

Original study

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A reappraisal of the species richness of *Euneomys* Coues 1874 (Rodentia, Cricetidae), with emendations of the type localities of *Reithrodon fossor* Thomas 1899 and *Euneomys mordax* Thomas 1912

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Abstract: The genus *Euneomys* is mostly distributed in the open environments of the central and southern Andes, adjacent Patagonian steppes of Argentina and Chile, and in several islands of the Tierra del Fuego Archipelago. This genus includes three living species: *E. chinchilloides*, *E. fossor*, and *E. mordax*. *Euneomys fossor* is a poorly known species, with an uncertain geographic provenance and known from a single specimen, whose distinction from the other species of the genus has not been accurately assessed. Here, using qualitative and quantitative morphological evidence, plus published information about karyotypes and genetic variation, we evaluate the taxonomic status of *E. fossor* and *E. noei*, a nominal form usually considered a synonym of *E. mordax*. Based on multivariate analysis of cranial measurements and morphological discrete traits, we recognize two main morphotypes within *Euneomys*, one referable to *E. chinchilloides* (with *dabbenei*, *petersoni*, and *ultimus* as

synonyms), and another including *E. fossor*, *E. mordax*, and *E. noei*. The recognition of two major groups within *Euneomys* is also supported by molecular and chromosomal data. By the principle of the priority, the names of *E. chinchilloides* and *E. fossor* applies for each one of these morphotypes. In addition, after discussing the pros and cons of replacing the name *mordax* by *fossor*, we emended the type localities of both forms.

Keywords: Andes; *Euneomys chinchilloides*; Sigmodontinae; species limits; taxonomy.

1 Introduction

Species of the genus *Euneomys* Coues 1874 (including *Chelemyscus* Thomas 1925) are distributed from west-central Argentina and central Chile to the archipelago of Tierra del Fuego, in southernmost South America (Braun and Pardiñas 2015); in addition, there is a dubious record from northwestern Argentina (see below). Species of this genus are typical dwellers of barren, rocky, windswept steppes, as well as open grassland with thickets of *Nothofagus* above the tree line in the Andes (Pearson and Christie 1991; Pine et al. 1979).

As is currently conceived, the genus *Euneomys* includes three species of medium-sized, heavy-bodied, herbivorous rats: 1) *Euneomys chinchilloides* (Waterhouse 1839), which includes *petersoni* J. A. Allen 1903 (for the unjustified recognition of this nominal form as a separate species see Braun and Pardiñas 2015), *dabbenei* Thomas 1919, and *ultimus* Thomas 1916; 2) *Euneomys fossor* (Thomas 1899); and 3) *Euneomys mordax* Thomas 1912, including *Euneomys noei* Mann 1944. As such, only seven specific nominal forms are associated to *Euneomys*.

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However, the number of recognized species within the genus has been unstable.

Thomas (1916, 1919) recognized six species under two genera, *Chelemyscus* (including *fossor*) and *Euneomys* (including *chinchilloides*, *dabbenei*, *mordax*, *petersoni*, and *ultimus*). Osgood (1943), in his review of Chilean mammals, listed *chinchilloides* (including *ultimus*) and *petersoni* (including *dabbenei*) under *Euneomys* and doubted about the generic distinction of *Chelemyscus*. Cabrera (1961) retained *Chelemyscus* as a subgenus of *Euneomys*, including as species *mordax* and *fossor* in the former, and *chinchilloides* and *petersoni* in the latter. Subsequently, Hershkovitz (1962) referred four living species under *Euneomys* (*chinchilloides*, *fossor*, *mordax* and *noei*), raising some doubts about the distinction of *fossor*, *mordax*, and *noei* from *chinchilloides*.

To the end of the decade of 1980, Yañez et al. (1987) considered *Euneomys* as monotypic, including all nominal forms under *E. chinchilloides*. At the beginning of the decade of 1990, *Euneomys* was reviewed by Reise and Gallardo (1990) and Pearson and Christie (1991). These authors agreed into recognize two species (i.e., *E. chinchilloides* and *E. mordax*), but disagreed about the taxonomic status of *noei*. Reise and Gallardo (1990) retained it as a subspecies of *E. chinchilloides*, while Pearson and Christie (1991) suggest its synonymy with *E. mordax*. In addition, Pearson and Christie (1991) linked *fossor* to *E. mordax*, mostly based on the measurements of the type.

More recently, phylogenetic analyses of mtDNA sequences corroborated the hypothesis that *Euneomys* includes two main lineages, for which the names *chinchilloides* and *mordax* were used (Lessa et al. 2010; Ojeda et al. 2015). In addition, these studies recovered a geographically structured genealogy for *E. chinchilloides*, which in addition to karyotypic evidence suggest that this taxon could include more than one lineage of species level (Lessa et al. 2010; Ojeda et al. 2015).

E. fossor is perhaps one of the least known sigmodontine rodents, being only known from its type specimen whose collection locality is uncertain (Braun and Pardiñas 2015; Pearson 1984; Pearson and Christie 1991; Teta and D'Elía 2019). Originally described as *Reithrodon fossor* by Thomas (1899), and successively included within *Euneomys* (Thomas 1901) and *Chelemyscus* (Thomas 1925), this name was based on one specimen from “Salta Province, N. Argentina.” (ca. -25°). This putative area is well apart from all other records of the genus, which occurs south of -33° (Braun and Pardiñas 2015; Vianna et al. 2011), raising doubts about the correctness of its attributed geographical origin (see Braun and Pardiñas 2015 for a more complete discussion about this still unresolved issue).

An additional inconvenient regarding the type and the only known specimen of *fossor* is that this animal is a combination of a skin of *Paynomys* (Sigmodontinae, Abrotrichini) and a skull of *Euneomys* (Pearson 1984). Interestingly, Thomas (1899) already advanced doubts about the correspondence between the skin and skull of this individual, selecting for nomenclatorial purposes the skull as the type of the nominal form. However, some years later, Thomas (1925) used both the skin and skull to describe *Chelemyscus*, a new genus in which he placed *fossor*.

In turn, *E. noei* was described by Mann (1944), based on specimens from “«Valle de la Junta», Cajón del Río Volcán, a 2,400 m de altura.” (Santiago, Chile). Pine et al. (1979) added a second locality for this species in central Chile, suggesting that the type series of *noei* could be composed of two different sympatric species.

In this contribution, on the largest sample of *Euneomys* analyzed so far, we conducted an analysis of qualitative and quantitative morphological traits, to reevaluate the taxonomic status of *E. fossor* and *E. noei*. The uncovered pattern of morphologic variation was contrasted with available chromosome and molecular data. Based on our results, we made some comments about the taxonomy of *Euneomys* and the lineages that compound the genus.

2 Materials and methods

The specimens that form the basis of this study are housed in the following scientific collections (see also Appendix): CMI, Colección Mamíferos del IADIZA, Instituto Argentino de Investigaciones de Zonas Áridas (Mendoza, Argentina); CNP-E, Colección de Material de Egagrópilas y Afines “Elio Massoia”, Centro Nacional Patagónico (Puerto Madryn, Argentina); FMNH, Field Museum of Natural History (Chicago, USA); MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina); MHNSR, Museo de Historia Natural de San Rafael (San Rafael, Argentina); MVZ, Museum of Vertebrate Zoology (Berkeley, USA); UACH, Colección de Mamíferos, Universidad Austral de Chile (Valdivia, Chile); and USNM, United States National Museum of Natural History (Washington, DC, USA). Both the holotypes of *E. fossor* (BM [British Museum of Natural History] 99.2.22.25) and *E. noei* (USNM 391817) were examined, the first through high resolution photographs and the second directly. We also reviewed (all through high resolution photographs) the holotypes of *E. chinchilloides* (BM 55.12.26.111), *E. mordax* (BM 55.12.24.199), *Euneomys petersoni* (USNM 84198), and *Euneomys ultimus* (BM 43.11.16.26).

Studied specimens ($N = 223$) were grouped into three main operational groups based on previous results of phylogenetic analysis of mtDNA sequences (see Lessa et al. 2010) and discrete morphological traits (cf. Tammone et al. 2016). One group is composed by populations traditionally referred to *E. mordax*

(localities 4, 6, 7, 9, 11, 13, 20, 21), while the other two correspond to the two allopatric haplogroups or clades recognized within *E. chinchilloides* (Lessa et al. 2010). The latter two are labelled as north (localities 1–19 and 21–27; Figure 1), encompassing samples from northern Mendoza to northern and central Chubut (Argentina), and south (localities 28 to 44; Figure 1), including those specimens from southwestern Chubut to the island of Tierra del Fuego and adjoining southern islands (Argentina and Chile).

Anatomical terminology for cranial and dental features follows Stepan (1995) and Pardiñas et al. (2015). Surveyed characters included those previously described in the literature (e.g., Osgood 1943; Pearson and Christie 1991; Reise and Gallardo 1990; Tammone et al. 2016) and others newly reported herein.

Eleven skull variables were measured to 0.01 mm using digital calipers under a dissecting microscope (measurements are defined by Patterson [1992], Teta and Pardiñas [2014] or explained between brackets): breadth of rostrum (BR); breadth of nasals (BN); breadth across zygomatic notches (BZN, greatest distance between the outer border of zygomatic notches); interorbital breadth (IOB); breadth of zygomatic plate (BZP); length of incisive foramen (LIF); breadth across incisive foramina (BIF); palatal bridge (PB, least distance between the posteriormost point of the incisive foramen and the posterior border of the palate); palatal width at the upper first molar (BM1); palatal width at the upper third molar (BM3); alveolar length of maxillary tooth row (MTR). Most cranial dimensions were restricted to the anterior part of the skull, due to the incomplete nature of most specimens recovered from owl pellet samples. Some measurements of the type of *fossor* were taken from Thomas (1899), while others were recorded using the tpsDig2 digitization software (Rohlf 2013).

Skull variables were analyzed to summarize patterns of variation within and among the studied populations using standard descriptive statistics (mean, range, standard deviation) and principal component analysis (PCA). To conduct the PCA, we firstly transformed the skull measurements to logarithms (base 10). PCA were extracted from the variance-covariance matrix of the whole set of analyzed specimens. A second PCA was carried out limited to specimens from localities where *E. chinchilloides* and *E. mordax* were detected living in sympatry (Pearson and Christie 1991; Tammone et al. 2016, Figure 1). All statistical procedures were implemented using the software PAST v. 2.17 (Hammer et al. 2001).

3 Results

The studied specimens exhibit two distinctive morphotypes. Morphotype 1 includes specimens broadly referred to *E. chinchilloides*, including the holotypes of this nominal form, *E. petersoni* and *E. ultimus*, and a nearly topotypes of *Euneomys dabbenei* (locality 39; Figure 1). Overall, these animals are smaller (Table 1), with the upper incisors with a laterally positioned groove, less expanded nasals and rostri, and have the fossa containing the posterolateral palatal pits more ovate and not extended anteriorly as a groove (Table 2). Morphotype 2 includes specimens traditionally referred to *E. mordax*

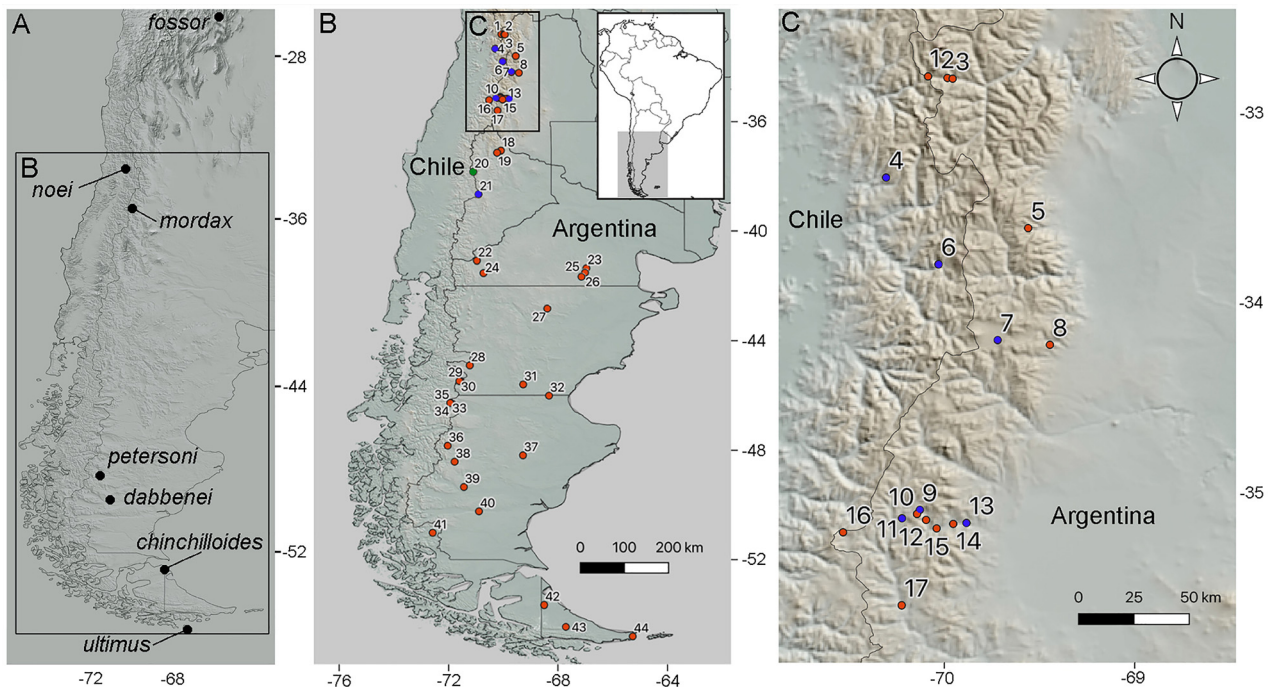


Figure 1: (A) Map of southern South America depicting the placement of the type localities of the nominal forms included within *Euneomys*. (B) Map of southern South America depicting the collection localities of the specimens of *Euneomys* studied in this work. (C) Amplified area in Mendoza Province and neighboring areas of Chile.

Colors are as follow: green circle, *Euneomys fossor*; red circles, *E. chinchilloides*; blue circles, documented sympatries between these taxa.

(Figure 2) as well as the holotypes of *E. fossor* (Figure 3) and *E. noei* (Figure 4). These specimens are characterized by larger skulls (Table 1), upper incisors with a centrally positioned groove, broader nasals and rostri, and by having the fossa containing the posterolateral palatal pits transversally compressed and extended anteriorly as a groove (Table 2). In addition, the morphotype 1 has proportionally much larger tympanic bullae and a broader mesopterygoid fossa than the morphotype 2 (Table 2; Figure 5).

PCA revealed that all variables were positively correlated with the first principal component (PC1, 61.9% of the total variance), suggesting that it mostly correspond to a size vector (Figure 6A, Table 3). Along this PC, the highest

loadings correspond to BN, BR and BZN. In the PC2 (11.3%), the most important variables were LIF, BM1 and BM3. Overall, the samples north and south of *E. chinchilloides* broadly overlap in the multivariate space defined by the first two PCs, at the time that completely segregate from those referred to *E. mordax* and the holotypes of *fossor* and *noei* (Figure 6A). The holotypes of *E. fossor* and *E. noei* fall well within the multivariate space defined by the specimens currently assigned to *E. mordax* (Figure 6A). The clear separation of the studied specimens in two main morphometric groups is in accordance with the distribution of the morphotypes described above. The PCA for sympatric specimens of both morphotypes depict the same general results (Figure 6B, Table 3). Both morphometric groups

Table 1: Summary statistics (mean, SD, range) of cranial measurements (in mm) of adult samples (*N*) of *Euneomys*.

	<i>E. chinchilloides</i> (north)					<i>E. chinchilloides</i> (south)					<i>E. fossor</i> (= <i>E. mordax</i>)					<i>E. fossor</i> ^a	<i>E. noei</i> ^b
	<i>N</i>	Mean	SD	Min.	Max.	<i>N</i>	Mean	SD	Min.	Max.	<i>N</i>	Mean	SD	Min.	Max.		
BR	90	5.65	0.24	4.98	6.12	113	5.22	0.29	4.6	6.51	17	6.77	0.32	6.07	7.27	7.06	6.12
BN	90	4.86	0.25	4.07	5.44	113	4.44	0.24	3.91	5.28	17	5.81	0.24	5.30	6.10	6.00	5.47
BZN	90	7.18	0.39	6	8.08	113	6.91	0.36	5.96	7.7	17	8.37	0.59	7.13	9.31	8.86	7.90
IOC	90	3.83	0.17	3.41	4.2	113	3.74	0.18	3.26	4.3	17	4.44	0.23	4.18	4.80	4.40	4.52
BZP	90	3.08	0.19	2.53	3.5	113	2.92	0.2	2.43	3.43	17	3.53	0.28	2.98	4.13	2.88	3.09
LIF	90	7.93	0.4	6.5	8.73	113	7.7	0.4	6.67	9.09	17	8.10	0.57	6.49	8.98	8.50	7.58
BIF	90	1.83	0.15	1.4	2.22	113	1.75	0.12	1.49	2.04	17	2.24	0.15	1.97	2.60	2.14	2.10
PB	90	5.78	0.35	5.11	6.48	113	5.38	0.3	4.65	6.07	17	6.52	0.50	5.82	7.68	6.36	6.33
BM1	90	2.65	0.31	1.98	3.37	113	2.73	0.28	2.14	3.3	17	2.78	0.22	2.34	3.12	2.66	2.64
BM3	90	4.15	0.33	3.2	4.87	113	4.04	0.29	3.3	4.69	17	4.34	0.35	3.63	5.21	4.72	3.69
MTR	90	5.85	0.22	5.35	6.37	113	5.58	0.21	5.14	6.25	17	6.45	0.28	5.84	6.98	6.50	6.83

See the text for an explanation of variable abbreviations. ^aHolotype, BM 99.2.22.25. ^bHolotype, USNM 391817.

Table 2: Selected traits for a qualitative morphological differentiation between *Euneomys chinchilloides* and *E. fossor* (= *mordax*).

	<i>E. chinchilloides</i>	<i>E. fossor</i>	References
Dorsal coloration	Usually brownish, variable washed with buff or gray	Darker and grayer	Pine et al. 1979
Dark band on top of tail	Broad	Narrow	Pine et al. 1979
Anterior third of nasals	Expanded	Widely expanded	Pine et al. 1979
Fossa containing posterolateral palatal pits	Transversally compressed	Ovate	Pine et al. 1979, Tammone et al. 2016
Anterior border of mesopterygoid fossa	With a palatine process	Rounded	Tammone et al. 2016
Mesopterygoid fossa	Proportionally broad	Proportionally narrow	This work
Tympanic bullae	Proportionally larger	Proportionally smaller	This work
Position of grooves on upper incisors	Lateral	Medial	Pine et al. 1979, Pearson and Christie 1991
M3	Without a remnant of paraflexus	With a remnant of paraflexus	Tammone et al. 2016
m1 prociungulum	With anteromedian flexid, isolated from the rest of the tooth	Without anteromedian flexid, connected to the rest of the tooth	Tammone et al. 2016



Figure 2: Lateral, dorsal, and ventral views of the skull, and labial view of the mandible of the holotype of *Euneomys mordax* Thomas 1912 (BM 55.12.24.199). Scale = 5 mm. Photographs courtesy of the British Museum of Natural History, The Natural History Museum, London.



Figure 3: Lateral, dorsal, and ventral views of the skull, and labial view of the mandible of the holotype of *Reithrodon fossor* Thomas 1899 (BM 99.2.22.25). Scale = 5 mm. Photographs courtesy of the British Museum of Natural History, The Natural History Museum, London.



Figure 4: Lateral, dorsal, and ventral views of the skull, and labial view of the mandible of the holotype of *Euneomys noi* Mann 1944 (USNM 391817). Scale = 5 mm.

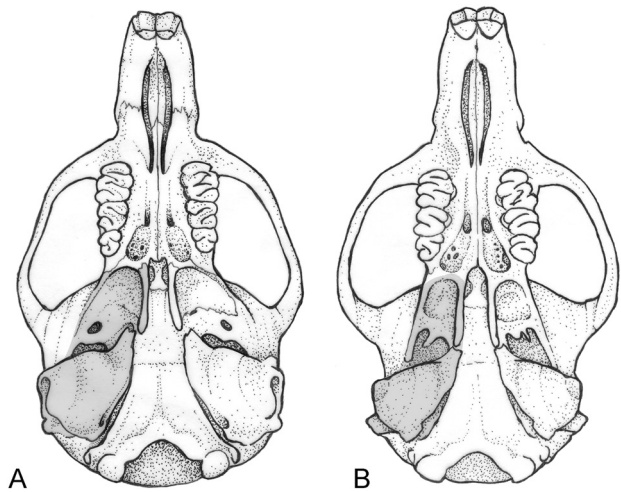


Figure 5: Schematic representations of the skull of *Euneomys chinchilloides* (A) and *E. fossor* (B). Note the differences in shape and relative size of mesopterygoid fossa and tympanic bullae (shadow area). Also conspicuous is the difference in the position of grooves on the upper incisors. Figures are not in scale to facilitate comparisons.

have a complete separation. In this case, all specimens can be differentiated along the PC1 (67.4%), being the BZN the most important variable along this axis.

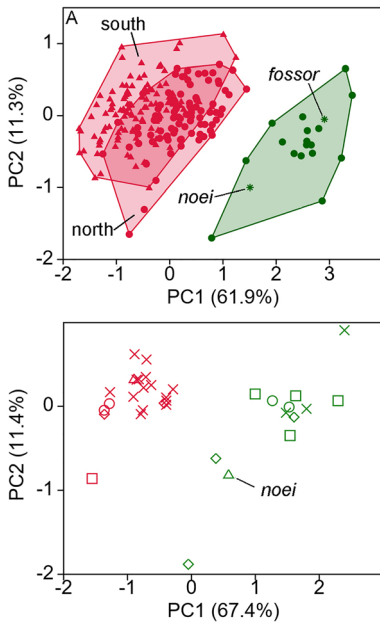


Figure 6: (A) Specimen scores for principal components 1 and 2 for the two main groups of *E. chinchilloides* (in red, see the text for more details), and *E. fossor* (in green), and the holotypes of *E. fossor* and *E. noei*. (B) Specimen scores for principal components 1 and 2 for sympatric specimens referred to *E. chinchilloides* (red) and *E. fossor* (green); each locality is referred by the same symbol with different color as follow: circles, La Parva [Santiago, Chile]; crosses, Laguna de la Niña Encantada [Mendoza, Argentina]; diamonds, Paso de Pino Hachado [Araucanía, Chile]; squares, Las Leñas [Mendoza, Argentina]; triangles, Valle de La Junta [Santiago, Chile].

Table 3: Results of principal components analyses (PCA) performed on three operational groups of *Euneomys* and the holotypes of *E. fossor* and *E. noei* (first and second columns; see also Figure 6A) and for a subset of samples from localities in which *E. chinchilloides* and *E. fossor* (= *E. mordax*) occur in sympatry (third and fourth columns; see also Figure 6B).

	PC 1	PC 2	PC 1	PC 2
BR	0.4722	-0.0823	0.4203	-0.0917
BN	0.4198	-0.0979	0.3776	-0.1544
BZN	0.4777	-0.0315	0.6275	0.2889
IOC	0.1688	-0.1588	0.2086	-0.3233
BZP	0.1800	0.0409	0.2146	0.0767
LIF	0.2521	0.6671	0.0937	0.7612
BIF	0.1392	-0.0056	0.1443	-0.1412
PB	0.3581	-0.3417	0.2979	-0.1717
BM1	0.0789	0.4373	0.1308	0.0378
BM3	0.1621	0.4298	0.1015	0.2529
MTR	0.2602	-0.1334	0.2269	-0.2988
% Variance	61.91	11.30	67.40	11.13
Eigenvalue	1.0243	0.1870	1.4122	0.2333

See the text for an explanation of variable abbreviations.

4 Discussion

Qualitative and quantitative morphological traits allow to clearly separate two main morphotypes within *Euneomys* (Table 2; Figure 5; Supplementary Figures 1s–3s). This distinction agrees with molecular and cytogenetic evidence that showed two main clades within this genus, characterized each by different chromosome complements (Ojeda et al. 2005, 2015; Reise and Gallardo 1990). For the first morphotype ($2n = 34$ or 36), applies the name *chinchilloides* (including *dabbenei*, *petersoni*, and *ultimus* as synonyms), while the name for the other morphotype ($2n = 42$), usually referred to *E. mordax*, is discussed below. Overall, our results are in accordance with those reached by Pine et al. (1979), Pearson and Christie (1991), Reise and Gallardo (1990) and Lessa et al. (2010).

Morphological evidence strongly suggests that *E. fossor*, *E. noei*, and *E. mordax* are conspecific. Based on the principle of priority, we include *mordax* and *noei* under the synonymy of *fossor*. While the inclusion of *noei* under the synonymy of *mordax* has not major implications and it is currently accepted by some authors (e.g., Braun and Pardiñas 2015), the case of *fossor* is distinct as both forms are currently regarded as represent distinct species (e.g., Teta et al. 2018). Antedating *mordax* by 13 years, the name *fossor* has priority if both taxa are considered as synonyms. However, previous authors (e.g., Pearson and Christie 1991) suggested that considering *fossor* as the senior synonym presents several inconveniences, given the uncertain provenance of the holotype of *fossor* and its incomplete nature. We note, however, that both the skulls of the type specimens of *fossor* and *mordax* are fragmentary. That of *fossor* is incomplete, inasmuch lacks part of one zygomatic arch and a portion of the occipital (Figure 3). However, it is more complete than that of the type of *mordax*, which is severely damaged, lacking their nasals, parts of both zygomatic arches, the braincase and the occipital (Figure 2). As such, the skull of the type of *fossor* is more informative than that of *mordax*. It is also true that the type of *fossor* lacks a skin (see below), while the type of *mordax* includes a skin.

Similarly, the types localities of both species are problematic. That of *mordax* was recorded by Thomas (1912) as “Fort San Rafael, Mendoza Province,” but as Pearson and Lagiglia (1992) discussed, based on historical and biogeographical arguments, it is much more likely that the type of *mordax* has been captured near the Peteroa volcano, along the border between Argentina and Chile. The reasoning behind this assertion is that the

environment around San Rafael (shrubby steppes of the Monte Desert) do not accomplished the type of habitat occupied by *mordax* (i.e., high altitude grasslands with low bushes or thickets of *Nothofagus*, wet “alpine” meadows with deep soil; cf. Pearson and Christie 1991; Pine et al. 1979; Braun and Pardiñas 2015). Accordingly, Ojeda et al. (2005) considered as topotypes specimens collected at Valle Hermoso (Mendoza, Argentina), which is placed ca. 28 km E from the Peteroa volcano. We view the consideration made by Ojeda et al. (2005) as correct; however, these authors did not formally amend the type locality of *mordax*. As such, here we formally do it, amended it to “Valle Hermoso (35.09794° S, 70.10247° W, 2460 m), departamento de Malargüe, provincia de Mendoza, (Argentina), 28 km al este del volcán Peteroa,” which is the locality where Ojeda et al. (2005) collected the specimens by them karyotyped.

The type locality of *fossor* was recorded by Thomas (1899) as “Salta Province, N. Argentina.” However, no additional specimens of *Euneomys* has been collected at such latitude (i.e., ca. -25°) during the 120 years followed the description of *fossor* (see for example Díaz et al. 2000). That area in the province of Salta is more than 750 km N from the nearest documented record of *Euneomys*. Based on our current knowledge of this genus, it seem unlikely that *fossor* had been caught in northwestern Argentina (see Tammone et al. 2016 for a model of the predicted probability of occurrence of this species). In addition, the skin associated to the skull of *fossor* correspond to a specimen of *Paynomys* (Supplementary Figure 2s), a rodent genus widely sympatric with *Euneomys* in central-western and southern Argentina and central and southern Chile and unknown from northwestern Argentina (cf. Teta et al. 2014). Therefore, all available evidence indicates that the type locality of *fossor* is incorrect, a fact that need to be emended (Article 76, Recommendation 76A.2 of the ICZN [1999]). The type of *fossor* was sent as a fluid-preserved specimen to Oldfield Thomas by Francisco P. Moreno, by this time the director of the Museo de La Plata (Thomas 1899). As no additional data is accompanying the original material, nor collector’s notes or itineraries seems to exists, in accordance to recommendation 76A.2 (“A statement of a type locality that is found to be erroneous should be corrected”) of the ICZN (1999) here we amend the type locality of *fossor* Thomas 1899. In doing so, we followed recommendation 76A.1.4 (“as a last resort, and without prejudice to other clarification, localities within the known range of the taxon or from which specimens referred to the taxon had been taken”; ICZN 1999) and set the type locality of *fossor* at “Paso de Pino Hachado, Neuquén, Argentina

($-38^\circ40'$, $-70^\circ54'$).” Pino Hachado is a border crossing at the frontier between Argentina and Chile. A small sample of nearly topotypes, housed at the UACH, has been caught on the Chilean side of the border and includes karyotyped specimens ($2n = 42$; FN = 66; Reise and Gallardo 1990). Even when it is unknown if the type of *fossor* was caught by Moreno himself, it is at least interesting to note that he traveled across the province of Neuquén in 1896, visiting several localities in which this species might occur, including Paso de Pino Hachado (Moreno 1897).

Besides *E. chinchilloides* is not the focus of our study, it is worth to highlight the moderate to high overlap in the multivariate space among the two main sets of specimens of *E. chinchilloides* grouped at the light of the pattern of mtDNA variation (Lessa et al. 2010). Neither the DNA genealogies (e.g., Lessa et al. 2010) nor the morphologic variation as revealed here, sustain the recognition of *E. petersoni* as a distinct species. In this context, the relatively high values of cytochrome-b genetic divergence ($>3\%$) between northern (for which no name is available) and southern populations (including *dabbenei*, *petersoni*, and *ultimus*; see Figure 1) and karyotypical evidence suggest that as is currently understood, *E. chinchilloides* could be a highly structured species or a complex of two morphologically cryptic species. Even more, Ojeda et al. (2015) recognized some chromosomal, morphological and molecular (COI gene) differences within the northern clade, suggesting that differences on diploid and fundamental numbers between populations in northern and southern Mendoza can be enough to lead to reproductive isolation. Further studies, including the inspection of more karyotypes and other molecular markers, are needed to better address the distinction between populations of *E. chinchilloides*.

Species of *Euneomys* occurs sympatrically, although not necessarily syntopically, along the central Andes, from -33° to -39° (cf. Novillo and Ojeda 2012, 2014; Figure 1; Pearson and Christie 1991). This situation has led to the confusion of some authors, which failed to recognize or minimized the differences among individuals at some localities. For example, Mann (1944) include in the type series of *E. noei* specimens referable to *E. chinchilloides* (USNM 391818, USNM 391819) and *E. fossor* (USNM 391817), a fact first adverted by Pine et al. (1979). Similarly, at least two of the geographical groups defined in the study of Reise and Gallardo (1990) (i.e., “La Parva” and “Paso de Pino Hachado”) were composed of members of both taxa, a fact that caused that these authors regarded as outliers some specimens. As was previously reported (Pearson and Christie 1991; Pine et al. 1979; Tammone et al. 2016), both

species are clearly diagnosable, being each characterized by a unique combination of external, cranial and dental traits (see Table 2). To the differences indicated by these authors, we added that *E. fossor* has proportionally much smaller tympanic bullae and a narrower mesopterygoid fossa than *E. chinchilloides* (see Table 2; Figure 5).

The taxonomy of the genus *Euneomys* during the XIX and XX centuries was assessed using small sample sizes, widely scattered across most of the southern cone of South America, from -33° to the islands of the Cabo de Hornos. For example, Osgood (1943), in his review of the mammals from Chile, studied only 21 individuals collected along more than 1000 linear kilometers. Subsequent authors encountered the same problem, highlighting also the large distances among known localities (Pine et al. 1979). This scenario began to change around the decade of 1980, when more specimens became available due to field collection of specimens, including several recovered from owl pellet (e.g., Pardiñas et al. 2003); in this regard was relevant the discovery that *Euneomys* lives in habitats so bare and open that previously were rarely sampled by collectors (Pearson 1987; Pearson and Christie 1991). However, additional integrative studies are needed, especially regarding the situation of *E. chinchilloides*, which judging by molecular and karyotypic data could include more than one lineage of species level.

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Appendix: List of the specimens examined in this study and their localities.

Species allocation follows the taxonomic scheme here proposed (see text). Acronyms are as follows: CMI, Colección Mamíferos del IADIZA, Instituto Argentino de Investigaciones de Zonas Áridas (Mendoza, Argentina); CNP-E, Colección de Material de Egagrópilas y Afines Elio Massoia,” Centro Nacional Patagónico (Puerto Madryn, Argentina); FMNH, Field Museum of Natural History (Chicago, USA); MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina); MVZ, Museum of Vertebrate Zoology (Berkeley, USA), MHNSR, Museo de Historia Natural de San Rafael (San Rafael, Argentina), UACH, Colección de Mamíferos, Universidad Austral de Chile (Valdivia, Chile); USNM, United States National Museum of Natural History (Washington, DC, USA). Numbers between brackets correspond to those on Figure 1.

E. chinchilloides ($N = 204$): ARGENTINA: Chubut: [32] Escalante, 13 km SW de Holdich (CNP-E-342), [27] Gastre, Carhue Niyeu (CNP-E-631); [28] Río Senguer, 41 km O Alto Río Senguer (CNP-E-473), [31] Sarmiento, 17 km W Sarmiento (CNP-E-506); Mendoza: [1] Las Heras, Cristo Redentor, 3401 m (CMI 7409), [2] Las Heras, Los Horcones, 2854 m (CMI 7405), [3] Las Heras, Parque Provincial Aconcagua (CNP-E-390); [15] Malargüe, 10 km S de Las Leñas, margen del río Salado, 1900 m (CMI 6803), [17] Malargüe, Arroyo El Seguro, 2800 m (CMI 7418), [11] Malargüe, camino a Valle Hermoso, 2460 m (CMI 7388), [13] Malargüe, Laguna de la Niña Encantada (CNP-E-55), [10] Malargüe, Laguna Escondida (CMI 7389), [16] Malargüe, Los Azufres, Peteroa (CMI 7419), [14] Malargüe, Los Molles (CMI 7435), [8] San Carlos, Valle de Uco, 6 km O Gral Alvarado (CMI 7328); [5] Tunuyán, Refugio Scaravelli (CMI 7353, CMI 7403); Neuquén: [18] Chos Malal, 12 km NE Parque Provincial Tromen (CNP-E-529), Catán Lil (MACN-Ma 13573), [19] Chos Malal, Cueva de las Mil Chivas (CNP-E-638); Río Negro: [22] Pilcaniyeu, Cerro Microondas (UACH 1741, UACH 1742), 9 de Julio, Somuncurá, without precise locality (MACN-Ma 19139), [26] 9 de Julio, Somuncurá, Cañadón Bajada de las Nacientes (CNP-E-4), [25] 9 de Julio, Cerro Corona Grande (CNP-E-31, CNP-E-76), [23] 9 de Julio, Laguna del Paraguay (CNP-E-73), [24] Ñorquinco, Escorial de Chenquienyen,

Cerro Las Bayas, 9 km SSW Las Bayas (CMI 7009); Santa Cruz: [37] Deseado, Puesto El Cuero (CNP-E-442), [40] Lago Argentino, Cerro Fortaleza (CNP-E-500), [39] Lago Argentino, Cordón del Bagual (CNP-E-421), [36] Río Chico, Parque Nacional Perito Moreno, Alero Destacamento Guardaparque (CNP-E-386), [38] río Chico, 4.5 km aguas arriba de Estancia El Portezuelo (USNM 84198 [holotype of *E. petersoni*]); Tierra del Fuego, Antártida e Islas del Atlántico Sur: [42] Río Grande, Estancia San Julio (CNP-E-410), [43] Río Grande, Lago Fagnano (FMNH 50736), [44] Ushuaia, Bahía Buen Suceso (USNM 482138, USNM 399402, USNM 482140). CHILE: Araucanía: [21] Lonquimay, Paso de Pino Hachado (UACH 3837, UACH 3840, UACH 3844); Aysén: [35] 0.5 km N Puerto Ibáñez (FMNH 134181, FMNH 134482, FMNH 134483, FMNH 134486), [34] 2 km N Puerto Ibáñez (FMNH 133088, FMNH 133089, FMNH 134233), [33] 4 km N Puerto Ibáñez (FMNH 134184), [30] Coyhaique Alto (UACH 3671), [29] Coyhaique Alto, 4.5 km E, Fundo El Largo (FMNH 133081, FMNH 133082, FMNH 133083, FMNH 133085); Región Metropolitana: [6] La Junta, Lo Valdez, 2500 m (USNM 391818), [4] La Parva, 3000 m (USNM 399404, USNM 399405); Magallanes y de la Antártida Chilena: [41] Última Esperanza, Lago Lazo (FMNH 50592, FMNH 50593, FMNH 50595, FMNH 50596, FMNH 50597, FMNH 50584, FMNH 50585, FMNH 50587, FMNH 50588, FMNH 50589, FMNH 50590).

E. fossor ($N = 19$): ARGENTINA: Mendoza: without precise locality (MHNSR 1238), [9] Malargüe, camino a Valle Hermoso, 2460 m (CMI 7388), [13] Malargüe, Laguna de la Niña Encantada (CNP-E-55), [12] Malargüe, Las Leñas (CMI s/n ; four individuals), [7] San Carlos, Valle de Uco, Laguna del Diamante, 3982 m (CMI 7417); Neuquén: [20] Ñorquin, 1.5 km S Copahue (town) (MVZ 183288, MVZ 183289). CHILE: Araucanía: [21] Lonquimay, Paso de Pino Hachado (UACH 3841, UACH 3850), Región Metropolitana: [6] La Junta, Lo Valdez, 2500 m (USNM 391817), [4] La Parva, 3000 m (USNM 399400, USNM 399401).

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