetic and Phylogenetic analyses

Sequences were aligned using CLUSTAL X (Thompson et al. 1997), with alignment parameters set to default values. Sequences were trimmed to identical lengths (i.e., 801 bp) and visually inspected for stop codons and reading frame shifts. Observed percent of sequence divergence was estimated as p distances using MEGA X (Kumar et al. 2018). Phylogenetic relationships were assessed using maximum likelihood **(ML)** and Bayesian **(BA)** analyses based on the best-fit model of molecular evolution (HKY + I + G) identified with the Bayesian Information Criterion **(BIC)** using jModeltest2 (Darriba et al. 2012). ML analysis was conducted using the IQ-TREE web server (Trifinopoulos et al. 2016), with analyses based on the best fit model of molecular evolution, a perturbation strength of 0.5, and 100 unsuccessful iterations. Branch support **(BS)** was determined based on 1000 replicates of ultrafast bootstrapping. BA was performed in MrBayes 3.1 (Ronquist and Huelsenbeck 2003), with two runs consisting of three heated and one cold Markov chains each.

Runs lasted 10 million generations and trees were sampled every 1000 generations. The first 25% of the trees were discarded as burn-in and the remaining trees resulting from this analysis were used to compute a 50% majority-rule consensus tree with posterior probability **(PP)** estimates for each clade.

Specimens examined in the morphological analyses

We studied a total of 37 museum specimens of *Ctenomys* (see Appendix 1; Fig. 1) consisting of skulls and skins deposited at the following institutions: Fundación de Historia Natural "Félix de Azara" (**CFA**; Ciudad Autónoma de Buenos Aires, Argentina); Instituto Argentino de Investigaciones de Zonas Áridas (**CMI**; Mendoza, Argentina); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (**MACN-Ma**; Ciudad Autónoma de Buenos Aires, Argentina). Samples in our study included the topotypes of *C. fochi* and *C. mendocinus*.

Anatomical descriptions and cranial measurements

Anatomical terminology used to describe external and cranial traits follow Brook et al. (2022) and De Santi et al. (2020, 2021). Fur coloration was defined following the nomenclature of Ridgeway (1912). Standard external measurements were taken from field catalogs or specimen tags and included: **TOTL**, total length; **TAIL**, tail length; **HFL**, hind foot length (including the claw); **EAR**, ear length; and **W**, weight. Fifteen craniodental measurements were taken on each specimen, using a digital caliper (nearest to 0.01 mm) following the definitions provided by Contreras and Contreras (1984): **TLS**, total length of the skull; **CIL**, condyle-incisive length; **NL**, nasal length; **NW**, nasal width; **RW**, rostral width; **FL**, frontal length; **IOC**, interorbital constriction; **ZB**, greatest zygomatic breadth; **BB**, braincase breadth; **BIB**, width between the auditory meatae; **IFH**, infraorbital foramen height; **DL**, upper diastema length; **PL**, palatal length; **UIW**, upper incisors width; and **TRL**, upper toothrow length.

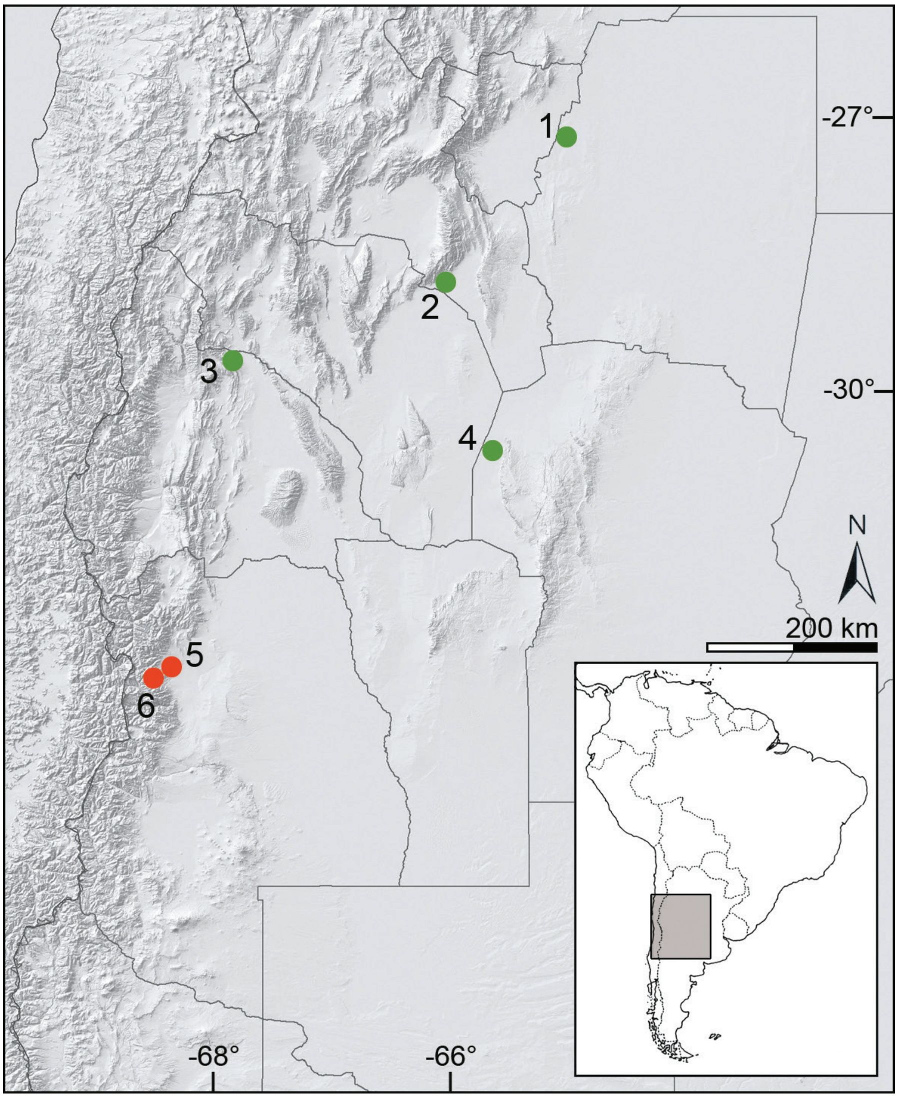

Figure 1. Map of west-central Argentina depicting the studied samples. Green and red dots correspond to *Ctenomys fochi* and *Ctenomys uco* **sp. nov.**, respectively. Numbers indicate the following localities: **1** Finca Zorro Pozo (Santiago del Estero); **2** Chumbicha (Catamarca); **3** El Chepical (San Juan); **4** Estancia La Providencia (Córdoba); **5** Finca Caicayén II (Mendoza); **6** Cajón de Arenales (Mendoza).

Morphological analyses

Morphological analyses were guided by the results of the phylogenetic analyses of molecular data (see below), geography, and current taxonomy (for a similar approach see Teta and D'Elía 2020, and Teta et al. 2023). We employed descriptive statistics (i.e., mean, minimum and maximum values, standard deviation) and multivariate statistical analyses, to assess the patterns of variation among lineages. A Principal Component Analysis **(PCA)**, based on the covariance matrix of log 10-transformed data, was conducted to investigate the main independent trends in craniometric variation. Morphometric discriminatory trends were explored using a Canonical Variate Analysis **(CVA)**. Both sexes were pooled together to obtain larger samples in the statistical analyses (for a similar procedure, see Kelt and Gallardo 1994; Teta et al. 2020, Teta and D'Elía 2020). All statistical analyses were made with the software PAST v4.13 (Hammer et al. 2023).

Results

Phylogenetic relationships

The phylogenetic analyses recovered a strongly supported monophyletic group of *Ctenomys* (BS = 100; PP = 1; Fig. 2). Within it the *C. mendocinus* species group appears well supported (BS = 98; PP = 0.96) and is formed by the same 12 main lineages as reported by Teta et al. (2023), which in-turn also shows high levels of support (Fig. 2). Relationships among these main lineages are, in general, well resolved and resemble those of Teta et al. (2023). One of these lineages, with significant support in the ML tree (BS = 99; PP = 0.76) has been called "Arenales-Tupungato," and includes the haplotypes referred by Parada et al. (2011) as "Tupungato" and by Mapelli et al. (2017) as "Arenales," as well as new haplotypes from Tupungato and Arenales generated in the current study. This group is recovered as sister group (BS = 99; PP = 0.96) of *C. fochi* (BS = 98; PP = 0.61), which contains haplotypes from topotype specimens from Chumbicha (Catamarca) and haplotypes from localities in Santiago del Estero, Córdoba, and San Juan provinces. The average genetic distance between the "Arenales-Tupungato" clade and *C. fochi* is 1.85 %. The most diverse clade within the *C. mendocinus* species group is that of *C. mendocinus* sensu stricto,

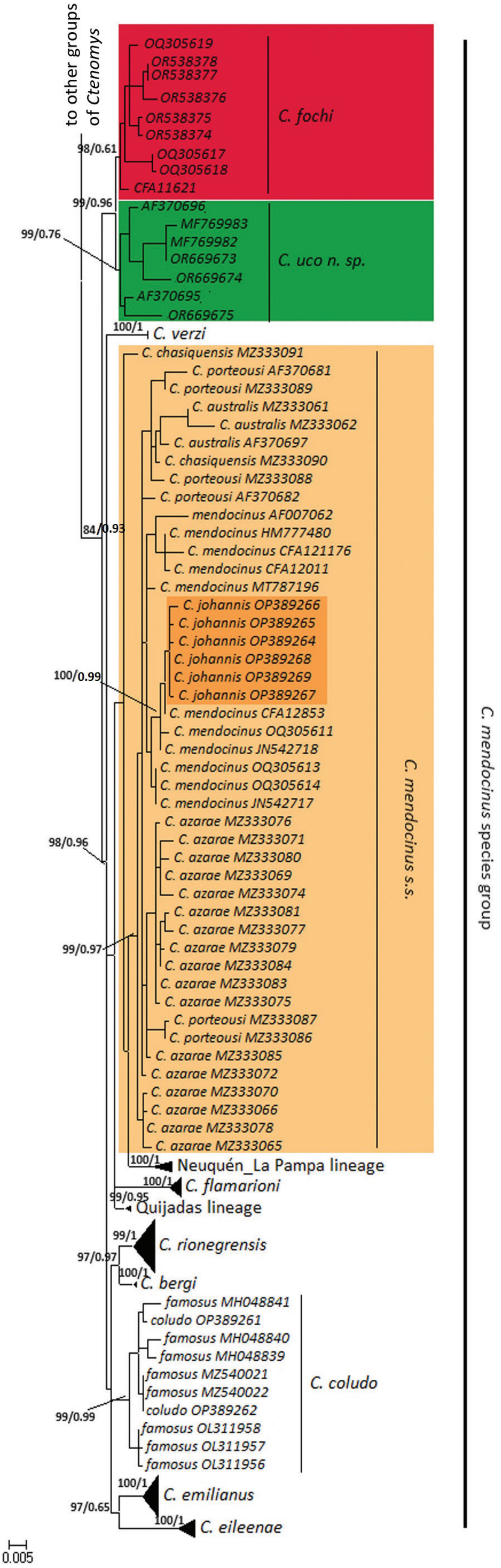

Figure 2. Phylogenetic analysis of mitochondrial DNA sequences. Maximum Likelihood tree (ln = –8860.2974) obtained in the analysis of 186 cytochrome *b* gene sequences of *Ctenomys*. Numbers indicate bootstrap (right of the diagonal) and posterior probability (left of the diagonal, found in a Bayesian analysis) values of adjacent nodes; a missing value indicates that the given node has less than 50% of posterior probability. Terminal labels indicate species name and GenBank accession numbers.

Table 1. Percentage of average genetic variation (p distances), based on cytochrome *b* sequence data, observed within and between pairs of species and lineages of the *Ctenomys mendocinus* species group.

		intraspecific	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1	*C. rionegrensis*	0.63											
2	*C. flamarioni*	0.22	2.39										
3	*C. coludo*	0.73	2.16	2.74									
4	*C. verzi*	0.00	2.22	2.60	1.92								
5	*C. emilianus*	0.47	2.56	2.62	2.27	2.40							
6	*C. mendocinus*	1.17	2.44	2.33	2.36	2.33	2.71						
7	*C. bergi*	0.13	1.45	2.26	1.67	1.64	1.98	2.08					
8	Neuquén-La Pampa lineage	0.69	2.70	2.74	2.95	2.45	2.97	2.11	2.68				
9	*C. fochi*	1.04	2.46	2.78	2.37	2.13	2.36	2.33	2.12	2.61			
10	*C. uco* **sp. nov.**	1.14	2.52	2.90	2.62	2.26	2.68	2.89	2.03	3.06	1.85		
11	*C. eileenae*	0.63	3.51	3.45	3.13	3.00	3.08	3.33	2.93	3.76	3.31	3.46	
12	Quijadas lineage	0.28	2.09	2.59	1.86	1.25	1.92	0.02	1.14	2.43	1.96	1.94	3.04

Table 2. Summary statistics (N), mean, S.D., range (min.–max.) of cranial measurements (in mm) of adult samples (N = 35) of three species of the genus *Ctenomys*. See Materials and Methods for abbreviations.

	C. fochi						***C. mendocinus***						***C. uco* sp. nov.**				
	N	Mean	S.D.	min.	max.		N	mean	S.D.	Min.	max.		N	Mean	S.D.	min.	max.
TLS	10	40.64	1.97	37.99	43.72		19	39.68	1.55	37.1	41.7		6	40.74	1.65	38.16	42.35
CIL	10	39.17	1.82	36.68	41.99		19	38.37	1.35	36.11	40.51		6	37.26	0.97	35.75	38.15
NL	10	14.32	0.94	12.61	15.61		19	13.21	0.91	11.74	14.92		6	14.81	0.58	14.25	15.58
NW	10	6.33	0.37	5.98	6.99		19	5.83	0.37	5.15	6.48		6	5.85	0.23	5.55	6.20
RW	10	9.25	0.63	8.67	10.63		19	8.77	0.46	7.91	9.49		6	9.17	0.34	8.80	9.60
FL	10	11.41	0.53	10.47	12.15		19	12.34	0.89	10.76	13.95		6	11.64	0.50	11.05	12.35
IOC	10	8.51	0.59	7.75	9.79		19	7.77	0.50	6.89	8.79		6	8.29	0.50	7.44	8.80
ZB	10	24.2	1.01	22.86	26.04		19	23.37	1.12	21.11	25.49		6	23.36	0.95	22.26	24.9
BB	10	16.73	0.74	15.82	18.35		19	16.45	0.70	15.16	17.72		6	16.68	0.75	15.65	17.55
BIB	10	26.21	0.74	24.93	27.37		19	24.93	0.97	23.3	26.24		6	25.75	1.56	23.86	27.4
IFH	10	7.63	0.53	6.87	8.51		19	7.25	0.43	6.41	7.96		6	7.63	0.23	7.30	8.02
DL	10	10.23	0.61	9.51	11.39		19	10.03	0.70	8.94	11.16		6	10.38	0.32	10.03	10.9
PL	10	16.94	1.13	15.47	18.97		19	16.63	0.82	15.2	17.81		6	17.73	1.03	16.11	18.9
UIW	10	5.99	0.46	5.52	6.99		19	5.58	0.29	5.18	6.11		6	5.78	0.30	5.25	6.06
TRL	10	8.50	0.39	7.96	9.11		19	8.43	0.46	7.61	9.19		6	9.00	0.38	8.40	9.40

which shows a genealogy that lacks geographic structure. As in Teta et al. (2023) within this clade, we recovered haplotypes assigned to the considered distinct species *C. australis*, as well as haplotypes recovered from topotype specimens of *C. johannis*, which form a well-supported subclade with haplotypes of *C. mendocinus* sensu stricto (BS = 100, PP = 0.99). Observed averages of percentage of sequence divergence between pairs of species/lineages within the *C. mendocinus* species group are shown in Table 1.

Morphological variation

Qualitative differences between samples, including the external coloration and morphology of the skull, in particular those involving the "Arenales-Tupungato" lineage, are detailed below (see the Discussion). Descriptive statistics of cranial measurements (i.e., mean, standard deviation and range are summarized in Table 2.

The first 2 axes of the PCA accounted for 78.6% of the total variance (PC1 = 69.1%; PC2 = 9.5%; Fig. 3A, Table 3). In the first principal component (PC1) all variables had loadings with positive values, indicating that this axis corresponds mostly to the general size of the skull. For the PC1, the variables with the highest loading were TLS (0.56) and CIL (0.43), followed by BIB (0.33) and ZB (0.32). On PC2, NL (0.57) has the highest loading, followed by CIL (–0.53), FL (–0.51) and IOC (0.19). Plots of individual scores show that *C. fochi*, *C. mendocinus* and the "Arenales-Tupungato" lineage mostly segregates along the PC2.

The CVA correctly classified all individuals according to their taxonomic reference. Overall, this analysis was consistent with the PCA results (Fig. 3B, Table 3). In fact, on the space defined by the first two axes (64.2% and 35.8% of the total variance, respectively) the same three sets of species were identified (i.e., *C. fochi*, *C. mendocinus* and the "Arenales-Tupungato" lineage), but with a much greater separation. The measures that contributed most to the separation among samples were BIB (0.19), NL (0.18), TLS (0.15), and FL (–0.14) on the first axis and CIL (–0.25), NL (0.17) and PL (0.16) over the second.

Table 3. Results of principal components analysis performed on adult specimens of three species of *Ctenomys* (N = 35). See Materials and Methods for explanation of abbreviations.

	PC1	PC2	CV1	CV2
TLS	0.5590	0.0397	0.1514	0.0974
CIL	0.4317	–0.5297	0.0933	–0.2549
NL	0.2578	0.5718	0.1819	0.1766
NW	0.0740	–0.0400	0.0689	–0.0384
RW	0.1405	0.0988	0.0740	0.0271
FL	0.0620	–0.5135	–0.1404	–0.0393
IOC	0.1296	0.1890	0.1121	0.0271
ZB	0.3287	–0.1622	0.1141	–0.0724
BB	0.1559	–0.0073	0.0429	0.0141
BIB	0.3305	0.1675	0.1931	0.0311
IFH	0.1025	0.0585	0.0592	0.0327
DL	0.1827	0.0448	0.0340	0.0425
PL	0.2916	0.0891	0.0606	0.1591
UIW	0.0907	0.0491	0.0605	–0.0015
TRL	0.1003	0.0991	0.0196	0.0906

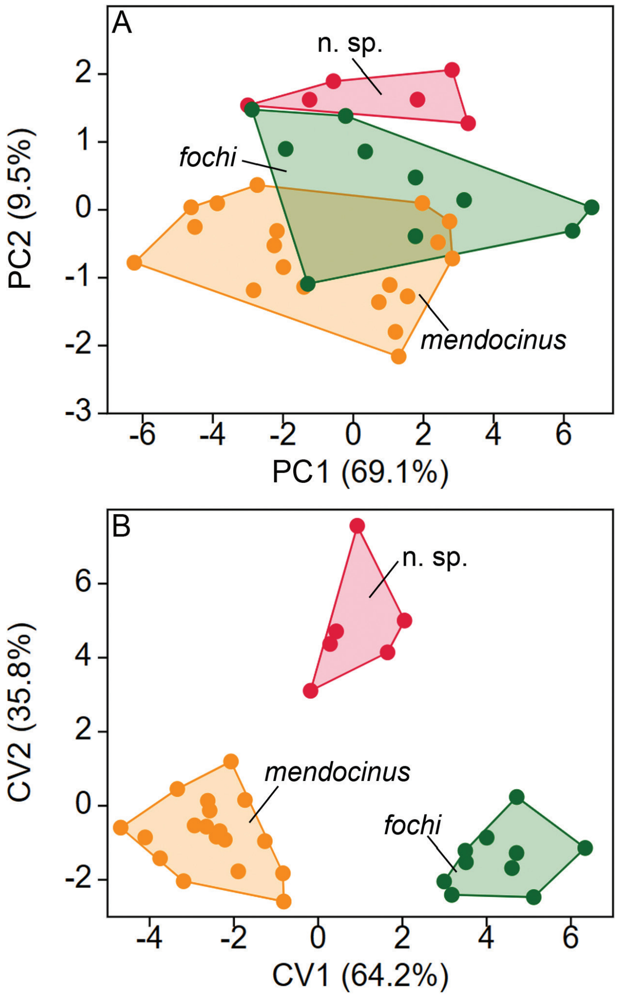

Figure 3. Multivariate statistics for three species of *Ctenomys* from west-central Argentina. Individual scores of adult specimens of *Ctenomys* from west-central Argentina (N = 35) for (**A**) principal components 1 and 2; **B** canonical variates 1 and 2, extracted from three taxonomical group discriminant function analysis.

Discussion

Phylogenetic analysis of molecular markers (reciprocal monophyly) and genetic divergences of the cyt *b* gene suggest that the Arenales-Tupungato is an independent lineage of *Ctenomys*. The evaluation of integumental and craniodental morphological traits indicate this lineage is morphologically distinct and diagnosable, all of which provide strong evidence for its recognition as a new species of the genus, which is sister to *C. fochi*. As no name is available for it, here we describe it as a new species.

Ctenomys uco sp. nov.

https://zoobank.org/797C39B9-EADE-4A18-8BD4-4875AD374443

Figures 4–7

Chresonymy.
Ctenomys mendocinus – Slamovits et al. (2001: 1709)
[*Ctenomys*] *mendocinus* 3 – Parada et al. (2011 :682)
[*Ctenomys*] Arenales – Mapelli et al. (2017: 134)
Ctenomys mendocinus Tupungato – Tammone et al. (2021: 1413)
[*Ctenomys*] “Arenales-Tupungato” lineage – Teta et al. (2023: 454)

Holotype. An adult male (CMI 7712), including skin, skeleton, and tissues, collected on 28 April 2023 by Raquel Alvarado-Larios, Pablo Cuello, Agustina Ojeda, Andrea P. Tarquino-Carbonell, and Paula Cornejo (original field number RCAL 91) (Figs 4, 5). An 801 base-pair sequence of the cyt *b* gene has been deposited in GenBank with accession number (OR669674).

Type locality. Argentina: Mendoza Province, Tunuyán Department, Cajón de Arenales, alongside Ruta Provincial N° 34, 2710 m a.s.l. (33.6213°S, 69.5112°W; Fig. 1: locality 6).

Measurements of the holotype (in mm). TOTL, 226; TAIL, 70; HFL, 31; EAR, 6.5; TLS, 39.66; CIL, 37.71; NL, 15.58; NW, 5.66; FL, 11.31; RW, 8.91; ZB, 22.26; IOB, 7.44; BB, 15.65; BIB, 23.90; IFH, 8.02; DL, 10.21; PL, 16.89; UIW, 6.06; TRL, 8.71. Weight, 110 g.

Paratype. An adult male (CMI 7739), including skin, skeleton, and tissues, collected 28 April 2023 by Raquel Alvarado-Larios, Pablo Cuello, Agustina Ojeda, Andrea P. Tarquino-Carbonell, and Paula Cornejo (original field number RCAL 92). An 801 base-pair sequence of the cyt *b* gene has been deposited in GenBank with accession number (OR669673).

Measurements of the paratype (in mm). TOTL, 215; TAIL, 64; HFL, 31; EAR, 8; TLS, 38.16; CIL, 36.36; NL, 14.28; NW, 5.81; FL, 11.05; RW, 8.94; ZB, 22.77; IOB, 7.98; BB, 16.35; BIB, 23.86; IFH, 7.65; DL, 10.03; PL, 16.11; UIW, 6.00; TRL, 8.40. Weight, 109 g.

Other examined specimens. Three adult males (CMI 7735 [original field number RCAL 87], CMI 7737 [RCAL 89], CMI 7738 [RCAL 90]) and one adult female (CMI 7736 [RCAL 88]), including skin, skeleton, and tissues, collected 26 April 2023 by Raquel Alvarado-Larios, Pablo Cuello, Agustina Ojeda, Andrea P. Tarquino-Carbonell, and Paula Cornejo at the Finca Caicayén II (33.3925°S, 69.2007°W; Tupungato Department, Mendoza Province).

Etymology. We named this species in reference to the region where the type locality lays, the Valle de Uco (Uco Valley), which includes the Tupungato, Tunuyán, and San Carlos Departments in Mendoza Province, central western Argentina; this valley is well known for its fine wines.

Morphological diagnosis. A small-sized tuco-tuco of the *C. mendocinus* species group (TOTL, 215–263 mm; TAIL, 64–79 mm; HFL, 31–36 mm: EAR, 6–8 mm; Weight, 109–138 g); dorsum Drab to Dusky Drab, which turns lighter on flanks; venter Light Brownish Drab to Light Drab, with line separating from dorsum scarcely defined; a patch above nose and forehead, blackish. Skull moderately robust, with rostrum and nasals proportionally long and narrow; premaxillary-frontal suture evident anterior to the naso-frontal suture; interorbital region with posteriorly divergent outer margins. Zygomatic arches thin, slightly divergent backwards in dorsal view; dorsal profile of cranium with a marked ventral inflection in the parietal-occipital region; incisive foramina short and narrow, recessed in a common fossa of posteriorly divergent outer borders; interpremaxillary foramen small or nearly absent; sphenopalatine vacuities nearly tear-shaped; auditory bullae moderately inflated and nearly oval, with salient auditory tubes.

Morphological description. Pelage dense, fine, and silky, about 12–15 mm long over back and rump (Fig. 4); dorsum Drab to Dusky Drab, which turns lighter on flanks; individual hairs Dark Neutral Gray to Olive Gray, except for distal tips, which are lighter and brownish. A patch above nose and forehead are blackish. Sides of head and flanks with marked agouti effect. Color of ventral pelage Light Brownish Drab to Light Drab, with line separating from dorsum weakly defined; individual hairs dark gray basally, with distal tips whitish to cream. Chin, throat, part of chest and inguinal area darker. Fur of fore- and hindlimbs colored like dorsum, except for internal sides which are lighter. Specimens from Tupungato are lighter and brownish, with sides of nose tinged with Cinnamon, while those from Tunuyán are much darker overall (Fig. 4). Mystacial vibrissae surpassing dorsal edge of pinnae when laid back alongside head; superciliary vibrissae sparse, extending to base of pinnae when laid

Figure 4. External appearance of *Ctenomys uco* **sp. nov. A** CMI 7712 (holotype), from Cajón de Arenales, Tunuyán, Mendoza, Argentina; **B** CMI 7737, from Finca Caicayén II, Tupungato, Mendoza, Argentina.

back alongside head. Ears sparsely covered with short, blackish hairs. Manus covered by short blackish hairs, except on sides where they are whitish. Frontal claws, long (ca. 10 mm in third digit) and are sparsely covered by ungual tufts. Pes broad and dorsally covered by blackish hairs; all digits with ungual tufts of whitish stiff bristles, and strong claws. Tail short (ca. 43% of head and body length), darker above than below and sparsely covered by short hairs.

Skull moderately robust with rostrum proportionally long and narrow, interorbital region with posteriorly divergent outer margins, and zygomatic arches thin and slightly divergent posteriad in dorsal view (Fig. 5). Nasals slightly bowed, comparatively long, and narrow, with nearly straight lateral margins; their anterior tips are in–line to level of anterior end of upper diastema. Premaxillo-frontal suture placed slightly anterior to the naso-frontal suture. Supraorbital ridges well defined, without defined postorbital processes on frontals. Interparietal small and nearly triangular in outline. Temporal ridges not developed. Lambdoid crest weakly developed. Rostral masseteric fossa dorsal to alveolar sheath of the I1, deep and ending in curved crest at level with premaxillary-maxillary suture. The bottom of alveolar sheaths of upper incisors visible laterally located at level of DP4. Zygomatic arch broad, with well-developed and pointed postorbital processes of jugal and a slightly expressed jugal ventral process; jugal dorsal fossa well excavated; and jugal longitudinal crest well defined. Dorsal profile of cranium with marked inflection ventrad in parietal-occipital region. Incisive foramina short, narrow, recessed in a common fossa of divergent outer borders posteriad; interpremaxillary foramen small, nearly absent. Palatal bridge with two major palatine foramina at about level of M1. Mesopterygoid fossa "V"-shaped, reaching anterad to middle portion of M2; bony roof of mesopterygoid fossa with two moderate nearly tear-shaped sphenopalatine vacuities. Alisphenoid-basisphenoid bridge thin. Buccinator-masticatory foramen mediumsized, undivided. Paraoccipital processes well developed and axe-shaped. Auditory bullae moderately inflated, nearly oval, with salient auditory tubes (Fig. 5).

Mandible robust, markedly hystricognathous, with coronoid process long and pointed; condyloid process robust, bearing a poorly developed articulation flange. Postcondyloid process with small ventrolateral apophysis. Chin process small and moderately visible in lateral view; bottom of alveolar sheath of p4 weakly protruding (Fig. 5).

Upper incisors large, robust, and orthodont to slightly ophistodont; frontal enamel surface Orange. Maxillary tooth rows slightly divergent posteriad. M3 reduced, with posterolingual face flat with an anterior protruding lobe (Fig. 5).

Karyotype. One female from "Tupungato" has a 2n = 47, FN = 68 (Massarini et al. 1991).

Morphological and genetic comparisons. *Ctenomys uco* **sp. nov.** can be differentiated from *C. coludo* by its less inflated and proportionally smaller tympanic bullae, and its proportionally larger rostrum and narrower nasals. In addition, *Ctenomys uco* **sp. nov.** has large and wide incisive foramina, while in *C. coludo* these openings are short and wide.

Ctenomys uco **sp. nov.** differs from *C. fochi* (Figs 6, 7) by its less inflated tympanic bullae, larger rostrum, and larger and narrower nasals, in which the naso-frontal suture is placed behind the premaxillo-frontal suture (vs. both sutures at the same level in *C. fochi*; Fig. 7). In addition, the nasals of *Ctenomys uco* **sp. nov.** have straight and nearly parallel outer margins, while in *C. fochi* the nasals have a barrel-shaped outline in dorsal view (Fig. 7).

Ctenomys uco **sp. nov.** can be differentiated from both *C. mendocinus* (Fig. 6) and *C. tulduco* by its smaller and less globose tympanic bullae. Additionally, the tympanic bullae are scarcely visible from above in *Ctenomys uco* **sp. nov.**, while they are visible in the dorsal view in both *C. mendocinus* (Fig. 6) and *C. tulduco*.

Ctenomys uco **sp. nov.** differs from *C. verzi* by its less robust appearance, narrower nasals and rostrum, and by the presence of an interparietal bone. In addition, *Ctenomys uco* **sp. nov.** has orthodont to slightly ophistodont upper incisors, while those of *C. verzi* are more proodont (Fig. 6).

Pairwise genetic distances with other species of the *Ctenomys mendocinus* species group range from 1.85 to 3.76 % (Table 1).

Distribution. *Ctenomys uco* **sp. nov.** is known from only two localities, including its terra typica (see above) and Finca Caicayén II, near the small village of Sarmiento (33.3925°S, 69.2007°W; Tupungato Department, Mendoza Province) (Fig. 1). Both localities are separated by ca. 39 km. Two other specimens reported in the literature were referred as from "Tupungato" (see Slamovits et al. 2001, Parada et al. 2011), a reference that could apply both to the town (33.37°S, 69.14°W) or the department of the same name; due to this uncertainty, we do not map these specimens.

Natural history. Mostly unknown. Field work indicates the species has solitary habits. The two known localities for this species are placed between 1000–2710 m a.s.l. The landscape in this area corresponds to an ecotone between the Low Monte and the Southern Andean Steppe (sensu Olsen et al. 2001), characterized by a mosaic of grasslands, shrublands, and vineyards (Fig. 8A, B). Dominant plants at Cajón de Arenales correspond to grasses and shrubs of the genera *Stipa*, *Adesmia*, *Mulinum*, *Nassauvia*, *Larrea* and *Chuquiraga* (Fig. 8A). Populations at Finca Caicayén II mostly live in anthropogenic plantations of grape-bearing vines, digging their burrows at the foot of these plants (Fig. 8B). This region presented a mean annual temperature between 10°C and 15°C and a mean annual precipitation of 300 mm concentrated in winter months (Norte 2000). Valle de Uco is characterized for its temperate climate with harsh winters, hot summers with cool nights, and its closeness to the Andes.

Figure 5. Cranial anatomy of *Ctenomys uco* **sp. nov.** Lateral (above), dorsal (below, left), and ventral (below, right) views of the skull and labial view of the mandible (middle) of the holotype of *C. uco* **sp. nov.** (CMI 7712). Scale = 5 mm.

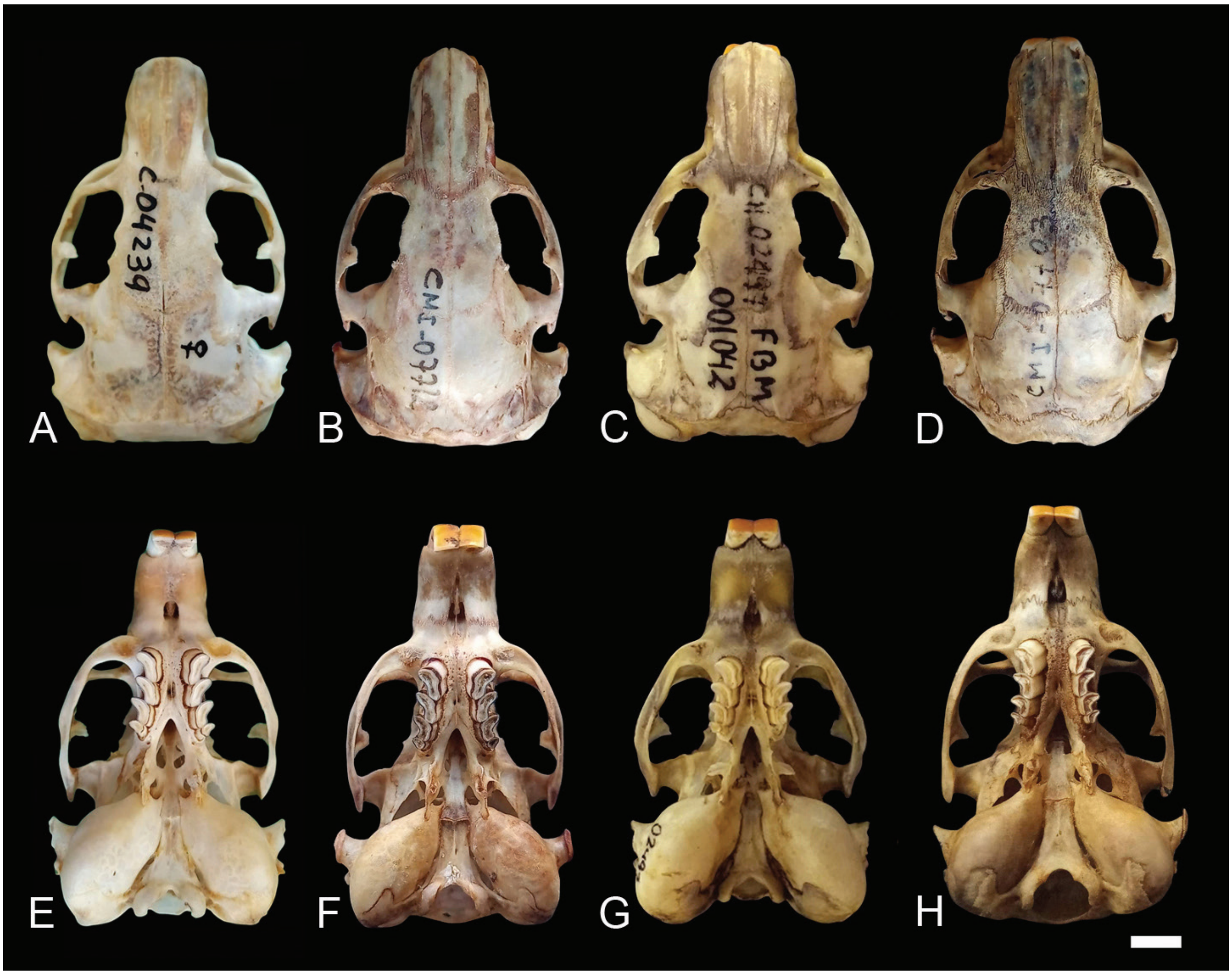

Figure 6. Cranial anatomy in four species of *Ctenomys* from west-central Argentina. Dorsal (A–D) and ventral (E–H) views of the skulls in four species of *Ctenomys* from west-central Argentina: **A**, **E** *C. fochi* (CFA-MA 12120); **B**, **F** *C. uco* **sp. nov.** (CMI 7712); **C**, **G** *C. mendocinus* (CMI 2497); **D**, **H** *C. verzi*. Scale = 5 mm.

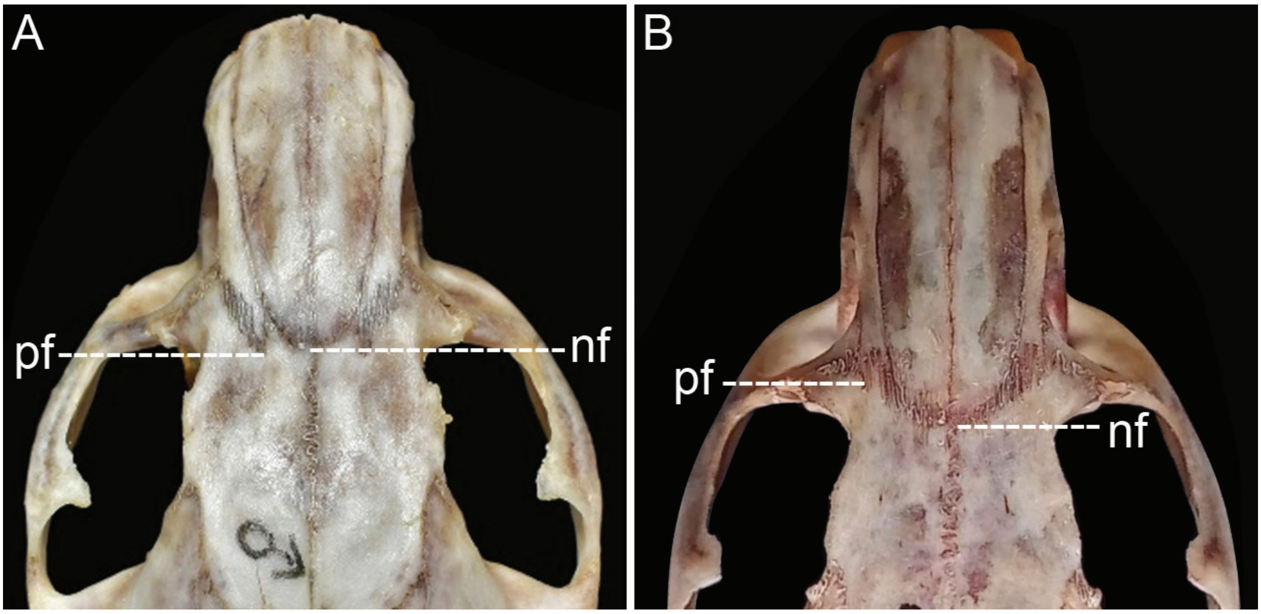

Figure 7. Selected traits of the skull anatomy in two species of *Ctenomys* from west-central Argentina. Comparative view of the nasals and rostri: **A** *C. fochi* (MACN-Ma 30875), **B** *C. uco* **sp. nov.** (CMI 7712). Abbreviations are as follows: nf, naso-frontal suture; pf, premaxillo-frontal suture.

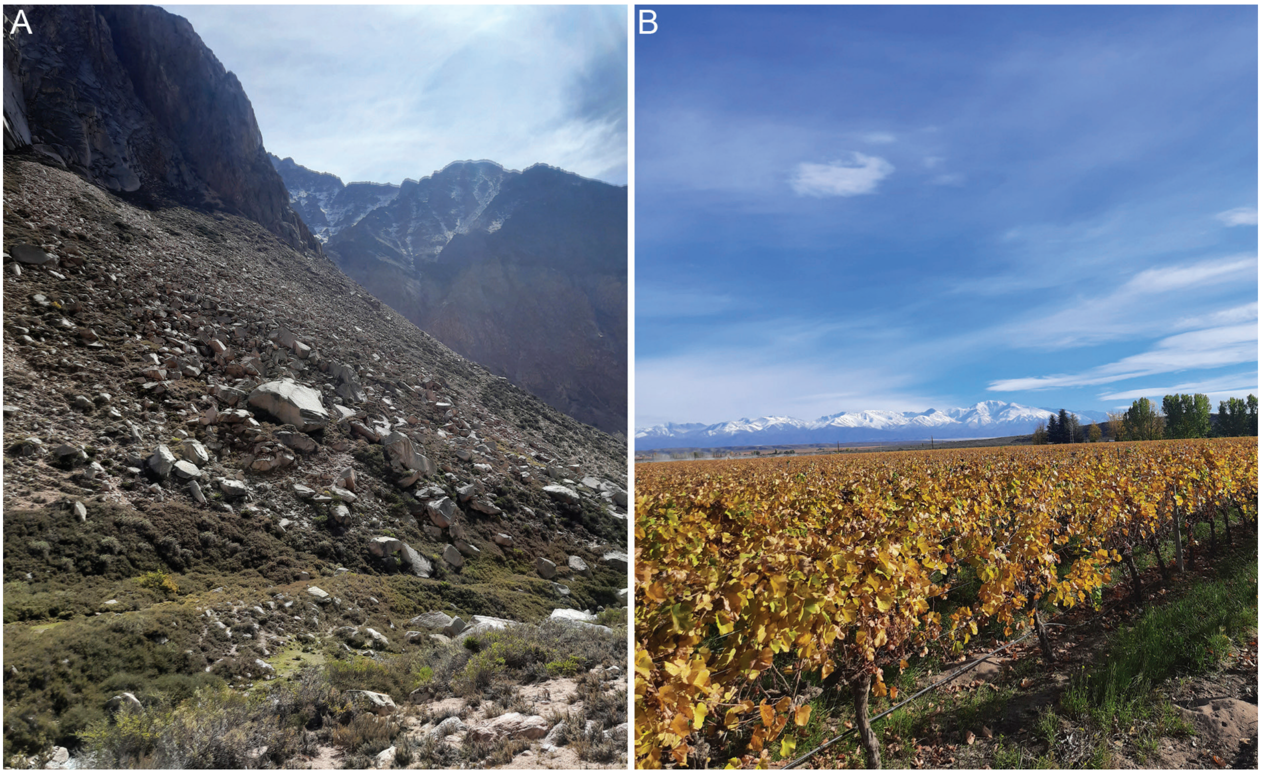

Figure 8. Views of the landscapes at the two known localities of *Ctenomys uco* **sp. nov.** **A** Mendoza, Tunuyán, Cajón de Arenales (type locality), **B** Mendoza, Tupungato, vineyards of Finca Caicayén II (note the burrows at the lower right corner on this photograph).

Conservation. *Ctenomys uco* **sp. nov.** apparently has a small geographic range (Fig. 1), which has a direct influence on its conservation status (Bidau et al. 2012; Caraballo et al. 2023). Even so, most species of tuco-tucos with restricted geographical distributions are traditionally viewed as Data Deficient (DD; see SAREM-MAyDS 2019; but see Teta et al. 2021; Caraballo et al. 2023). Similarly, given our lack of knowledge on *C. uco* **sp. nov.**, a DD categorization seems to best fit the available evidence. However, considering that *C. uco* **sp. nov.** is only known from two localities, one of them laying in an area strongly affected by the wine industry, to consider it as endangered or vulnerable seems to be more realistic. Additional field work is needed to better delineate the species distribution. Notwithstanding, it is possible that *C. uco* **sp. nov.** is present within some protected areas, including Reserva Natural Manzano- Portillo Piquenes and/or Reserva Paisajística y Natural Manzano Histórico; as said, additional field work is needed.

Final remarks. Taxonomic work with *Ctenomys* is far from complete. Ongoing studies suggest that some nominal forms will likely fall into synonymy with others, while there are still many candidate species whose distinction needs to be tested (e.g., the "Quijadas" lineage; see Mapelli et al. 2017; Teta et al. 2023), while additional field work would likely reveal additional undescribed species (e.g., Mapelli et al. 2022). There are only two other groups of Neotropical mammals undergoing a similar scenario, in which more than 8–10 species have been described in the last decade. These are species in the bat genus *Myotis* (see Novaes et al. 2023 and the references therein) and the sigmodontine rodents of the genus *Neacomys* (see Tinoco et al. 2023 and the references therein). Much of the recently discovered diversity in these two later genera is mostly cryptic and somewhat unexpected (for example, nobody would have predicted that the species richness of *Neacomys* would increase from six recognized species by 2015 to the currently 23 recognized species; Weksler and Bonvicino 2015; Mammal Diversity Web 2023). Meanwhile, the case of *Ctenomys* is distinct as its taxonomy has been largely considered as chaotic and unstable (Sage 1986; D'Elía et al. 2021), with several parts of the extensive adaptive diversification far from been resolved in terms of species boundaries (e.g., the so-called Corrientes and Boliviensis groups). Fortunately, the use of integrative approaches, together with a renewed interest in the exploration of the mammal faunas of little-known and understudied geographic areas in the southern Neotropics, have begun to reveal even more hidden diversity in species of *Ctenomys* (e.g., Gardner et al. 2014; Tammone et al. 2021; Sánchez et al. 2023; Teta et al. 2023). It is expected that, in this context, renewed interest in the taxonomy of these animals would cause new taxonomic arrangements, including the proposition of new species with additional species being recognized as either endangered or data deficient in terms of the IUCN categories.

The case of *C. fochi*, the sister species to *Ctenomys uco* **sp. nov.**, is an eloquent example of the limited ecological and systematic knowledge that characterizes most species of *Ctenomys*. During almost a century, this species was only known from four specimens, including its holotype, all coming from the species type locality (Teta and D'Elía 2019), and flipped between being considered as a distinct species or as a subspecies of *C. mendocinus* (e.g., Cabrera 1961; Bidau 2015). During the last year, individuals of this species were found in two additional localities, enlarging its known distribution ca. 200 km SE and 250 km NW (Teta et al. 2023; Jayat et al. in press), and was included for the first time in a phylogenetic analysis, recovering it as a distinct species within the *C. mendocinus* species group (Teta et al. 2023). Finally, herein we report a fourth locality (El Chepical, Valle del río Gualcamayo, Jáchal, San Juan), which enlarges its distribution ca. 240 km SW from the previous nearest known locality. Thus, when all these localities are considered together, in only one year, our knowledge about the distributional range of *C. fochi* extended from a single geographical point to an area of more than 61,900 km^2. This situation likely would change the conservation status of this nominal form, which was considered as Data Deficient by Sánchez and Tomasco (2019; see Jayat et al. in press).

Based on the results of the phylogenetic analysis conducted here, in which haplotypes of specimens assigned to *C. johannis* are nested within the clade corresponding to *C. mendocinus* and the morphological evidence provided by Teta et al. (2023) that indicates that phenotypically *C. johannis* is not distinct from *C. mendocinus*, we formally include *C. johannis* as a synynom of *C. mendocinus*. Under this assumption, the northern distribution of *C. mendocinus* extends to southern San Juan province, Argentina. Additionally, in that area, the species *C. tulduco* Thomas, 1921 is also known. Although this last species has not been so far included in any phylogenetic study, the description provided by Thomas (1921), including its external coloration and size of the tympanic bullae, is indicative that this nominal form is likely also a synonym of *C. mendocinus*. In fact, according to Sanchez et al. (2023), some samples from Pedernal (San Juan), a locality from which Thomas (1921) referred some specimens to *C. tulduco* in the original description of this species, are indistinguishable from *C. johannis* (= *C. mendocinus*; this work). Beyond the case of *C. tulduco*, whose synonymy under *C. mendocinus* has yet to be formalized, in just two years, the following nominal forms have been placed in the synonymy of *C. mendocinus*: *C. azarae*, *C. johannis*, *C. porteousi*, and *C. validus* (D'Elía et al. 2021, Teta et al. 2023; this study), indicating that just as there is still diversity to be described at the species level and the distinction of other nominal forms needs to be tested. As such, we expect that the taxonomy of *Ctenomys* will remain unstable during the next few years as more diversity is discovered and more descriptions result.

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Appendix 1

List of specimens included in morphological comparisons. See "Materials and methods" for explanation of acronyms.

Catalog number	Species	Locality
CFA-MA 12120	*Ctenomys fochi*^{t}	Argentina, Catamarca, Capayán, Chumbicha
CFA-MA 12118	*Ctenomys fochi*^{t}	Argentina, Catamarca, Capayán, Chumbicha
CMI 7707	*Ctenomys fochi**	Argentina, Córdoba, Cruz del Eje, Estancia La Providencia
CFA-MA 12028	*Ctenomys fochi*	Argentina, San Juan, Jáchal, Valle del río Gualcamayo, El Chepical
CFA-MA 11621	*Ctenomys fochi*	Argentina, San Juan, Jáchal, Valle del río Gualcamayo, El Chepical
CFA-MA 12031	*Ctenomys fochi*	Argentina, San Juan, Jáchal, Valle del río Gualcamayo, El Chepical
MACN-Ma 30872	*Ctenomys fochi*	Argentina, Santiago del Estero, Giménez, Isca Yacu, finca Zorro Pozo
MACN-Ma 30873	*Ctenomys fochi*	Argentina, Santiago del Estero, Giménez, Isca Yacu, finca Zorro Pozo
MACN-Ma 30874	*Ctenomys fochi*	Argentina, Santiago del Estero, Giménez, Isca Yacu, finca Zorro Pozo
MACN-Ma 30875	*Ctenomys fochi*	Argentina, Santiago del Estero, Giménez, Isca Yacu, finca Zorro Pozo
MACN-Ma 30876	*Ctenomys fochi*	Argentina, Santiago del Estero, Giménez, Isca Yacu, finca Zorro Pozo
CMI 7223	*Ctenomys mendocinus**^{t}	Argentina, Mendoza, Capital, Cerro de la Gloria
CMI 2806	*Ctenomys mendocinus*^{t}	Argentina, Mendoza, Capital, Cerro de la Gloria
CMI 2650	*Ctenomys mendocinus*	Argentina, Mendoza, Godoy Cruz, San Ignacio
CMI 2664	*Ctenomys mendocinus*	Argentina, Mendoza, Godoy Cruz, San Ignacio
CMI 2658	*Ctenomys mendocinus*	Argentina, Mendoza, Godoy Cruz, San Ignacio
CMI 2804	*Ctenomys mendocinus*	Argentina, Mendoza, Luján de Cuyo, Chacras de Coria
CMI 2806	*Ctenomys mendocinus*	Argentina, Mendoza, Luján de Cuyo, Chacras de Coria
CMI 2519	*Ctenomys mendocinus*	Argentina, Mendoza, Luján de Cuyo, La Puntilla
CMI 2777	*Ctenomys mendocinus*	Argentina, Mendoza, Luján de Cuyo, La Puntilla
CMI 2812	*Ctenomys mendocinus*	Argentina, Mendoza, Luján de Cuyo, La Puntilla
CMI 2810	*Ctenomys mendocinus*	Argentina, Mendoza, Luján de Cuyo, La Puntilla
CMI 2786	*Ctenomys mendocinus*	Argentina, Mendoza, Luján de Cuyo, La Puntilla
CMI 2515	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán
CMI 2646	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán
CMI 2514	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán
CMI 2513	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán
CMI 2489	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán
CMI 2510	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán

Catalog number	Species	Locality
CMI 2817	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán
CMI 2512	*Ctenomys mendocinus*	Argentina, Mendoza, Santa Rosa, Ñacuñán
CMI 7712	*Ctenomys uco* **sp. nov.**[h]	Argentina, Mendoza, Tunuyán, Cajón de Arenales
CMI 7739	*Ctenomys uco* **sp. nov.**[p]	Argentina, Mendoza, Tunuyán, Cajón de Arenales
CMI7735	*Ctenomys uco* **sp. nov.**	Argentina, Mendoza, Tupungato, Finca Caicayén II
CMI7736	*Ctenomys uco* **sp. nov.**	Argentina, Mendoza, Tupungato, Finca Caicayén II
CMI7737	*Ctenomys uco* **sp. nov.**	Argentina, Mendoza, Tupungato, Finca Caicayén II
CMI7738	*Ctenomys uco* **sp. nov.**	Argentina, Mendoza, Tupungato, Finca Caicayén II
*Specimen not included in multivariate statistical analyses; h, holotype; p, paratype; t, topotype		

Supplementary Material 1

Table S1

Authors: Alvarado-Larios R, Teta P, Cuello P, Jayat JP, Tarquino-Carbonell AP, D’Elía G, Cornejo P, Ojeda AA (2024)
Data type: .xlsx
Explanation notes: List of cytochrome *b* gene sequences of specimens of the *Ctenomys mendocinus* species group included in the genetic-based analyses. For each sequence, details of species/lineage (see text), GenBank accession numbers and geographic provenance are given. Sequences gathered here are indicated with an #. For these sequences catalog numbers are also provided (see collection acronyms in the main text). Species/lineage assignment follows the taxonomy discussed in the text, following Teta et al. (2023).

Link: https://doi.org/vz.74.e115242.suppl1