



An appraisal of the species richness of the *Ctenomys mendocinus* species group (Rodentia: Ctenomyidae), with the description of two new species from the Andean slopes of west-central Argentina

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Abstract

The genus *Ctenomys* of subterranean rodents is one of the most species-rich genera of Mammalia, with 66 living species currently recognized. However, the taxonomy of the genus is dynamic with several new species and new synonymies proposed during the last decade. One of the species groups that have undergone more changes in contents in the last years is the *Ctenomys mendocinus* species group. Here, based on phylogenetic analysis of mitochondrial DNA sequences and qualitative and quantitative morphological evidence, we conducted an appraisal of the species richness of tuco-tucos of the *C. mendocinus* species group, describing two new species from west-central Argentina. The new taxa are morphometrically distinctive when compared with other geographically or phylogenetically close species of the genus, showing qualitative differences in their craniodental anatomy. One of the new species is known from the eastern Andean slopes of La Rioja and San Juan provinces, occurring on montane grasslands and shrublands above 3,500 m a.s.l., while the other is endemic of southwestern Mendoza province, occurring on montane grasslands and shrublands between 2,400–2,700 m a.s.l. In addition, we include for the first time the nominal forms *C. fochi* and *C. validus* in a phylogenetic analysis of the genus *Ctenomys*, showing that both correspond to the *C. mendocinus* species group, being the second a junior synonym of *C. mendocinus*. Finally, we made some comments about other candidate species within this species group as well as highlight issues that need to be addressed to gain a robust picture of the specific richness of *Ctenomys*.

Keywords

Andean Highlands, Caviomorpha, Octodontoidea, species limits, taxonomy, tuco-tucos

Introduction

Arguably, Rodentia is the mammalian order with the most dynamic taxonomy. New species are routinely described (e.g., Rowsey et al. 2022; Zhang et al. 2022), at the time that the taxonomic status of its numerous nominal forms are changing because new species synonyms are advanced and names traditionally viewed as synonyms are considered full species (e.g., Abreu et al. 2021; Pradhan et al. 2021). As such, the species richness of Rodentia keeps increasing, although it is still far from being well characterized (for a synthesis of current trends on rodent taxonomy see D'Elía et al. 2019).

A genus that is a good representative of the scenario above mentioned is *Ctenomys* de Blainville, 1826, which is one of the most diverse of the order Rodentia (D'Elía et al. 2021). Currently, it is composed of 66 known living species, which are distributed from southern Peru to the archipelago of Tierra del Fuego in southernmost Argentina and Chile (Bidau 2015). Our knowledge about the alpha taxonomy of this genus is still far from complete (D'Elía et al. 2021) and is highly dynamic, as indicated by the fact that several nominal forms have been described in the last few years (Teta and D'Elía 2020; Brook et al. 2022; Mapelli et al. 2022), others were synonymized (Parada et al. 2012; Teta et al. 2020; D'Elía et al. 2021), or suggested as candidate species (e.g., Caraballo and Rossi 2017; Tammone et al. 2021, 2022a, 2022b). As the species of *Ctenomys* are morphologically conservative (e.g., Fornel et al. 2018), these advances have been mostly based on integrative taxonomic approaches, using karyotypic, molecular, and morphological datasets.

Based on phylogenetic studies of mitochondrial DNA sequences and morphologic traits, species of the genus *Ctenomys* are grouped into nine main species groups and several species without clear phylogenetic relationships (Parada et al. 2011; De Santis et al. 2021; see also Sánchez et al. 2019; Londoño-Gaviria et al. 2019; Leipnitz et al. 2020). Among these groups, the *C. mendocinus* species group is widely distributed through central Argentina between the Andes and the Atlantic coast (e.g., Mapelli et al. 2017), reaching eastern Uruguay and southernmost Brazil (D'Elía et al. 1999). Karyotypic studies (e.g., Massarini et al. 1991) and phylogenetic analysis of DNA sequences (e.g., Mapelli et al. 2017) show a complex evolutionary history for the *C. mendocinus* species group, which reflects the difficulty to establish species limits as well as the instability in the advanced taxonomic schemes. For instance, D'Elía et al. (2021) recently synonymized *C. azarae* Thomas, 1903 and *C. porteousi* Thomas, 1919 under *C. mendocinus* Philippi, 1869. As currently understood, six species (i.e., *C. australis* Rusconi, 1934; *C. bergi* Thomas, 1902, *C. famosus* Thomas, 1920; *C. flamarioni* Travi, 1981; *C. mendocinus*; and *C. rionegrensis* Langguth & Abella, 1970) are included within this group (D'Elía et al. 2021; Mapelli et al. 2022), but several others are likely linked to it, at least judging by their morphology and geographic distribution (e.g., *C. bonettoi* Contreras & Berry, 1982; *C. fochi* Thomas, 1919;

C. johannis Thomas, 1921, *C. tulduco* Thomas, 1921, and *C. validus* Contreras, Roig & Suzarte, 1977). The status of some of these species (e.g., *C. fochi*, *C. johannis*) is dubious as their descriptions were based on few specimens and their distinction have never been evaluated with contemporaneous approaches. Additionally, analyses of DNA sequences (Parada et al. 2011; Mapelli et al. 2017; Tammone et al. 2021, 2022a, 2022b) have identified other six candidate species within the radiation of this species group that needs to be further reviewed to corroborate or refute their distinction from other species. One of these candidate species was erroneously referred in the literature as *C. fulvus* Philippi, 1860 and is found at the San Guillermo National Park, in the northernmost portion of the Andes of San Juan province (cf. Haene et al. 2001; for its reference to the *mendocinus* group, see Borghi and Giannoni 2007). A second one was recently reported for the highland areas of western La Rioja province, being documented for the Laguna Brava area (Tammone et al. 2022a). Interestingly, these two candidate species occur in the same environment above 3,500 m a.s.l., in the Central Andean Puna ecoregion (sensu Olson et al. 2001), being separated from each other by ca. 110 km. Finally, a third one was initially reported by Mapelli et al. (2017; labeled as “Las Leñas”) and later by Tammone et al. (2021; identified as “*Ctenomys* sp. 3”) and is so far known from Las Leñas Valley, southwestern Mendoza province.

In this contribution, we used cytochrome *b* (*cyt b*) sequences of the mitochondrial DNA and qualitative and quantitative morphological traits of skins and skulls to evaluate the species richness of the *C. mendocinus* species group. We describe two new species, based on the above-mentioned candidate species. One of the new species corresponds to those populations of northernmost San Juan and western La Rioja provinces, while the other encompasses the lineage of Las Leñas, in southwestern Mendoza province. Additionally, we test the phylogenetic position of *C. fochi* and *C. validus*, suggesting that both belong to the *C. mendocinus* species group and the latter is a synonym of *C. mendocinus*.

Materials and methods

Species concept

We follow the General Lineage Species Concept, which considers that species are metapopulation lineages recognized by their emergent properties (e.g., monophyly, morphological diagnosability; de Queiroz 1998, 2007), as an ontological (i.e., primary) species concept; additionally, we framed our contribution under the so-called Phylogenetic Species Concept (PSC; sensu Cracraft 1983), which considers that species are unique evolutionary lineages which exhibit unique combinations of qualitative and quantitative traits (the smallest diagnosable clusters of samples), as an operational (i.e., secondary) species concept.

Sampling for genetic and phylogenetic analyses

Genetic comparisons and phylogenetic analyses are based on DNA sequences of the mitochondrial *cyt b* gene. We used an extensive sampling of DNA sequences of specimens of the *C. mendocinus* species group; we included 164 sequences that were retrieved from all species belonging to the group (sensu D'Elia et al. 2021), five of the six candidate species, as well as from *C. fochi* and *C. validus* that likely belong to the group (see Supplementary Material 1). Of the sequences of the *C. mendocinus* species group, 17 were gathered by us as indicated below. Additionally, our sampling included sequences of each of the other 42 species of *Ctenomys* available in GenBank (by November 2022) plus *C. pilarensis* Contreras, 1993 (specimen TK66077 from the Natural Science Research Laboratory, Texas Tech University); the sequence of *C. pilarensis* was gathered by us (see below). This is, up to now, the phylogenetic study with the broadest specific sampling of *Ctenomys*. The outgroup was formed with sequences of a representative of each of the genera of Octodontidae, the sister family of Ctenomyidae, with complete sequences available in GenBank. In the light of preliminary analyses (conducted also as indicated below) we excluded three sequences downloaded from GenBank from the final analyses. Sequences MZ333073 and MZ333064 identified in GenBank as of *C. azarae* (a synonym of *C. mendocinus*; D'Elia et al. 2021) fall outside the *C. mendocinus* species group and related to *C. talarum* Thomas, 1898. These two sequences are quite similar to those of *C. talarum*; then considering that they were retrieved from specimens collected in Coronel Suárez (Buenos Aires, Argentina), and Arroyo Sauce Chico (Buenos Aires, Argentina), two areas where so far only *C. talarum* is known, they likely belong to specimens of this species. Sequence MZ333063 labeled in GenBank as *C. australis* falls outside the clade of the *C. mendocinus* species group. A close inspection of this sequence allows us to suggest that it may have some editing problems that likely affect their phylogenetic placement and it was also excluded from the analyses. Details of all sequences of the *C. mendocinus* species group used in the final genetic-based analyses are included in Supplementary Material 1. GenBank accession numbers of all sequences, including those of specimens that do not belong to the *C. mendocinus* species group, are provided in Fig. 1. Sequences acquired here (some of them from dry skins) were obtained using primers MVZ 05 and MVZ 16 (da Silva and Patton 1993) and MVZ 103 and MVZ 14 (Smith and Patton 1993) following the protocol outlined in Cadenillas and D'Elia (2021). Amplicons were purified and sequenced by Macrogen Inc., Korea. New sequences were deposited in GenBank (OQ305611–OQ305627; OQ319606).

Genetic and Phylogenetic analyses

Clustal, as implemented in MEGA 6 (Tamura et al. 2013) and using the default values for all alignment param-

eters, was employed to perform sequence alignment. Alignment was straightforward and no adjustment by eye was needed; the alignment has no gaps. The constructed matrix was subjected to Bayesian (BA; Rannala and Yang 1996) and Maximum Likelihood (ML; Felsenstein 1981) analyses. The HKY+G+I model, selected with jModelTest (Darriba et al. 2012), was specified in both analyses. BA was performed in MrBayes 3.1 (Ronquist and Huelsenbeck 2003), by means of 2 independent runs with 3 heated and 1 cold Markov chains each. 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 lasted for 10 million generations, with trees being sampled every 1,000 generations. Run convergence on a stable log-likelihood value was checked by plotting Log-likelihood values against generation time and by checking that Potential Scale Reduction Factor converged to 1. The 1st 25% of the trees sampled were discarded as burn-in; the remaining trees, sampled within the convergence zone, were used to compute a 50% majority rule consensus tree and to obtain posterior probability (PP) estimates for each clade. The ML analysis was conducted with IQ-TREE (Nguyen et al. 2015) using the online implementation W-IQ-TREE (<http://iqtree.cibiv.univie.ac.at>; Trinouopoulos et al. 2016), with perturbation strength set to 0.5 and stopping rule set to 100. Clade support was calculated with 1000 ultrafast bootstrap pseudo-replications (BS; Hoang et al. 2018). The 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.

Studied specimens in the morphological analyses

Morphological analyses of qualitative and quantitative external and cranial traits were carried out on 131 adult specimens of *Ctenomys* collected at 36 localities in west-central Argentina and northern Chile (Fig. 2; see Supplementary Material 2 for details). Studied specimens are housed in the following biological collections: Facultad de Ciencias Naturales e Instituto Miguel Lillo (CML; San Miguel de Tucumán, Argentina); 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); Natural History Museum, (NHMUK; London, United Kingdom); Universidad Nacional de Río Cuarto (CUNRC; Río Cuarto, Argentina); and Universidad Austral de Chile (UACH; Valdivia, Chile). Studied specimens correspond both to species of the group of *C. mendocinus* (e.g., *C. bergi*, *C. emilianus* Thomas & Saint Leger, 1826, *C. fochi*, *C. mendocinus*), as well as other taxa distributed in the Andean ranges of central Argentina and Chile (e.g., *C. fulvus* Philippi, 1860; *C. maulinus*

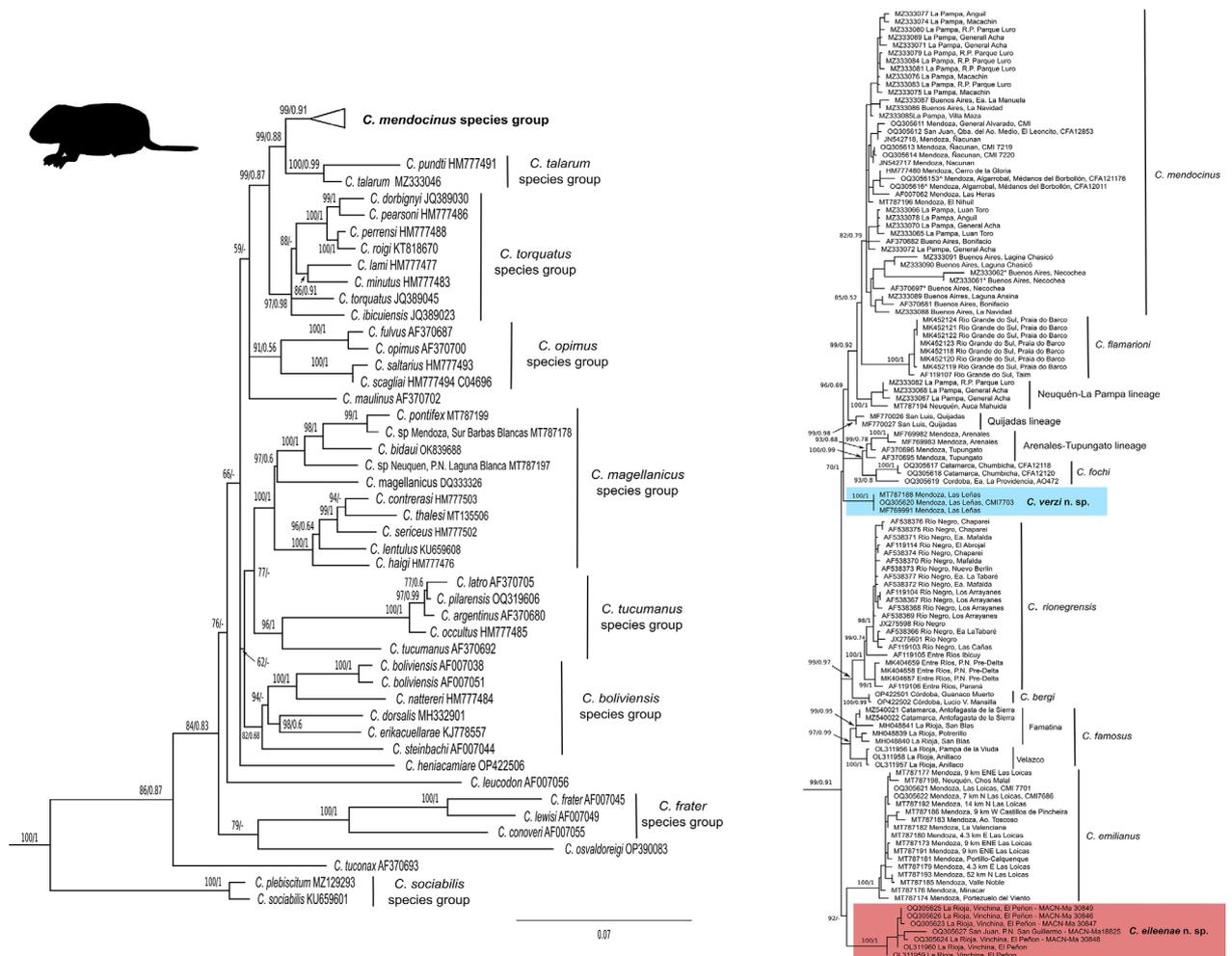


Figure 1. Maximum Likelihood tree ($\ln = -12720.876$) obtained in the analysis of 164 cytochrome *b* gene sequences of the *Ctenomys*. Numbers indicate bootstrap (right of the diagonal) and posterior probability (left of the diagonal) values of adjacent nodes; a missing value indicates that the given node has less than 50% of posterior probability; a dash indicates that the given node was not recovered in the Bayesian analysis. For clarity the tree is split into two. In the left panel the general tree of *Ctenomys* is shown (outgroup not shown); species groups (sensu D'Elia et al. 2021) are indicated with bars (the two main clades of *C. famosus* are also labeled as in Tammone et al. 2022a). In the right panel the focus is on the *Ctenomys mendocinus* species group. Terminal labels indicate species name and GenBank accession numbers. For the species of the *Ctenomys mendocinus* species group, terminal labels include Province/State/Department and abbreviated locality (see more details in Supplementary File 1). The silhouette of *Ctenomys* was taken from PhyloPic and was made available by Chloé Schmidt under a license CC BY 3.0.

Philippi, 1872). Skins and skulls of specimens of *C. coludo*, *C. famosus* and *C. knighti* Thomas, 1919 were examined through photographs (Sánchez et al. 2019; SayDS-SAREM 2019; Tammone et al. 2022a).

Anatomical descriptions and cranial measurements

Anatomical terms employed 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 Ridgway (1912). Standard external measurements were taken from field catalogs or specimen tags, including: TOTL, total length; TAIL, tail length; HFL, hind foot length (including the claw); EAR, ear length; and W, weight. Sixteen craniodental measurements were taken on each specimen with a digital caliper

(nearest to 0.01 mm), following the definitions provided by Contreras and Contreras (1984). Reported measurements are: TLS, total length of the skull; CIL, condylo-incisive length; NL, nasal length; NW, nasal width; RW, rostral width; FL, frontal length; IOC, interorbital constriction; ZB, greatest zygomatic breadth; BB, braincase breadth; MB, mastoid breadth; IFH, infraorbital foramen height; DL, upper diastema length; PL, palatal length; UIW, upper incisors width; PM4L, upper fourth premolar length; and TRL, upper toothrow length.

Morphological analyses

Morphological comparisons were guided by the results of the analyses of molecular data (see below), geography, and current taxonomy. We use descriptive statistics (i.e., mean, minimum and maximum values, standard devia-

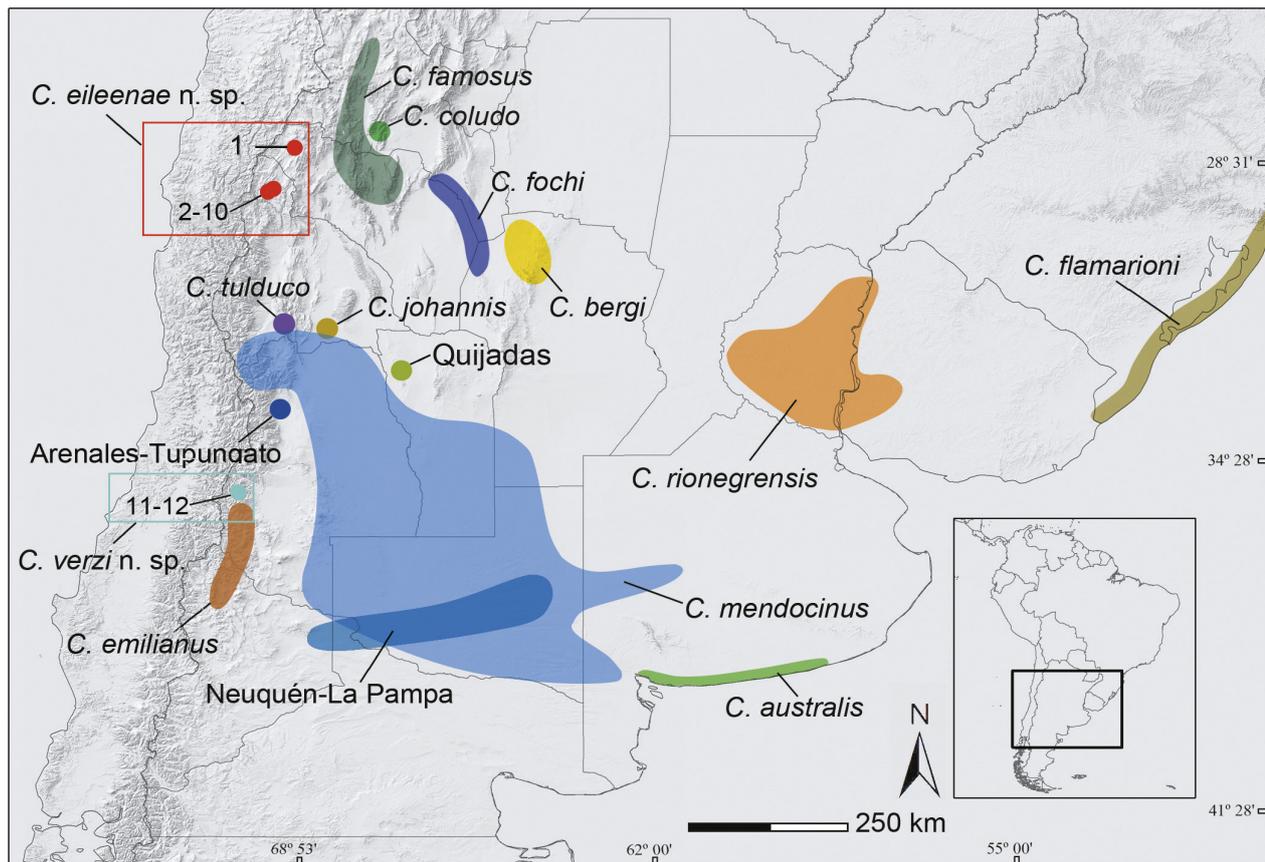


Figure 2. Map of central Argentina, southern Brazil and Uruguay, depicting the generalized distributional boundaries of the species and candidate species of the group of *Ctenomys mendocinus*. Numbers 1–10 and 11–12 correspond to the known localities for the “La Rioja-San Juan lineage,” and “Las Leñas lineage,” respectively (for reference of the numbers, see the text).

tion) and multivariate statistical analyses to assess the patterns of variation among lineages. Principal component analysis (PCA) was computed using sixteen craniodontal measurements, all of which were previously log₁₀ transformed. The PCA was conducted with exploratory aims in order to identify the contribution of each measurement to the total variance, extracting them from a variance-covariance matrix (Strauss 2010). Data from both males and females were pooled with the aim to obtain more robust samples for its inclusion in the statistical analyses (see Kelt and Gallardo 1994; Teta et al. 2020, Teta and D’Elia 2020). All statistical analyses were carried out with the software PAST v2.17 (Hammer et al. 2001).

Results

Phylogenetic relationships

The phylogenetic analyses strongly recovered the monophyly of *Ctenomys* (BS = 100; PP = 1; Fig. 1). In turn, the basal dichotomy of the clade leads on one hand to the clade formed by *C. plebiscitum* and *C. sociabilis* (BS = 100; PP = 1) and the clade formed by all other species of the genus (BS = 86; PP = 0.87). Within the latter clade, all species groups are recovered monophyletic with vary-

ing levels of support (Fig. 1). *Ctenomys pilarensis* falls within the *C. tucumanus* species group (BS = 96; PP = 1).

The clade corresponding to the *C. mendocinus* species group appears highly supported (BS = 99; PP = 0.91) and it is composed of 12 main lineages. The two haplotypes of *C. bergi* form a strongly supported clade (BS = 100; PP = 0.99), which is one of the main lineages of the *C. mendocinus* species group. *C. flamarioni* (BS = 100; PP = 1) and *C. rionegrensis* (BS = 100; PP = 1) also appear highly supported. Within the latter there are three main lineages; one (BS = 98; PP = 1) composed by haplotypes of Uruguayan specimens, which is sister (BS = 99; PP = 0.74) to the lineage composed by a single available haplotype from Ibicuy in southern Entre Rios province (Argentina), and the third one (BS = 99; PP = 1) composed by variants collected at two localities, Parana and Parque Nacional Pre-Delta, in west central Entre Rios province (Argentina). Average divergence value between the Uruguayan and the Ibicuy lineages is 0.13%, between the Uruguayan the Parana-Pre Delta lineages is 0.11% and between the Ibicuy and Parana-Pre Delta lineages is 0.14%. *C. famosus* is recovered monophyletic (BS = 97; PP = 0.99) and also shows internal geographical structure, including one clade (BS = 100; PP = 1) with haplotypes from medium elevations at the Velazco mountain chains (La Rioja) and another (BS = 99; PP = 0.95) with variants from the Famatina range (La Rioja) and Antofagasta de la Sierra (Catamarca). Average divergence value between

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

		intraspecific	1	2	3	4	5	6	7	8	9	10	11
1	Arenales Tupungato	1.00											
2	<i>C. bergi</i>	0.09	1.94										
3	<i>C. eileenae</i> sp. nov.	0.62	3.14	2.93									
4	<i>C. emilianus</i>	0.51	2.60	2.83	3.16								
5	<i>C. famosus</i>	0.86	2.37	1.97	3.17	2.53							
6	<i>C. flamarioni</i>	0.17	3.06	3.37	3.64	3.76	3.11						
7	<i>C. fochi</i>	0.85	1.86	2.46	3.47	2.62	2.74	2.88					
8	<i>C. mendocinus</i>	1.13	2.86	2.50	3.31	3.12	2.41	2.51	2.62				
9	Neuquén-La Pampa	0.75	2.94	2.88	3.68	3.26	2.83	3.01	2.97	1.98			
10	Quijadas	0.28	2.01	1.14	3.04	1.92	1.82	2.59	2.39	2.08	2.43		
11	<i>C. rionegrensis</i>	0.64	2.50	1.68	3.49	3.24	2.33	3.36	2.80	2.69	2.81	2.09	
12	<i>C. verzi</i> sp. nov.	0.00	2.08	1.71	2.99	2.47	1.93	2.82	2.35	2.33	2.42	1.25	2.30

both clades is 1.11 %. Another of the main lineages of the *C. mendocinus* species group is a clade (BS = 100; PP = 1) distributed in northern Neuquén and southern Mendoza provinces, that includes the haplotype of one individual of the type series of *C. emilianus* (see Tamonne et al. 2021). This clade is genetically homogenous (average percentage of intra clade p distance is 0.51 %) and is here tentatively referred to *C. emilianus*. Topotypic sequences of *C. fochi* form a well-supported clade (BS = 100; PP = 1) that is sister (BS = 93; PP = 0.80) to an haplotype of one individual (AO472) from Córdoba province. The latter differ on average by 1.21 % from sequences of *C. fochi*. Haplotypes from the nearby candidate species identified by Mapelli et al. (2017) as “Arenales” and by Parada et al. (2011) as “Tupungato” form a clade (BS = 93; PP = 0.68) that is sister (BS = 100; PP = 0.99) to the clade containing the haplotypes of *C. fochi* and the specimen from Córdoba. Average genetic divergence between the “Arenales-Tupungato” clade and that containing haplotypes from topotypes of *C. fochi* and specimen AO472 is 1.86 %. A geographically wide clade (BS = 82; PP = 0.79) is that corresponding to *C. mendocinus* sensu stricto; this clade shows some genealogical structure although lacks geographic structure. Haplotypes from paratypes of *C. validus* (OQ305615 and OQ305616) fall within the clade of *C. mendocinus* sensu stricto. Moreover, three haplotypes (AF370697; MZ333061, MZ333062) labeled in GenBank as *C. australis* also fall in the clade of *C. mendocinus* sensu stricto. Another main lineage (BS = 100; PP = 1) of the *C. mendocinus* species group is formed by sequences from a specimen of Auca Mahuida in eastern Neuquén Province, referred as *C. sp. 4* by Tamonne et al. (2021) and three other haplotypes from two localities, General Acha and Reserva Provincial Parque Luro, from east-central La Pampa Province (labeled by Carnovale et al. 2021 as *C. azarae*, which is now regarded as a synonym of *C. mendocinus*); here, we refer to this clade as of the “Neuquén-La Pampa lineage”. Remarkably, haplotypes of other specimens collected at the two mentioned Pampean localities (see collection details in Carnovale et al. 2021: table 1) form part of the *C. mendocinus* s.s. clade.

Finally, there are three main lineages of the *C. mendocinus* species group with no available name. One of these (BS = 99; PP = 0.98) is formed by sequences retrieved from specimens from Quijadas (San Luis) which are here informally referred to, following Mapelli et al. (2017), as the “Quijadas lineage”. The second one is formed by haplotypes from specimens collected in the mountains of La Rioja and San Juan (BS = 100; PP = 1) and is here referred to as the “La Rioja-San Juan lineage”. The last one, which include the haplotypes of three individuals collected in Las Leñas, Mendoza province, form a well-supported clade (BS = 100; PP = 1) that is here referred to as “Las Leñas lineage”.

Relationships among the 12 main lineages of the *C. mendocinus* species group remain mostly unresolved; the single relationship that gets significant support in both analyses is that of the clade formed by *C. rionegrensis* and *C. bergi* (BS = 99; PP = 0.97). Both analyses recovered a clade formed by the “Quijadas lineage”, the “Neuquén-La Pampa lineage”, *C. flamarioni*, and *C. mendocinus* sensu stricto, but it only gets significant support in the ML tree (BS = 96; PP = 0.69); the same occurs for the clade formed by the “Neuquén-La Pampa lineage”, *C. flamarioni*, and *C. mendocinus* sensu stricto (BS = 99; PP = 0.92). Another relationship observed in both analyses, but that does not get significant support in any tree (BS = 85; PP = 0.92) is that of *C. flamarioni* and *C. mendocinus* sensu stricto. Meanwhile, in the ML tree there is a clade (BS = 92) formed by *C. emilianus* and the “La Rioja-San Juan lineage” that is not recovered in the Bayesian tree as both lineages fall to the polytomy observed at the base of the clade corresponding to the *C. mendocinus* species group. Observed averages of percentage of sequence divergence between pairs of species/lineages of the *C. mendocinus* species group are shown in Table 1.

Morphological variation

Qualitative morphological descriptions, including the listing of the traits that characterize each lineage, are discussed below in the context of the new species described

Table 2. Summary statistics (mean, SD, range) of cranial measurements (in mm) of adult samples (N) of eight species of the genus *Ctenomys*. See Materials and Methods for abbreviations.

Variable	<i>C. emilianus</i>					<i>C. fochi</i>					<i>C. fulvus</i>					<i>C. johannis</i>	
	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	
TLS	3	50.89	4.55	45.74	54.35	2	39.89	1.1	39.11	40.67	47	54.9	3.32	47.09	61.51	1	45.29
CIL	3	46.84	2.78	44.31	49.82	2	39.26	1.22	38.39	40.12	47	51.56	3.13	43.6	57.56	1	44.11
NL	3	17.48	0.12	17.36	17.6	2	13.16	0.78	12.61	13.71	47	18.87	1.52	15.84	21.4	1	15.33
NW	3	8.13	0.72	7.32	8.71	2	6.58	0.59	6.16	6.99	47	9.03	0.84	7.03	10.78	1	6
RW	3	11.97	1.04	10.83	12.88	2	9.15	0.49	8.8	9.5	47	13.36	1.31	10.43	15.86	1	9.49
FL	3	14.55	1.43	13.01	15.84	2	11.79	0.5	11.44	12.15	47	14.71	1.01	12.29	16.42	1	12.86
IOC	3	10.48	0.87	9.94	11.49	2	7.98	0.33	7.75	8.21	47	11.76	1.13	9.85	14.33	1	8.25
ZB	3	29.19	1.97	26.99	30.81	2	23.86	0.11	23.78	23.94	47	33.81	2.72	28.64	39.7	1	26.93
BB	3	19.92	2.77	17.18	22.72	2	16.11	0.21	15.96	16.26	47	20.72	0.8	18.73	22.46	1	18.19
MB	3	28.21	2.13	25.79	29.77	2	23.66	0.47	23.33	24	47	33.04	2.41	28.92	37.67	1	25.75
IFH	3	9.68	0.81	8.84	10.45	2	7.68	0.29	7.48	7.89	47	11.37	0.9	9.55	13.05	1	8.57
DL	3	13.46	2.26	11.45	15.9	2	10.02	0.72	9.51	10.53	47	14.46	1.24	12.14	17.25	1	12.11
PL	3	21.77	1.71	20.09	23.51	2	16.91	0.57	16.51	17.32	47	23.23	1.75	19.32	26.71	1	19.37
UIW	3	7.68	0.96	6.82	8.71	2	5.76	0.26	5.58	5.95	47	8.67	0.87	6.99	10.49	1	6.5
PM4L	3	4.18	0.46	3.68	4.6	2	3.19	0.19	3.05	3.32	47	4.26	0.21	3.63	4.71	1	3.17
TRL	3	10.88	0.69	10.14	11.51	2	8.52	0.28	8.32	8.72	47	11.44	0.57	10.02	12.82	1	8.97
Variable	<i>C. maulinus</i>					<i>C. mendocinus</i>					<i>C. eileenae</i> sp. nov.					<i>C. verzi</i> sp. nov.	
	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	
TLS	8	46.55	4.1	41.63	53.4	33	41.16	2.74	37.1	47.44	23	46.49	3.2	41.73	53.96	1	43.58
CIL	8	44.66	4.04	39.45	51.67	33	39.91	2.68	36.11	46.42	23	44.75	3.1	40.08	51.69	1	40.68
NL	8	16.74	1.82	14.76	19.31	33	13.67	1.12	11.74	16.92	23	16.31	1.27	14.02	19.61	1	15.2
NW	8	6.87	0.88	5.77	8.44	33	6	0.45	5.15	7.44	23	7.17	0.59	5.86	8.39	1	7.65
RW	8	10.33	1.02	8.97	12.08	33	9.34	0.9	7.91	11.3	23	10.7	0.99	9.25	12.51	1	10.26
FL	8	13.01	1.02	12.18	15.4	33	12.15	0.84	10.1	13.95	23	13.43	0.71	12.51	15.35	1	12.31
IOC	8	8.79	0.66	7.87	9.74	33	7.93	0.49	6.89	9.12	23	9.11	0.59	8.05	10.12	1	8.42
ZB	8	26.14	1.89	23.22	29.68	33	23.96	1.54	21.11	27.59	23	27.23	1.69	25.12	30.2	1	25.04
BB	8	17.01	0.61	16.01	17.67	33	16.81	1.25	15.16	22.33	23	18.53	0.6	17.66	19.69	1	17.76
MB	8	23.84	2.3	21.43	28.84	33	23.75	1.4	20.04	26.63	23	27.03	1.43	24.95	29.51	1	23.36
IFH	8	9.34	0.72	8.07	10.12	33	7.47	0.56	6.41	9.07	23	8.74	0.77	7.78	10.67	1	8.33
DL	8	13.04	1.57	10.9	15.83	33	10.38	1.15	7.49	12.97	23	11.71	0.98	10.33	14.29	1	10.98
PL	8	20.71	2.09	18.16	24.48	33	17.54	1.46	15.2	20.67	23	19.01	1.66	17.16	22.7	1	18.2
UIW	8	6.92	0.69	6.03	7.99	33	5.99	0.6	5.18	7.43	23	6.79	0.68	5.61	8.3	1	6.58
PM4L	8	3.77	0.25	3.52	4.26	33	3.29	0.18	2.85	3.66	23	3.44	0.19	3.19	3.86	1	3.67
TRL	8	9.97	0.88	8.94	11.4	33	8.64	0.5	7.61	9.78	23	9.3	0.67	8.25	10.44	1	8.82

here. Descriptive statistics for cranial measurements are provided on Table 2.

The first two principal components (PCs) together accounted for 94.8% of the total variance (Fig. 3; Table 3). PCA revealed that all variables were positively correlated with the PC1 (93.3% of the total variance), suggesting that it mostly corresponds to a vector of size. Plots of individual scores shows that *C. bergi*, *C. mendocinus* (including *C. validus*), the “La Rioja-San Juan lineage”, and *C. fulvus* mostly segregate along PC1 from lower to higher values, while the latter three occupy similar range values along PC2. *C. emilianus* partially overlaps with *C. fulvus* and the “La Rioja-San Juan lineage.” *C. fochi* and *C. johannis* were included within the polygon of *C. mendocinus*. The “Las Leñas lineage” is placed in an intermediate position between *C. mendocinus* and the “La Rioja-San Juan lineage”. Secondarily, *C. maulinus* was

segregated from all other taxa along the second axis as it occupies lower values on this PC. Highest absolute loadings on PC1 corresponded to variables IFH, UIW and NW, while for the PC2 were DL, IOC and MB (Fig. 3; Table 3).

Discussion

Taken together, the molecular and morphological results provide strong evidence that the current taxonomic scheme does not reflect the species richness of the *Ctenomys mendocinus* species group. While one currently recognized species, *C. validus*, is not distinguishable from *C. mendocinus*, there are two molecular lineages (i.e.,

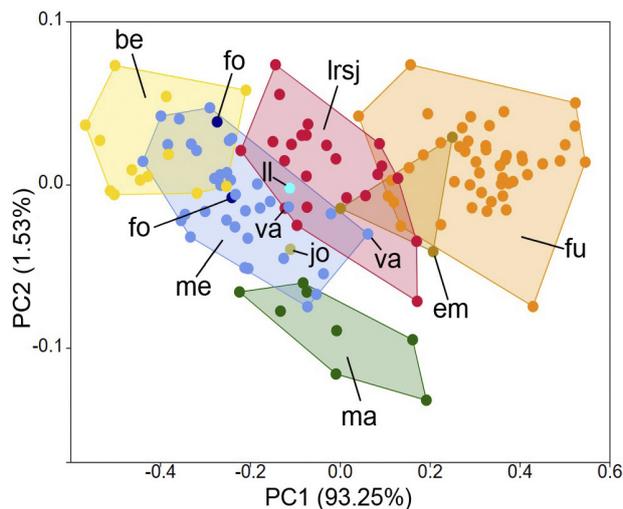


Figure 3. Individual scores of adult specimens of *Ctenomys* from west-central Argentina ($n = 131$) for: principal components 1 and 2. Abbreviations are as follow: be, *C. bergi*; em, *C. emilianus* (= Central Clade of Tammone et al. 2021); fo, *C. fochi*; fu, *C. fulvus*; jo, *C. johannis*; ma, *C. maulinus*; me, *C. mendocinus* (two paratypes of *C. validus* are depicted with a “va”); lrsj, La Rioja-San Juan lineage; ll, Las Leñas lineage.

those here referred to as “La Rioja-San Juan” and “Las Leñas”) that are also morphologically distinct from all other species of the group. As no names are available for them, we named and described them below. First, we erect a new species based on the “La Rioja-San Juan lineage” and then one based on the “Las Leñas lineage.” A third candidate species, the “Quijadas lineage”, remains awaiting a morphological and/or nuclear DNA evaluation of its distinction.

Contrary to the “La Rioja-San Juan lineage,” which is formalized below as a new species based on a large sample of individuals, the “Las Leñas lineage” is formalized as a new species on the base of morphological and genetic data of just one and three specimens, respectively. Descriptions based on one or few specimens are problematic, mainly because intraspecific variation, including sexual dimorphism and ontogenic changes, is poorly assessed. However, there are several recent examples of descriptions of new mammal species based on only one specimen, even within diverse and cryptic groups such as rodents (e.g., Teta et al. 2022). Under certain circumstances, and with some precautions, descriptions based on small samples of specimens can be well justified (e.g., Guayasamin et al. 2018). For instance, Köhler and Pádia (2016) expressed that the advantage of recognizing well-supported lineages as targets for further research and conservation, even when based on limited samples, greatly surpasses the possible inconveniences of naming them. In order to minimize the possibility of taxonomic errors, we follow Guayasamin et al. (2018), which provided a brief guide to describe species based on single (or few) specimens. Thus, beyond the congruence between our morphological and molecular datasets, that clearly shown the distinction of the species here described, we construct the morphological diagnosis based on traits

Table 3. Results of principal components analysis performed on adult specimens of four species of *Ctenomys* ($n = 119$). See Materials and Methods for explanation of abbreviations.

	PC 1	PC 2
TLS	0.2324	-0.0963
CIL	0.2132	-0.1464
NL	0.2506	-0.2531
NW	0.2935	0.3054
RW	0.2851	-0.0510
FL	0.1538	0.2413
IOC	0.2812	0.4107
ZB	0.2621	0.1298
BB	0.1597	0.3209
MB	0.2491	0.3616
IFH	0.3117	-0.0821
DL	0.2699	-0.4170
PL	0.2399	-0.3539
UIW	0.2962	-0.0848
PM4L	0.2081	-0.1377
TRL	0.2274	-0.1857
% variance	93.25	1.54
Eigenvalue	0.0816	0.0014

that present low intraspecific variation (e.g., size and shape of incisive foramina and tympanic bullae), and use well preserved specimens with precise collection locality data.

Ctenomys eileenae sp. nov.

<https://zoobank.org/F1355C16-11F3-40C9-8E40-3C90EEE2C2F9>

Figs 4–8

Ctenomys fulvus – Haene et al. (2001: 63)

Ctenomys sp. 1 – Borghi and Giannoni (2007:158)

Ctenomys sp. (Laguna Brava) – Tammone et al. (2022a: 5)

Eileen’s tuco-tuco

Tuco-Tuco de Eileen

Holotype. An adult male (MACN-Ma 30847), including skin, skeleton, and tissues, collected on 14 May 2022 by J. P. Jayat (original field number JPJ 2821) (Figs 4–6). An 801 base-pair sequence of the *cyt b* gene has been deposited in GenBank with accession number OQ305623.

Type locality. Argentina: La Rioja Province, Vinchina Department, Refugio El Peñón, on road to Laguna Brava, 3,609 m a.s.l. (-28.4765° , -68.8376° ; Fig. 2: locality 1).

Measurements of the holotype (in mm). TOTL, 285; TAIL, 88; HFL, 44; EAR, 8; TLS, 49.68; CIL, 48.17; NL, 17.04; NW, 7.86; FL, 14.21; RW, 12.03; ZB, 29.90; IOB, 10.00; BB, 19.40; MB, 29.41; IFH, 9.92; DL, 12.62; PL, 21.68; UIW, 7.65; PM4L, 3.67; TRL, 10.44. Weight, 275 g.

Paratypes. Three specimens as follows. An adult female (MACN-Ma 30846), including skin, skeleton, and tissues, collected on 2 October 2021 by J. P. Jayat (original field number JPJ 2762) at the species type locality; an 801 base-pair sequence of the *cyt b* gene of this specimen has been deposited in GenBank with accession number OQ305626. A young female (MACN-Ma 30848), including skin, skeleton, and tissues, collected on 16 May 2022 by J. P. Jayat (original field number JPJ 2871) at the species type locality; an 801 base-pair sequence of the *cyt b* gene of this specimen has been deposited in GenBank with accession number OQ305624. An adult female (MACN-Ma 30849), including skin, skeleton, and tissues, collected on 17 May 2022 by J. P. Jayat (original field number JPJ 2884) at the species type locality; an 801 base-pair sequence of the *cyt b* gene of this specimen has been deposited in GenBank with accession number OQ305625. See Supplementary Material 3 for measurements of the paratypes.

Other examined specimens. Argentina: La Rioja Province: Laguna Brava (CFA 12410, CFA 12411, CFA 12412 [Fig. 2, locality 1]). San Juan Province: Parque Nacional San Guillermo, without precise locality (CML 430, CML 772); Parque Nacional San Guillermo, Cerro Agua del Indio (MACN-Ma 18820, MACN-Ma 18821, MACN-Ma 18823 [Fig. 2, locality 2]); Parque Nacional San Guillermo, Cerro Imán (MACN-Ma 18817, MACN-Ma 18819, MACN-Ma 18828 [Fig. 2, locality 3]); Parque Nacional San Guillermo, Los Caserones (MACN-Ma 18816, MACN-Ma 18818 [Fig. 2, locality 4]); Parque Nacional San Guillermo, Mina La Brea (MACN-Ma 18824; [Fig. 2, locality 5]); Parque Nacional San Guillermo, Puesto Agua del Godo (MACN-Ma 18813, MACN-Ma 18814, MACN-Ma 18815 [Fig. 2, locality 6]); Parque Nacional San Guillermo, Refugio del Macho Muerto (MACN-Ma 18825; [Fig. 2, locality 7]); Parque Nacional San Guillermo, Rincón del Río (MACN-Ma 18826, MACN-Ma 18827 [Fig. 2, locality 8]); Parque Nacional San Guillermo, Vega Agua del Godo (CML 430, CML 1916 [Fig. 2, locality 9]); Parque Nacional San Guillermo, Vega del Infiernillo (MACN-Ma 18822 [Fig. 2, locality 10]).

Morphological diagnosis. A large-sized tuco-tuco of the *C. mendocinus* species group (TOTL, 244–289 mm; TAIL, 66–100 mm; HFL, 32–44 mm; EAR, 6–10 mm; W, 100–326 g), with moderately differentiated dorsal and ventral coloration; dorsum Dresden brown to Saccardo's olive, tinged with cinnamon brown in some individuals, becoming deep olive buff to olive buff on venter. Skull strongly built, slightly larger and robust than in other species of this group, and with a proportionally broader and shorter rostrum; zygomatic arches robust and with a rounded outline in dorsal view; edges of frontals posterior to the interorbital constriction moderately divergent; postorbital processes of frontals moderately well developed; premaxillo-frontal suture at the level of the naso-frontal suture; incisive foramina large and conspicuously broad, recessed in a common fossa of rhomboidal outer borders and completely separated by a bony sep-

tum; interpremaxillary foramen small; auditory bullae inflated and ovate; incisors orthodont.

Morphological description. Pelage dense, fine, and soft, about 20–22 mm long over back and rump; dorsum with fur ranging from Dresden brown to Saccardo's olive; individual hairs dark neutral gray colored, except for their distal thirds, which are buffy. Some individuals have the nose, crown and the dorsal midline tinged with cinnamon brown; others have the nose and crown mummy brown. Color of ventral pelage olive buff or buffy brown, with the line separating from dorsum indistinct; individual hairs dark gray basally, with distal tips whitish, olive buff or buffy brown. Fur of fore and hind limbs colored like dorsum, except internal sides which are pale olive buff. Top of manus and feet covered with brownish hairs. Mystacial vibrissae surpassing the dorsal edge of the pinnae when laid back alongside of head; superciliary vibrissae sparse, extending to the base of the pinnae when laid back alongside of head. Ears sparsely covered with short, brownish hairs. Pes broad, all digits with unguate tufts of stiff bristles, and strong claws. Tail short (40–51% of the head and body length), slightly darker above than below and sparsely covered by short buffy hairs; its distal third is covered by a dorsal fringe of dark brown, longer hairs (Fig. 4).

Skull strongly built and robust, with a proportionally broader and shorter rostrum and zygomatic arches broad and nearly rounded in dorsal view (Fig. 5). Nasals moderately bowed, long and narrow, with their broadest portion placed to the anterior third and with nearly straight to convex lateral margins; the anterior tips of nasals are in front of the level of the anterior end of upper diastema. Premaxillo-frontal suture placed in line with the naso-frontal suture. Supraorbital borders well defined, with moderately to well-developed postorbital processes on frontals. Persistent interfrontal fontanelles variably present. Interparietal large and narrow. Temporal ridges moderately developed in adult specimens. Lambdoid crest well developed. Rostral masseteric fossa dorsal to alveolar sheath of the I1, deep and ending in a curved crest slightly anterior to or level with premaxillary-maxillary suture. Zygomatic arch broad, with well-developed postorbital processes of jugal and a conspicuous lateral masseteric fossa. Incisive foramina large and conspicuously broad, recessed in a common fossa of rhomboidal outer borders (Fig. 6); interpremaxillary foramen small to well developed, although always evident. Palatal bridge with two major palatine foramina at about level of M1. Mesopterygoid fossae “V” shaped, reaching anteriorly the posterior portion of M2 (Fig. 5). Alisphenoid-basisphenoid bridge broad; bony roof of mesopterygoid fossa with two medium-sized and nearly pyriform sphenopalatine vacuities. Buccinator-masticatory foramen large, and divided in some individuals. Paraoccipital processes well developed, broad and comma-shaped. Auditory bullae well inflated and oval, with salient auditory tubes.

Mandible robust and markedly hystricognathous, with coronoid process long and pointed (Fig. 5). Condylod process robust, bearing a well-developed articulation

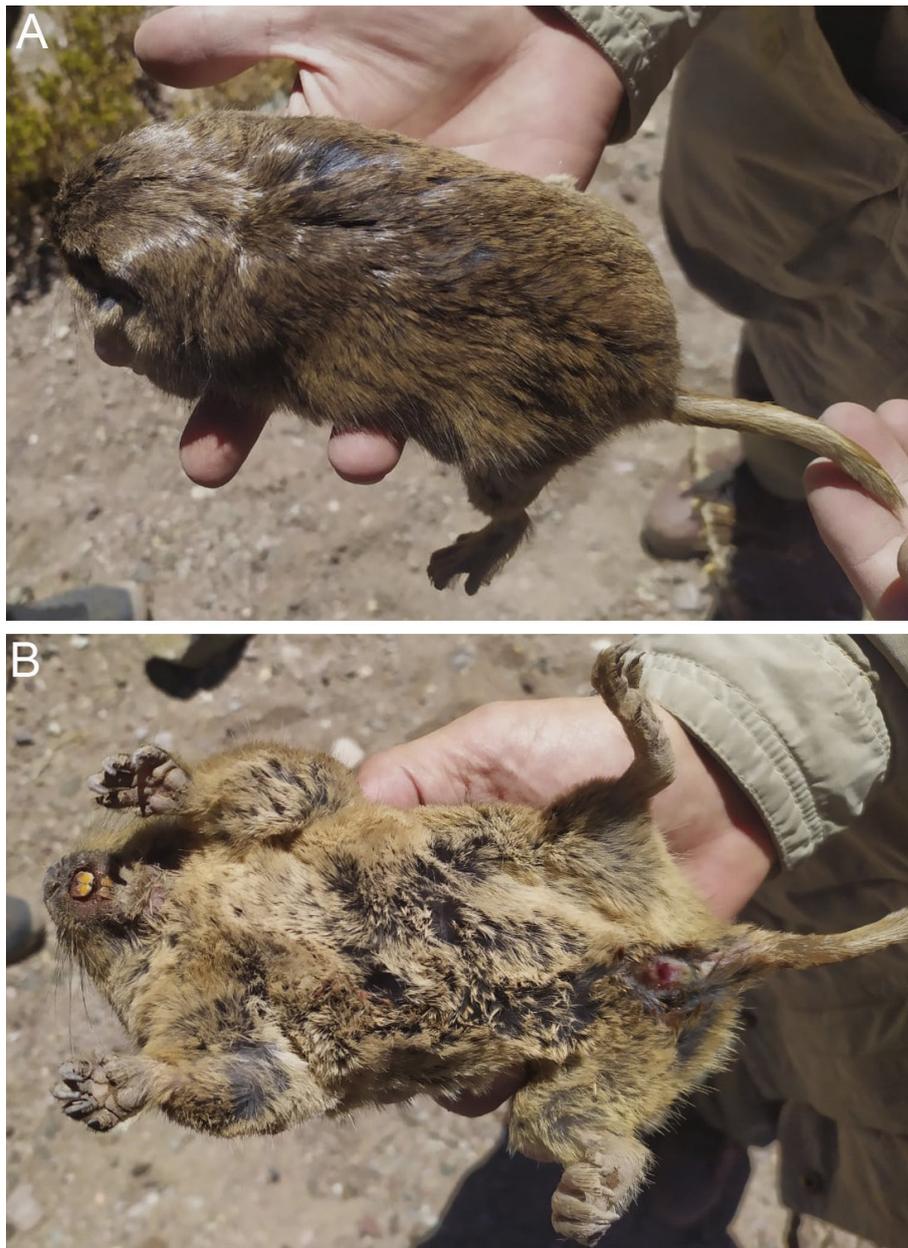


Figure 4. Dorsal (A) and ventral (B) views of the external appearance of the holotype of *C. eileenae* sp. nov. (MACN-Ma 30847).

flange. Postcondyloid process with a small ventrolateral apophysis. Masseteric crest nearly horizontal. Chin process well developed and visible in lateral view, located at the level of the p4. The bottom of the alveolar sheath of p4 does not protrude much (Fig. 5).

Upper incisors large, moderately robust, and nearly orthodont; frontal enamel surface orange. Maxillary tooth rows slightly divergent posteriad. M3 reduced (Fig. 5).

Descriptive statistics for external and cranial measurements are provided on Table 2; individual measurements are given on Supplementary Material 2 and 3.

Distribution. Known from several localities above 3,500 m a.s.l. in western La Rioja and northernmost San Juan provinces, west-central Argentina (Fig. 2).

Etymology. We named this species in honor of Eileen Lacey, a North American biologist devoted to studying the evolution of behavioral diversity of mammals. Among

others, the studies of Eileen have focused on subterranean rodents of the genus *Ctenomys*. Eileen is the current president of the International Federation of Mammalogists. The species name is a patronym in the genitive singular.

Comparisons. *Ctenomys eileenae* sp. nov. differs from *C. bergi*, *C. fochi*, *C. johannis*, *C. mendocinus*, and *C. tulduco* by its larger size (TLS = 41.7–53.9 vs. 37.4–44.7 mm), proportionally shorter nasals, lesser globose tympanic bullae, and proportionally wider and longer incisive foramina (Figs 6–8). Furthermore, the postorbital processes in *Ctenomys eileenae* sp. nov. are moderately to well developed, while in *C. bergi*, *C. fochi*, *C. johannis*, *C. mendocinus*, and *C. tulduco* are absent to slightly expressed.

Ctenomys eileenae sp. nov. can be differentiated from *C. coludo* and *C. famosus* by its larger size and more robust appearance, less inflated tympanic bullae and the pres-



Figure 5. Lateral (above), dorsal (below, left) and ventral (below, right) views of the skull and labial view of the mandible (middle) of the holotype of *Ctenomys eileenae* sp. nov. (MACN-Ma 30847). Scale = 5 mm.

ence of interparietal bone (cf. Thomas 1920a, 1920b). In addition, *Ctenomys eileenae* sp. nov. has moderately to well-developed postorbital processes, while in *C. coludo* and *C. famosus* this structure is mostly absent.

Ctenomys eileenae sp. nov. differs from *C. emilianus* (Fig. 9) by its more robust appearance, more developed postorbital process, and proportionally larger and broader incisive foramina. *C. eileenae* sp. nov. also has a moderately large interparietal bone, while in *C. emilianus* this bone is usually absent (when present is small).

Ctenomys eileenae sp. nov. differs from *C. fulvus*, which is endemic from northern Chile, by its much smaller size (TLS = 41.7–53.9 vs. 47.1–61.5 mm), narrower and less quadrate interorbital region, and proportionally narrower rostra and upper incisors (Fig. 7). In addition, *Ctenomys eileenae* sp. nov. has proportionally broader incisive foramina.

Ctenomys eileenae sp. nov. can be differentiated from *C. knighti* by its much narrower upper incisors, proportionally wider incisive foramina, smaller and lesser globose tympanic bullae, and less quadrate interorbital region, with posteriorly placed postorbital processes on frontals (vs. anteriorly placed in *C. knighti*) (Fig. 7 and 8).

Ctenomys eileenae sp. nov. can be differentiated from *C. verzi* sp. nov. by its larger size (TLS = 41.7–53.9 vs. 43.6 mm) and more robust appearance, and by its proportionally broader and shorter incisive foramina. Also, *Ctenomys eileenae* sp. nov. has moderately to well-developed postorbital processes, while in *C. verzi* sp. nov. these structures are absent.

Pairwise genetic distances with other species of the *Ctenomys mendocinus* species group range from 2.93 to 3.68 % (Table 1).

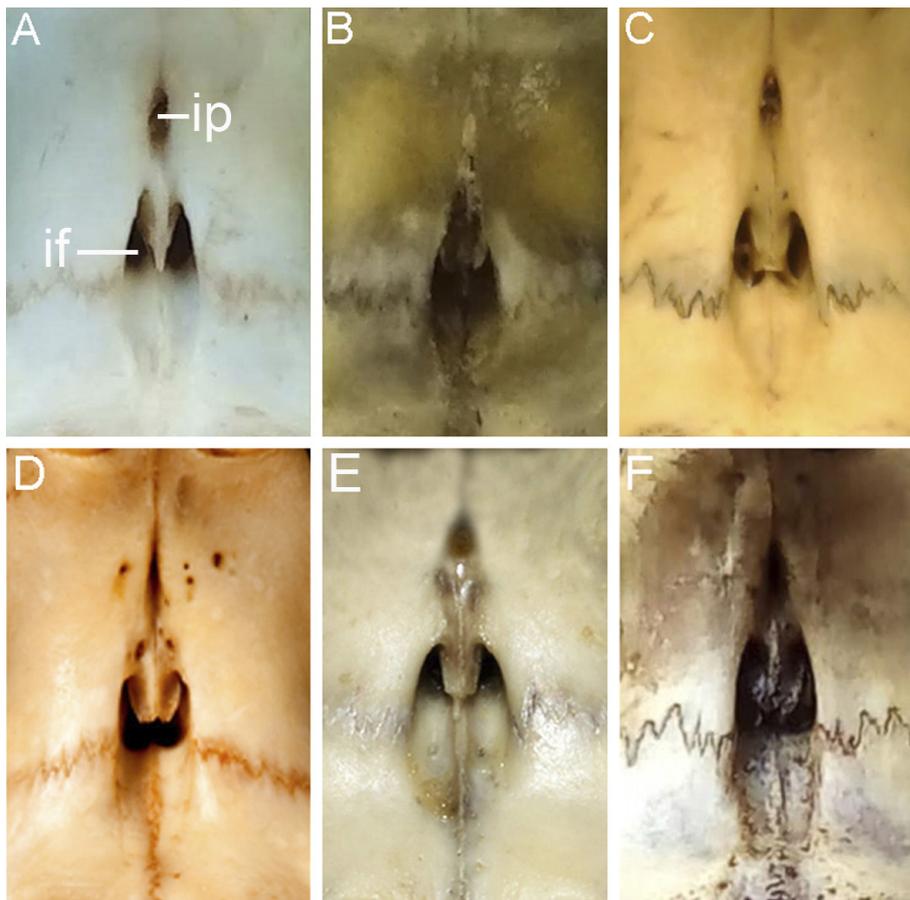


Figure 6. Ventral view of the incisive and interpremaxillary foramina in six species of *Ctenomys* from west-central Argentina: **A** *C. johannis* (CFA-Ma 12452); **B** *C. maulinus* (FMNH 23215); **C** *C. mendocinus* (CMI 2497); **D** *C. pontifex* (BM 60.5.1.2; holotype); **E** *C. eileenae* **sp. nov.** (MACN-Ma 30847; holotype); and **F** *C. verzi* **sp. nov.** (CMI 7703; holotype). Specimens are scaled to the same length.

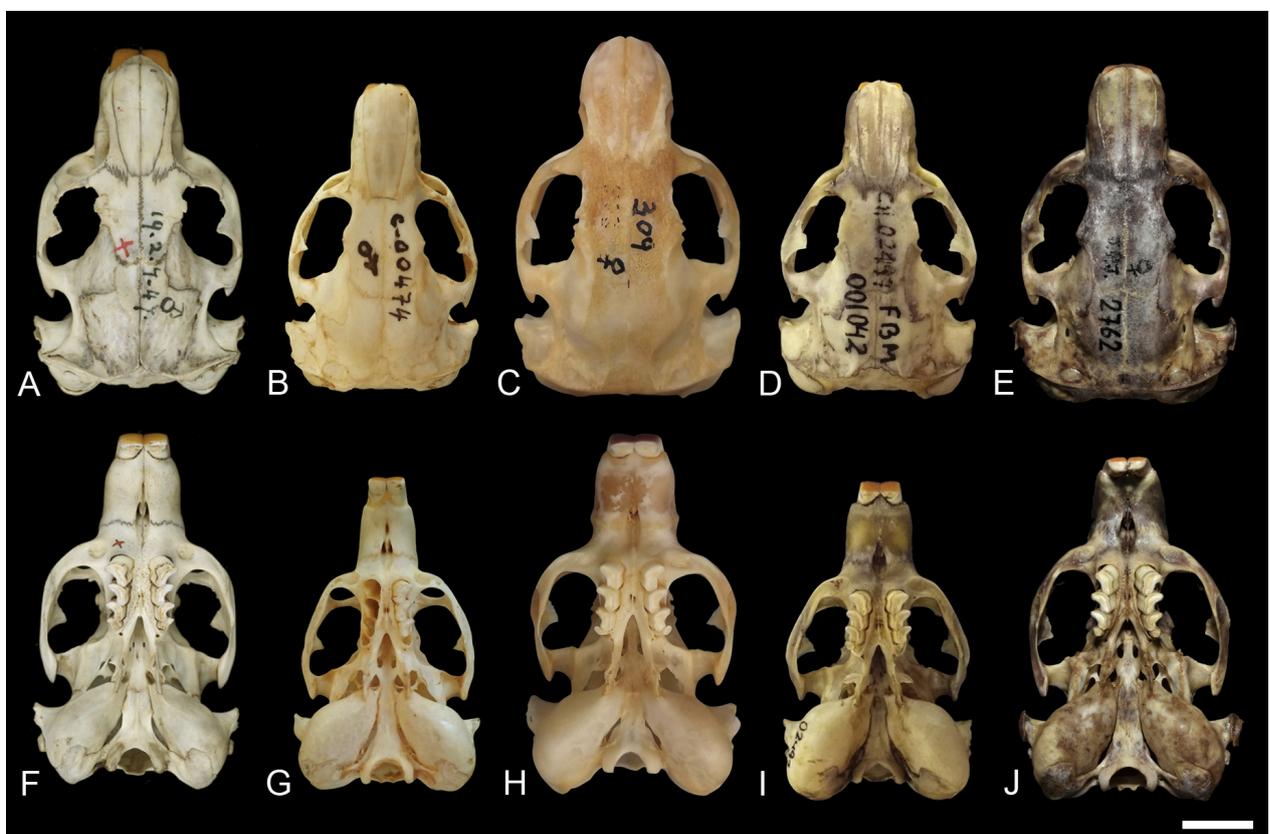


Figure 7. Dorsal (A–E) and ventral (F–J) views of the skulls in five species of *Ctenomys* from west-central Argentina and northern Chile: **A, F** *C. knighti* (NHMUK 1919.2.7.41); **B, G** *C. johannis* (CFA-MA 12452); **C, H** *C. fulvus* (UACH 309); **D, I** *C. mendocinus* (CMI 2497); and **E, J** *C. eileenae* **sp. nov.** (MACN-Ma 30846). Scale = 5 mm.

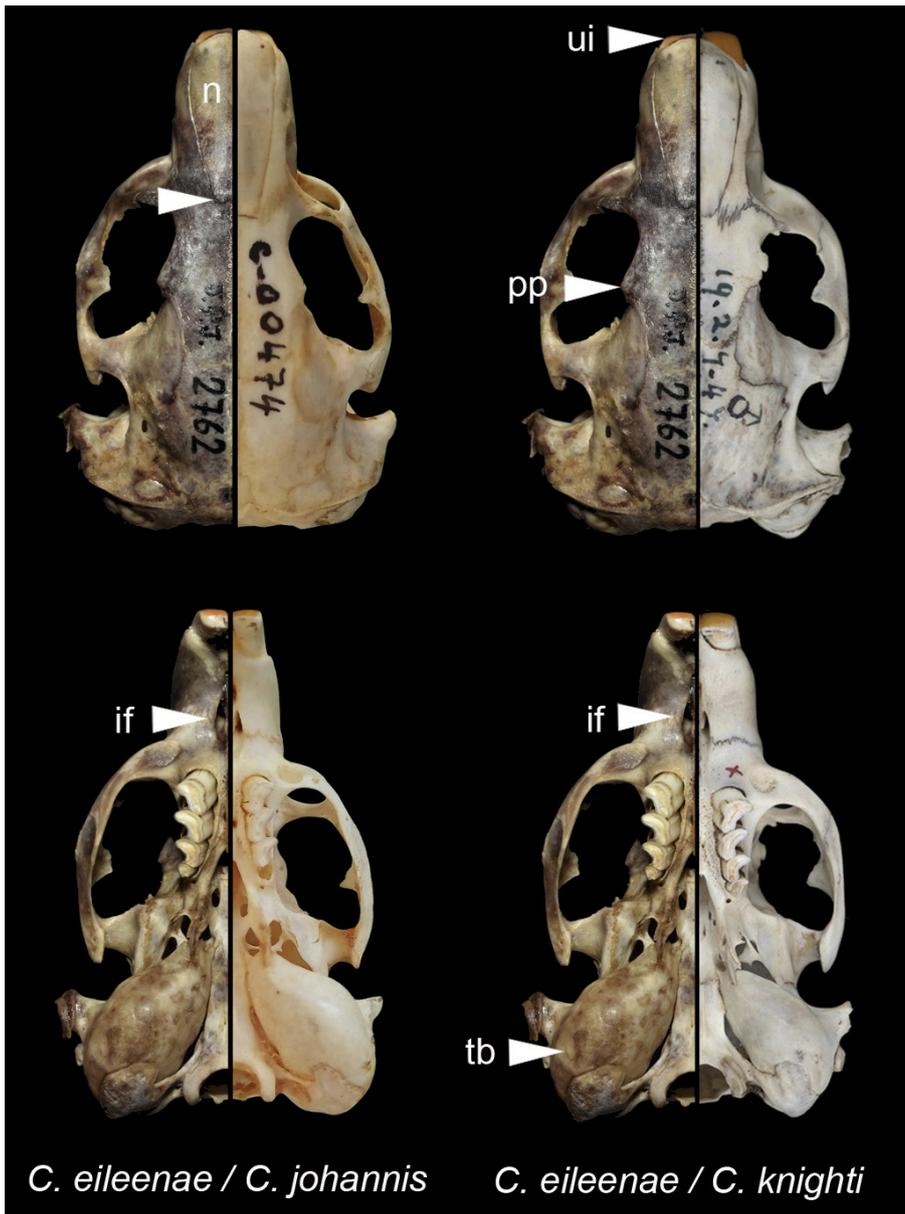


Figure 8. Selected differences comparing the cranial anatomy of *Ctenomys eileenae* sp. nov. (MACN-Ma 30846) and other *Ctenomys* species including *C. johannis* (CFA-MA 12452), and *C. knighti* (NHMUK 1919.2.7.41). Note that *C. eileenae* has proportionally shorter nasals (n) and much larger and broader incisive foramina (if) than *C. johannis* and narrower upper incisors (ui), posteriorly displaced postorbital process (pp), larger and broader incisive foramina, and more inflated tympanic bullae (tb) than *C. knighti*. Specimens are scaled to the same length.

Natural history. Mostly unknown; all known recording localities of Eileen’s tuco-tuco lay within the Central Andean Puna ecoregion. The flora in this area is characterized by montane shrublands, cushion plants, and grasslands. In the area of El Peñón, individuals of this new species were captured both on humid and organic soils of the “vegas” and in more dry and rocky grounds bordering these “vegas”. In the “vegas” vegetation type (areas of streams and river plains), the dominant plant types are *Festuca*, *Poa*, and *Cinnagrostis*. The more xeric microhabitats in this area are found on dry slopes and plateaus, the dominant species are saltbush (*Ephedra*), *Lycium* (Solanaceae) and *Senecio* (Asteraceae). One female captured in this locality in October 2021 was pregnant, but two females and one male were not sexually active in May 2022. The two females collected in October 2022 were molting. Other small mammals collected in El Peñón,

near the new species of *Ctenomys*, included *Abrothrix andina* (Philippi, 1858), *Akodon spegazzinii* Thomas, 1897, and *Phyllotis vaccarum* Thomas, 1912.

Conservation. *Ctenomys eileenae* sp. nov. is distributed over an area of ca. 900 km² in western La Rioja and northernmost San Juan provinces, west-central Argentina (Fig. 2). More than a half of its known distribution is included within the Parque Nacional San Guillermo, one of the few areas with effective protection in the central Andes of Argentina. Although the species does not seem to be threatened, being even locally abundant in some areas (e.g., in the vicinity of Laguna Brava), its restricted distribution, in an environment that suffers various anthropogenic pressures (e.g., megamining, cattle ranching), invites a careful review of its conservation status.

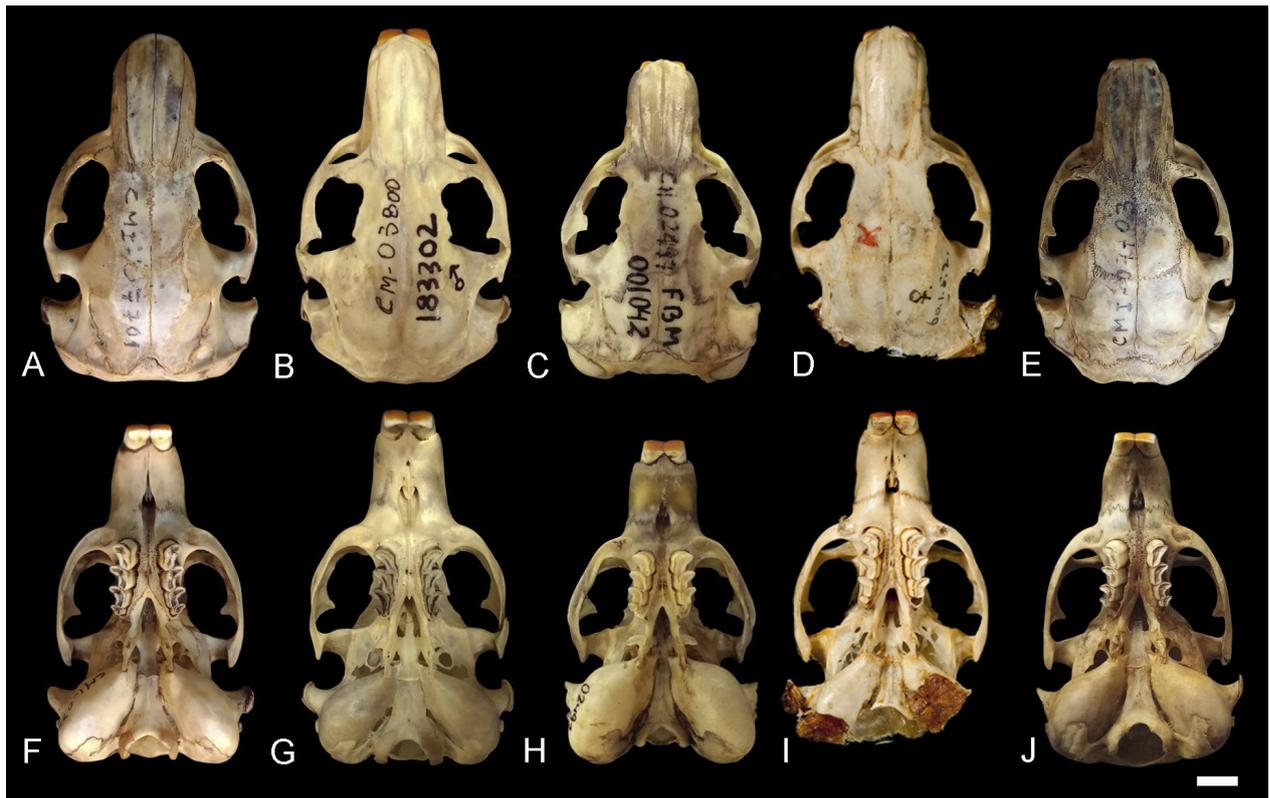


Figure 9. Dorsal (A–E) and ventral (F–J) views of the skulls in five species of *Ctenomys* from west-central Argentina: A, F *C. emilianus* (CMI 7701); B, G *C. maulinus* (CMI 3800); C, H *C. mendocinus* (CMI 2497); D, I *C. pontifex* (NHMUK 60.5.1.2; holotype); and E, J *C. verzi* sp. nov. (CMI 7703). Scale = 5 mm.

Ctenomys verzi sp. nov.

<https://zoobank.org/935F6E2F-0B11-40E5-98A4-ECB-57F73E160>

Figs 6, 9–12

Ctenomys sp. Las Leñas – Mapelli et al. (2017: 133)

Ctenomys sp. 3 – Tammine et al. (2021: 1407)

Verzi's tuco-tuco

Tuco-Tuco de Verzi

Holotype. CMI 7703, adult male; skin, skull, and partial skeleton collected on 27 March 2008 by Pablo Cuello (original field number PC06) (Figs 6, 9–12). An 801 base-pair sequence of the *cyt b* gene has been deposited in GenBank with accession number OQ305620.

Type locality. Argentina: Mendoza Province, Malargüe Department, 10 km by road NW Las Leñas, 2,799 m a.s.l. (–35.0973°, –70.1363°; Fig. 2: locality 11).

Measurements of the holotype (in mm). TOTL, 260; TAIL, 89; HFL, 40; EAR, 7; TLS, 43.58; CIL, 40.68; NL, 15.20; NW, 7.65; FL, 12.31; RW, 10.26; ZB, 25.04; IOB, 8.42; BB, 17.76; MB, 23.36; IFH, 8.33; DL, 10.98; UIW, 6.58; PL, 18.20; PM4L, 3.67; TRL, 8.82.

Morphological diagnosis. A medium-sized tuco-tuco of the *C. mendocinus* species group, with dorsal and ven-

tral coloration well differentiated; dorsum light brownish olive, becoming deep olive-buff on flanks; venter olive-buff, with the line separating from dorsum moderately defined. Skull moderately robust, with rostrum proportionally short and broad and interorbital region with posteriorly divergent outer margins; zygomatic arch relatively broad, with well-developed postorbital processes of jugal and a conspicuous lateral masseteric fossa; dorsal profile of the cranium with a marked inflection downwards at the parietal-occipital region; incisive foramina moderately long and broad, recessed in a common fossa of nearly straight outer borders; interpremaxillary foramen moderately large; sphenopalatine vacuities large; auditory bullae moderately inflated, and pyriform.

Morphological description. Pelage dense, fine, and soft, about 10–12 mm long over back and rump; dorsum with fur light brownish olive, becoming deep olive-buff on flanks; individual hairs dark neutral gray colored, except for the distal tips, which are lighter. Nose brownish olive. Color of ventral pelage olive buff, with the line separating from dorsum moderately defined; individual hairs dark gray basally, with distal tips whitish to olive buff. Fur of fore and hind limbs colored like dorsum, except for their internal sides which are lighter. Mystacial vibrissae surpassing the dorsal edge of the pinnae when laid back alongside of head; superciliary vibrissae sparse, extending to the base of the pinnae when laid back alongside of head. Ears sparsely covered with short, brownish olive hairs. Manus covered by silvery to brownish hairs,



Figure 10. Dorsal (A) and ventral (B) views of the skin of the holotype of *C. verzi* sp. nov. (CMI 7703). Scale = 10 mm.

with long claws (ca. 11 mm in the third digit). Pes broad and dorsally covered by silvery to brownish hairs; all digits with ungueal tufts of stiff bristles, and strong claws. Tail short (ca. 52% of the head and body length), darker above than below and sparsely covered by short hairs (Fig. 10).

Skull moderately robust, with rostrum proportionally short and broad, interorbital region with posteriorly divergent outer margins, and zygomatic arches broad and nearly parallel-sided in dorsal view (Fig. 11). Nasals relatively flat, moderately long and narrow, broadest anteriorly, and with nearly straight lateral margins; their anterior tips are in line to the level of the anterior end of

upper diastema. Premaxillary-frontal suture in line with the naso-frontal suture. Supraorbital ridges well defined, without postorbital processes on frontals. Interparietal completely fused. Temporal ridges not developed. Lambdoid crest slightly developed. Rostral masseteric fossa dorsal to alveolar sheath of the I1, deep and ending in a curved crest slightly anterior to or level with premaxillary-maxillary suture. Bottom of the alveolar sheaths of the upper incisors are visible laterally and located at the level of DP4. Zygomatic arch broad, with well developed postorbital processes of jugal and a conspicuous lateral masseteric fossa. Dorsal profile of cranium with a marked inflection downwards in the parietal-occipital region. In-



Figure 11. 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. verzi* sp. nov. (CMI 7703). Scale = 5 mm.

cisive foramina moderately long and broad, recessed in a common fossa of nearly straight outer borders; interpremaxillary foramen moderately large (Fig. 6). Palatal bridge with two major palatine foramina at about level of M1. Mesopterygoid fossa “V” shaped, reaching anteriorly the middle portion of M2. Alisphenoid-basisphenoid bridge thin; bony roof of mesopterygoid fossa with two large and nearly pyriform sphenopalatine vacuities. Buccinator-masticatory foramen large and divided. Paraoccipital processes well developed and comma-shaped. Auditory bullae moderately inflated and pyriform, with salient auditory tubes (Fig. 11).

Mandible robust and markedly hystricognathous, with coronoid process long and pointed; condyloid process robust, bearing a poorly developed articulation flange. Postcondyloid process with a small ventrolateral apophysis. Chin process poorly developed and moderately visible in

lateral view; bottom of alveolar sheath of p4 does not protrude much (Fig. 11).

Upper incisors large, moderately robust, and nearly orthodont; frontal enamel surface orange. Maxillary tooth rows slightly divergent posteriad. M3 reduced, with the posterolingual face flat and an anterior lobe protruding (Fig. 11).

Distribution. Only known from the type locality (see above) and its surroundings (RP22, 5.8 km N de Las Leñas; see Tamzone et al. 2021; Fig. 2, locality 12), at the Andes of southwestern Mendoza in west-central Argentina (Fig. 2; localities 11–12). The only two known localities are separated by less than 3.2 km.

Etymology. We named this species in honor of Diego Verzi, an Argentinean mammalogist and paleontologist

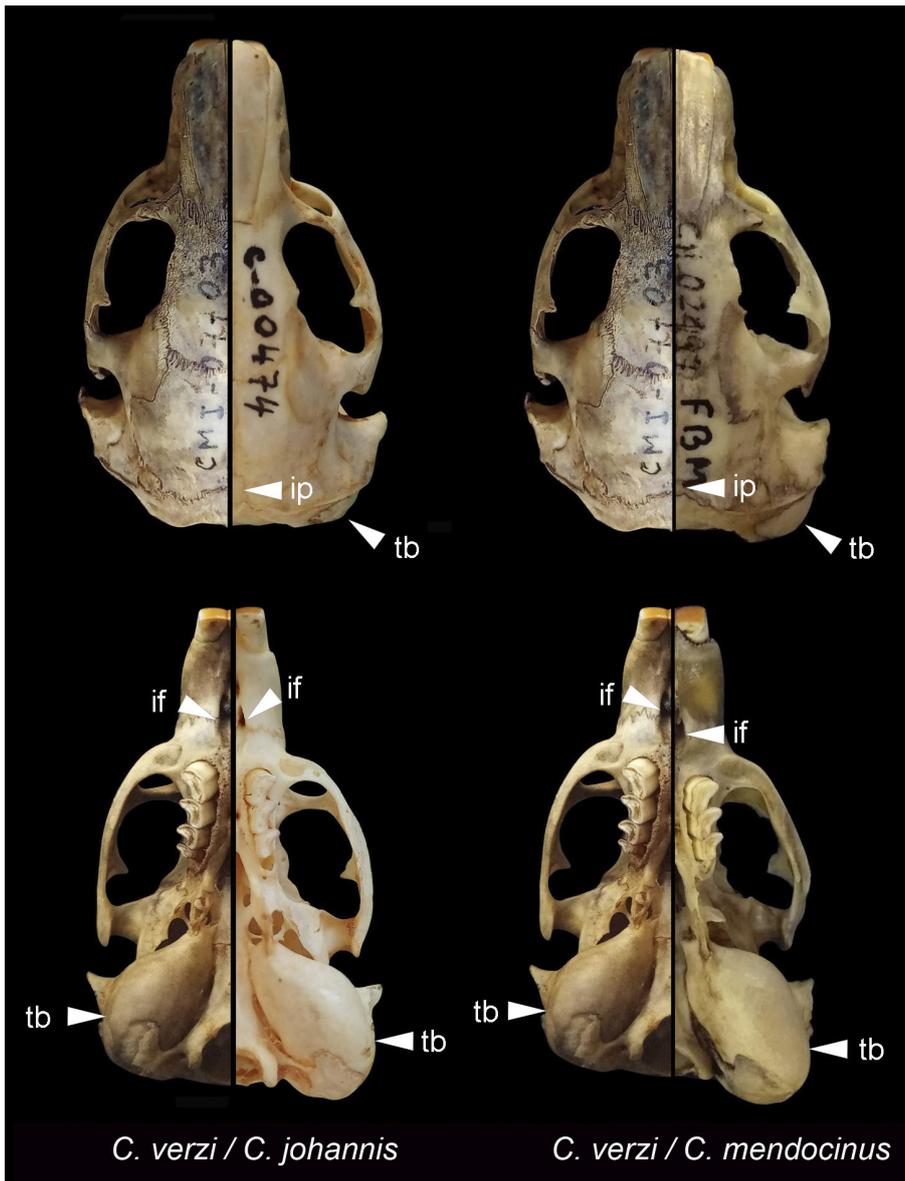


Figure 12. Selected differences comparing the cranial anatomy of *Ctenomys verzi* **sp. nov.** (CMI 7703) and other *Ctenomys* species including *C. johannis* (CFA-MA 12452), and *C. mendocinus* (CMI 2497). Note that *C. verzi* **sp. nov.** lacks interparietal (ip), has proportionally larger and broader incisive foramina (if), and smaller and not visible from above tympanic bullae (tb). Specimens are scaled to the same length.

devoted to the study of mammal evolution and systematics. Diego has a large publication record on living and fossil octodontoid rodents, including ctenomyids. The species name is constructed as a noun in apposition based on the name of a man.

Comparisons. *Ctenomys verzi* **sp. nov.** can be differentiated from *C. johannis* and *C. mendocinus* by its less globose tympanic bullae, absence of interparietal bone and larger incisive foramina (Figs 9, 12). Additionally, the tympanic bullae are not visible from above in *Ctenomys verzi* **sp. nov.**, while they are visible in dorsal view in both *C. johannis* and *C. mendocinus* (Fig. 12).

Ctenomys verzi **sp. nov.** can be differentiated from *Ctenomys eileenae* **sp. nov.** by its smaller size (TLS = 43.6 vs. 41.7–53.9 mm), less robust appearance, and by its proportionally more narrow and larger incisive foramina. In addition, the skull of *Ctenomys verzi* **sp. nov.** lacks postorbital processes, while these structures are moderately to well developed in *Ctenomys eileenae* **sp. nov.**

Ctenomys verzi **sp. nov.** differs from *C. emilianus* by its smaller size (TLS = 43.6 vs. 45.7–54.3 mm) and less robust appearance, smaller sphenopalatine vacuities, and less proodont upper incisors (Fig. 9). In addition, the interpremaxillary foramen is large and closely placed to the incisive foramina in *Ctenomys verzi* **sp. nov.** and large but well separated from the incisive foramina in the *C. emilianus* (Fig. 6).

Ctenomys verzi **sp. nov.** differs from *C. maulinus* by its smaller size (TLS = 43.6 vs. 41.6–53.4 mm) and less robust appearance, smaller sphenopalatine vacuities, more pyriform tympanic bullae, and proportionally longer incisive foramina. In addition, the interpremaxillary foramen is large and closely placed to the incisive foramina in *Ctenomys verzi* **sp. nov.** and large but well separated from the incisive foramina in *C. maulinus* (Fig. 9).

Ctenomys verzi **sp. nov.** differs from *C. pontifex* by its more pyriform tympanic bullae (vs. narrow and nearly tubular in *C. pontifex*), shorter rostrum, and proportion-

ally longer incisive foramina (Fig. 6). Also, in *Ctenomys verzi* the premaxillofrontal suture lies at the same line of the nasofrontal suture, while in *C. maulinus* the former is extended behind the second (Fig. 9).

Pairwise genetic distances with other species of the *Ctenomys mendocinus* species group range from 1.25 to 2.99 % (Table 1).

Natural history. Mostly unknown; the two known localities for this species are placed within the same valley, at 2,400–2,700 m a.s.l. The landscape in this area corresponds to the Southern Andean Steppe ecoregion, which is characterized by montane shrublands and grasslands. Most plants between 1,900 to 2,700 m a.s.l. correspond to the genera *Stipa*, *Adesmia*, *Mulinum*, *Nassauvia*, and *Chuquiraga*. The climate is cold and desert, with most precipitation and snow falling during winter. Other small mammals collected in Las Leñas, syntopically with the new species, included *Abrothrix hirta* (Thomas, 1895), *A. olivacea* (Waterhouse, 1837), *Euneomys chinchilloides* (Waterhouse, 1839), *E. fossor* (Thomas, 1899), *Loxodontomys micropus* (Waterhouse, 1837), *Paynomys macronyx* (Thomas, 1894), and *Phyllotis pehuenche* Jayat et al., 2022.

Conservation. As currently defined, Verzi's tuco-tuco has a small geographic range, which constitutes a proxy of its conservation status (Bidau et al. 2012; Caraballo et al. 2023). Most other species of tuco-tucos with restricted ranges were traditionally referred to as Data Deficient (DD; see SAREM-MAYDS 2019; but see Caraballo et al. 2023). However, the use of this category (DD) is not exempt of inconveniences; overall, it is uninformative as species may be categorized as such for different reasons, limiting the chances to enact conservation measures or to support additional scientific investigation on these taxa (see Teta et al., 2021). Taking into account that the new species is only known from two localities, its consideration as endangered or vulnerable seems to be more appropriate. This situation could be aggravated by tourism and the infrastructure associated with this activity, as in this valley (Las Leñas) occurs one of the largest Argentinian sky centers, being visited each year by numerous people. Additional surveys are much needed to evaluate more accurately its conservation status.

Final Remarks

The description of two new species of *Ctenomys* is not unexpected; in fact, the use of integrative approaches, coupled with specimen collection in non-sampled areas and the assessment of specimens already housed in biological collections, resulted in the recognition of 9 new living species in this genus during the last 10 years (e.g., Gardner et al. 2014; Brook et al. 2022; Mappeli et al. 2022). The wide identification of several other candi-

date species suggests that more new species of *Ctenomys* will be discovered and described in the near future. At the same time, other nominal forms have been recently synonymized as a result of taxonomic efforts (e.g., Teta et al. 2020; Teta and D'Elía 2020; D'Elía et al. 2021). Additionally, several species have been recently included in phylogenetic analyses, allowing the clarification of their placement within the radiation of *Ctenomys* (e.g., Sánchez et al. 2019; Londoño-Gaviria et al. 2019). In this regard, our analysis indicates that *C. pilarensis* is a member of the *C. tucumanus* species group, corroborating an early result, based on a short DNA fragment and a narrow taxonomic sampling, presented by Mascheratti et al. (2000). One of the species groups that have undergone more changes in the last decade is the *C. mendocinus* species group, which is the group to which belong the two new species described here. The analysis of qualitative and quantitative character traits strongly suggests that the species described here are distinguishable from other closely distributed or phylogenetically related taxa. Within the group of *C. mendocinus*, *C. eileenae* **sp. nov.** is proportionally larger and more robust (see comparisons above), inhabiting in a higher altitudinal range than other taxa of this group (> 3,500 m a.s.l.). Additionally, both morphological and molecular evidence clearly separates it from *C. fulvus*, which belongs to the *C. fulvus* species group. Finally, we also ruled out a possible conspecificity between *C. eileenae* **sp. nov.** and *C. knighti*, as was suggested by Tammone et al. (2022a), since both species depict largely distinct cranial morphologies (see comparisons above). Similarly, *C. verzi* **sp. nov.** has a unique combination of character traits, including a moderately robust skull with a markedly inflected dorsal profile at the parietal-occipital region; moderately long and broad incisive foramina and moderately inflated and pyriform auditory bullae. Additionally, the morphological and molecular evidence clearly separates it from *C. maulinus* and *C. pontifex*, other two species distributed in nearby Andean regions.

In addition to providing evidence for the existence of the new species described above, our results are relevant for other aspects of the specific diversity of the *C. mendocinus* species group. These issues include the suggestion of a novel synonymy (i.e., *C. validus* under *C. mendocinus*; see discussion below), the inclusion of a species in the species group (i.e., *C. fochi*), as well as the corroboration of the existence of other candidate species whose distinction needs to be further evaluated (see discussion below).

Two haplotypes recovered from paratype specimens of *C. validus* are part of the clade corresponding to *C. mendocinus* sensu stricto; moreover, they fall in a subclade with an haplotype of a topotype of *C. mendocinus*. Previous studies, based on multivariate statistical analysis of cranial measurements, also suggest a close similarity between topotypical samples of *C. validus* and *C. mendocinus* (Rosi et al. 1992). The only two specimens of *C. validus* that we studied are slightly larger than those analyzed belonging to *C. mendocinus* (cf. Fig. 3); however, we were unable to find qualitative craniodental dif-

ferences between *C. validus* (see Supplementary Material 4) and *C. mendocinus*, despite some minor distinction in their external coloration (i.e., studied specimens of *C. validus* have a conspicuous collar of whitish hairs). Together, the molecular and morphological evidence allows us to formally suggest that *C. validus* is a synonym of *C. mendocinus*; this taxonomic hypothesis should be tested with the analysis of nuclear DNA sequences.

Although we lack DNA sequences for specimens indisputably assignable to *C. johannis*, both the original description and the examination of one topotype of this nominal form, allow us to hypothesize that *C. johannis* is also a synonym of *C. mendocinus* or at least a closely related cryptic species (see also Fig. 3). In fact, we were unable to find qualitative or quantitative differences between them; both taxa are characterized by relatively globose, well visible in dorsal view, tympanic bullae, and have proportionally short and broad incisive foramina (cf. Fig. 12).

In a novel result of this study, the phylogenetic analysis of mitochondrial DNA sequences placed haplotypes of two topotypes of *C. fochi* within the clade of the *C. mendocinus* species group, indicating that *C. fochi* is a member of this species group. Interestingly, sister to the clade formed by sequences of *C. fochi* appears the sequence of one individual (AO472) from Córdoba province. The latter differs on average by 1.21 % from topotypic sequences of *C. fochi*, a value that is observed in intraspecific comparisons of *Ctenomys* (e.g., Londoño-Gaviria et al. 2019; Teta et al. 2020). Considering this and based on its overall cranial morphology (see Supplementary Material 4), we tentatively assign this specimen to *C. fochi*, extending as such the known distribution of this species ca. 200 km to the southeast. Similarly, haplotypes from the candidate species identified by Mapelli et al. (2017) as “Arenales” form a clade with those of the nearby candidate species “Tupungato” identified by Parada et al. (2011); this clade (i.e., “the Arenales-Tupungato lineage”) is relatively homogenous (average percentage of genetic distance among the four included haplotypes: 1.00) and sister to the clade containing the haplotypes of *C. fochi*. Average genetic divergence between the “Arenales-Tupungato lineage” and that containing haplotypes of *C. fochi* is 1.86 %. Additional studies, including the assessment of morphological evidence, are needed to evaluate the status of these populations allied to *C. fochi* (i.e., Córdoba and in particular of the “Arenales-Tupungato lineage”).

In accordance with previous contributions, our analysis depicts that there are other lineages within the *C. mendocinus* species group that may represent distinct species; in some cases, no names appear to be available for them. Along with the above mentioned case of the “Arenales-Tupungato lineage”, there is the “Quijadas lineage”, from San Luis province, first identified by Mapelli et al. (2017). In any case, their distinction as different species needs to be further tested with other sources of evidence. Unfortunately, no vouchers associated with all these sequences are available, as some sequences were gathered from biopsies from animals later released. Finally, *C. famosus*, whose mitochondrial variation was recently de-

scribed as arranged into two allopatric clades (“Velazco” and “Famatina” clades, sensu Tammone et al. 2022a), a result corroborated and expanded here, also needs to be further evaluated. According to our results, some samples from Antofagasta de la Sierra (Catamarca), first reported by Lacey et al. (2022) as *Ctenomys* sp., also belong to *C. famosus* (as part of the “Famatina clade” of Tammone et al. 2022a), enlarging to the north the distribution of this species ca. 260 km.

Of particular interest is the novel finding of a clade formed by the sequence of one specimen from Auca Mahuida, eastern Neuquén province (referred as *C. sp. 4* by Tammone et al. 2021) and haplotypes of specimens (labeled by Carnovale et al. 2021 as *C. azarae*, which is now regarded as a synonym of *C. mendocinus*) from two localities, General Acha and Reserva Provincial Parque Luro, in La Pampa province (as stated above, we refer to this clade as to the “Neuquén-La Pampa lineage”). This is remarkable because the Pampean localities are in the distributional area of *C. mendocinus* (see D’Elía et al. 2021) and at both localities where collected other specimens whose sequences, gathered by Carnovale et al. (2021), form part of the clade *C. mendocinus* sensu stricto. Remarkably, the clades corresponding to the Neuquén-La Pampa lineage and *C. mendocinus* sensu stricto are not sister to each other, as *C. mendocinus* sensu stricto appears sister to *C. flamarioni*; this suggests that the mitochondrial lineage referred to as the Neuquén-La Pampa lineage appears to be of species level. The possibility that two species of *Ctenomys* (i.e., *C. mendocinus* and the Neuquén-La Pampa lineage) occurring at General Acha and Reserva Provincial Parque Luro cannot be ruled out. Having said that, we note that no case of strict sympatry involving two or more species of *Ctenomys* is known, although at some areas, distinct species (e.g., *C. australis* and *C. talarum*; *C. flamarioni* and *C. minutus*) are distributed next to each other (see details in Bidau 2015). However, we note that a single coordinate was given in Carnovale et al. (2021), for each of these localities, meaning that if *C. mendocinus* and the Neuquén-La Pampa lineage are in fact distinct species, they occur in sympatry. Another possibility is that *C. mendocinus* and the Neuquén-La Pampa lineage represent a single species (i.e., *C. mendocinus*) that is paraphyletic with respect to *C. flamarioni* at the mitochondrial genome. This scenario is not unexpected, as several cases of non-monophyletic species at the mitochondrial genome are known (i.e., Rengifo et al. 2023); this is particularly true for species that are widespread and presumably have large effective population sizes. Unfortunately, no voucher specimens were secured for the samples from General Acha and Reserva Provincial Parque Luro, as DNA was extracted from tail tips of specimens that were later released (Carnovale et al. 2021: 3); as such, the phenotype of the specimens representative of these two mitochondrial lineages cannot be assessed in order to clarify if the Neuquén-La Pampa lineage represents a distinct species than *C. mendocinus* sensu stricto. This situation should be taken as a strong call of attention on the need to collect complete specimens and preserve

them in biological collections, especially in groups, such as *Ctenomys*, whose alpha taxonomy is far from being well understood and stable.

Another fact of much interest is that three analyzed sequences (AF370697, MZ333061, MZ333062) labeled in GenBank as *C. australis*, fall within the clade of *C. mendocinus*. *C. australis* is a species with a geographic distribution along the southern Atlantic coast of Buenos Aires province and that is easy to distinguish morphologically from other nearby species (i.e., *C. talarum*) and those of the *C. mendocinus* species group (see details in Bidau 2015). As such, we maintain that *C. australis* represents a distinct lineage at the species level. Unfortunately, as in the case mentioned above, no voucher specimens are associated with these three sequences referred to as *C. australis*. As such, we cannot check the phenotype of these individuals to evaluate if they correspond to that of *C. australis* or other species (we mention that the only other species of *Ctenomys* known in the area where these specimens were collected, around the city of Necochea, is *C. talarum*, a species that does not belong to the *C. mendocinus* species group and is morphologically distinct from *C. australis*). Therefore, our results may reflect a case of incongruence between the gene and the species trees (see review in D'Elía et al. 2019), likely caused by retention of an ancestral polymorphism or introgression (in this later case of mtDNA of *C. mendocinus* into a genomic background of *C. australis*). More data, which should be gathered from vouchered specimens, are needed to clarify this scenario.

Recent advances in the taxonomy of the genus *Ctenomys* have greatly benefited from the use of biological collections; not only in the traditional ways (i.e. through the inspection of the phenotype of large specimen series) but also from the extraction of DNA from the skins of individuals collected decades ago (e.g., Teta and D'Elía 2020; Teta et al. 2022; this study). This last point highlights again the value of the specimens housed in biological collections, which can be studied through new methodologies in ways that were unsuspected at the time of their capture (e.g., Gardner et al. 2021). This reason invites us to continue collecting specimens in the field, both to fill geographic and temporal sampling gaps, which along current used approaches, would allow implementing data gathering and analyses not yet envisioned.

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Supplementary Material 1

File 1

Authors: Teta P, Jayat JP, Alvarado-Larios R, Ojeda AA, Cuello P, D'Elía G (2023)

Data type: .docx

Explanation note: 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). Sequences with a * correspond to samples referred in Genbank as of *C. australis* (see the discussion in the main text). Sequences identified with a ^ were gathered from paratypes of *C. validus* (see discussion in the main text). Species/lineage assignment follows the taxonomy discussed in the text.

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Link: <https://doi.org/10.3897/vz.73.e101065.suppl1>

Supplementary Material 2

File 2

Authors: Teta P, Jayat JP, Alvarado-Larios R, Ojeda AA, Cuello P, D'Elía G (2023)

Data type: .xlsx

Explanation note: Individual measurements for specimens of *Ctenomys* used in the morphological analysis. For collection acronyms and measurement abbreviations see the section of “Materials and methods”.

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Link: <https://doi.org/10.3897/vz.73.e101065.suppl2>

Supplementary Material 3

File 3

Authors: Teta P, Jayat JP, Alvarado-Larios R, Ojeda AA, Cuello P, D'Elía G (2023)

Data type: .xlsx

Explanation note: External measurements (in mm) of the paratypes of *Ctenomys eileenae* n. sp. See the text for abbreviations.

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Link: <https://doi.org/10.3897/vz.73.e101065.suppl3>

Supplementary Material 4

File 4

Authors: Teta P, Jayat JP, Alvarado-Larios R, Ojeda AA, Cuello P, D'Elía G (2023)

Data type: .docx

Explanation note: Supplementary figures.

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