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A chronology of the genus *Thylamys* (Didelphidae, Thylamyini), with emphasis in the forms occurring in Argentina

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Abstract: The genus *Thylamys* includes several species of small mouse opossums living predominantly in arid and semi-arid regions of South America. In Argentina, where the genus has more species, different species have been recognized (*T. bruchi*, *T. citellus*, *T. pallidior*, *T. pulchellus*, *T. sponsorius*, and *T. venustus*), but their taxonomy is still confusing. Here, I summarize what we know of the systematics and taxonomy of *Thylamys* in Argentina, including the main sources of controversy between species. I also provide a differential diagnosis for the species I recognize, a chresonymy, and current distribution maps. Finally, I describe the main issues that should be addressed to improve our understanding of the genus in Argentina.

Keywords: Didelphimorphia, distribution, marsupials, mouse opossums

Resumen: Una cronología del género *Thylamys* (Didelphidae, Thylamyini), con énfasis en las formas que habitan Argentina. El género *Thylamys* incluye varias especies de pequeños marsupiales que viven predominantemente en regiones áridas y semiáridas de Sudamérica. En Argentina, donde el género tiene más especies, se han reconocido diferentes especies (*T. bruchi*, *T. citellus*, *T. pallidior*, *T. pulchellus*, *T. sponsorius*, and *T. venustus*), pero su taxonomía sigue siendo confusa. En este trabajo, resumo lo que sabemos sobre la sistemática y taxonomía de *Thylamys* en Argentina, incluyendo las principales fuentes de controversia entre especies. También proporciono diagnosis diferenciales para las especies que reconozco, una cresonimia y mapas de distribución actuales. Finalmente, describo los principales problemas que deben abordarse para mejorar nuestra comprensión del género en Argentina.

Palabras clave: Didelphimorphia, distribución, marmosas, marsupiales

INTRODUCTION

The genus *Thylamys* Gray (1843) comprises a group of small opossums (Marsupialia, Didelphimorphia, Didelphidae) that primarily inhabit the arid and semi-arid regions of South America; from central Perú to central Chile to the west of the Andes, and northeastern Brazil, central and southern Bolivia, Paraguay, western Uruguay, and most of Argentina to 45° 44' S (Solari, 2003; Carmignotto & Monfort, 2006; Albanese & Martin 2019a,b; Martin, 2019a,b,c; Martin *et al.,* 2019).

Externally, the species of the genus are characterized by having silky fur with a tricolor pattern, large ears, small feet, and they can store fat in their tails, like it does in *Lestodelphys* (Tate, 1933). The skull is mainly characterized by the presence of parallel or subparallel nasals, which slightly widen at the naso-fronto-maxillary suture. The dentition presents the following characteristics: upper molars compressed antero-posteriorly with greater labiolingual development, lower molars with a subequal or smaller talonid compared to the trigonid, laterally compressed premolars, small incisors, and have more or less developed canines, typical features of an omnivorous-animalivorous diet (Reig *et al*., 1987; Goin, 1997; Voss & Jansa, 2003).

The name *Thylamys* was originally proposed as a genus by Gray (1843) to separate it from the genera *Didelphis* and *Marmosa*, including only the species *Didelphis elegans* Waterhouse, 1839. Later, it was considered a subgenus of *Marmosa*

by Cabrera (1919), grouping the forms he differentiated from the typical subgenus (*Marmosa*) which included *carri* and *keaysi* (now within *Marmosops*; see Voss *et al*., 2004a), the *microtarsus* group of Tate (1933) (now part of *Cryptonanus* Voss *et al*., 2005, and *Gracilinanus* Gardner and Creighton, 1989), and *formosus* (now in the genus *Chacodelphys* Voss *et al*., 2004b).

In 1933, Tate offered the first comprehensive review of *Marmosa*, at that time considered a full genus that included all small didelphids, except for the species of *Monodelphis* Burnett,1830 and *Lestodelphys halli* (Thomas, 1921d). In that work, Tate (op. cit.) divided *Marmosa* into five groups, of which four were considered natural and one probably artificial (*i.e.*, *microtarsus*): *elegans*, *cinerea*, *microtarsus*, *murina*, and *noctivaga*. The *elegans* group included two sections (*elegans* and *pallidior-venusta*) and the following forms and subspecies: *elegans elegans*, *elegans coquimbensis*, *elegans soricina*, *janetta*, *marmota marmota*, *marmota verax*, and *pusilla* (in the *elegans* section); *venusta venusta*, *venusta cinderella*, *venusta sponsoria*, *pallidior*, *bruchi*, *formosa*, and *velutina* (in the *pallidior-venusta* section). A couple of years earlier, Marelli (1931) had nominated a subspecies for the form from southwestern Buenos Aires Province: *Marmosa elegans fenestrae*, which was not included in Tate's monograph (1933). A new species was proposed by Cabrera (1934) for a specimen captured in Santiago del Estero Province, which he named *Marmosa* (=*Thylamys*) *pulchella*.

From Cabrera's work (1958), *Thylamys* began to be used as a subgenus of *Marmosa s.l.*, including all forms from Tate's (1933) *elegans* and *microtarsus* groups. Almost immediately after, two new species were described: *Marmosa tatei* Handley, 1957 for Perú, and *Marmosa karimii* Petter, 1968 for Brazil, which were also assigned to the subgenus *Thylamys* (Handley, 1957; Petter, 1968).

During the 1980s, starting with Osvaldo Reig's work (1981), different authors accepted the separation of *Thylamys* at the genus level (*e.g.*, Marshall, 1981; Creighton, 1984; Reig *et al*., 1985, 1987), including the forms from the *microtarsus* group, which would first become a single genus (*i.e.*, *Gracilinanus* Gardner & Creighton, 1989), and later be separated into four (*i.e.*, *Chacodelphys*, *Cryptonanus*, *Gracilinanus*, and *Hyladelphys*; see Voss *et al*., 2001, 2004a,b, 2005).

In the last decade of the 20th century and the early 21st century, various works attempted to elucidate different aspects of *Thylamys'* taxonomy, now as a full genus (*e.g.*, Palma, 1994, 1995a,b; Palma & Yates, 1996, 1998; Flores *et al*., 2000; Meynard *et al*., 2002; Solari, 2002, 2003; Braun *et al*., 2005; Carmignotto & Monfort, 2006; Teta *et al*., 2009) but only a few of them (*e.g.*, Flores *et al*., 2000; Solari, 2003; Braun *et al*., 2005; Giarla *et al*., 2010; Palma *et al.*, 2014), included specimens from Argentina in their analyzes, where the genus has a wide distribution and the greatest specific richness on the continent.

The genus *Thylamys* in Argentina: Chronology

The first record of *Thylamys* in Argentina was documented by Burmeister (1879), for specimens probably referable to *Thylamys pallidior* from Mendoza Province. These specimens were assigned to different species by various authors, namely: *Didelphys elegans* (Burmeister, 1879), *Marmosa* (*Thylamys*) *pusilla bruchi* (Cabrera, 1958), *Thylamys pallidior* (Tate, 1933; Solari, 2003; Flores, 2006). Strangely, Cabrera (1919) did not mention these specimens in his notable monograph Genera Mammalium. Previously, Thomas (1888:353–354) included Burmeister's (1879) citation (as *D. elegans*) but restricted the species' distribution to "South Brazil and Chili."

Based on specimens collected by Emilio Budin during different campaigns in central and northwestern Argentina, Thomas (1902b, 1921b,c) described the forms *bruchi*, *cinderella*, *pallidior*, and *sponsorius*, the first as a full species and the latter two as subspecies of *elegans*. The form *bruchi* was collected in Alto Pencoso, San Luis Province, and is recognized here as a different species from *T. pallidior* due to its smaller size and several dental traits (see below). Regarding *cinderella* and *sponsorius*, Thomas proposed recognizing them as species due to the geographical distance separating them from *venustus*, whose collection localities are mostly in the Yungas of Bolivia. Between 1919 and 1921, the first specimens of *T. pallidior* from La Rioja and Jujuy provinces were described by Thomas, also from specimens collected by E. Budin. In 1926, and again thanks to Budin's fieldwork, specimens collected in Neuquén Province reached Thomas. All these records are notable for their areas of origin, far apart from each other, and the few specimens collected at each locality.

In 1931, Dr. Carlos A. Marelli, in a study on vertebrates exhibited in the Plata zoological gardens, named a subspecies (*Marmosa elegans fenestrae*) for *Thylamys* from Sierra de la

Ventana (Buenos Aires Province), in addition to mentioning *Marmosa elegans* for north-western Argentina and *Marmosa pusilla* for Paraguay. Unfortunately, there are no references to the material in question, nor is there a description of the new subspecies (see below and Martin, 2009 for an account of *T. fenestrae*).

The most important review conducted in the first half of the 20th century corresponds to Tate's (1933) monograph, discussing the main traits and distribution of the following forms for Argentina: *Marmosa pusilla* (=*citellus*), *M. venusta cinderella*, *M. venusta sponsoria*, *M. pallidior*, and *M. bruchi* (also including *M. formosa*, now recognized as *Chacodelphys formosus*; Voss *et al*., 2005). Immediately afterward, Cabrera (1934) named the subspecies *M. janetta pulchella*, for a specimen from Santiago del Estero Province, which he associated with *Marmosa janetta* from Bolivia, a form described by Thomas (1926a). The relationship between these forms was established based on the general appearance of the skull (with more expanded zygomatic arches and a shorter face) and the presence of supraorbital ridges (Cabrera, op. cit.).

In the second half of the 20th century, notable works include those by Ringuelet (1955, a new mention of *Thylamys* [as *T. pallidior*] for Sierra de la Ventana), and the fundamental *Catálogo de los mamiferos de America del Sur* ("Catalogue of the Mammals of South America") by Ángel Cabrera (Cabrera, 1958), where *Thylamys* appears as a subgenus of *Marmosa*. Cabrera (1958) has been used as a mandatory bibliographic reference for at least five decades, where the following species were mentioned for Argentina (information about the species' habitats is included in brackets): *Marmosa elegans cinderella* ["...distributed in northwestern Argentina, in the mountainous zone from Jujuy to Tucumán and northern Catamarca..."]; *M. elegans venusta* ["...a specimen from Vermejo, in Bolivia, which is most likely from the Argentine locality of Bermejo, ...province of Salta..."]; *M. pusilla bruchi*, including *M. pulchella* as a junior synonym ["...from Santiago del Estero, La Rioja, Mendoza, Neuquén, Río Negro, to the mountains of southern Buenos Aires Province, ...the pampasic district and the northern part of the Patagonian."], *M. pusilla pallidior* ["mountainous zone...of northwestern Argentina, up to Tucumán and Catamarca, where there is probably intergradation with the bruchi form."]; *M. pusilla pusilla* ["...northeastern Argentina (Formosa, Chaco, Corrientes, Entre Ríos)."]. Notably, Cabrera grouped the forms *bruchi*, *pallidior*, and *pusillus* as subspecies of *M. pusilla*, without arguing for this grouping. From this moment, there would be problems of specific assignment for the different forms inhabiting central and eastern Argentina, problems that persist to this day (see, for example, Birney *et al*., 1996; Galliari *et al*., 1996; Braun *et al*., 2005; Voss *et al*., 2009). Later works already show the afore-mentioned confusion, for example: Crespo (1964), Contreras (1968, 1973), and Reig *et al*. (1977) use the name *Thylamys pusillus* to refer to specimens captured in Buenos Aires Province (referable to *T. fenestrae* in Martin (2009) or *T. pallidior* by other authors; see below); and Daciuk (1974) uses the name *Marmosa pusilla bruchi* for specimens of *T. pallidior* captured in Valdés peninsula (Chubut Province). Most works during the 80's and 90's by researchers from the Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, Mendoza Province) use the name *T. pusillus* for the species inhabiting the Monte biogeographic province, instead of *T. pallidior* (*e.g.,* Ojeda *et al*., 1998; Corbalán, 2004).

Among the literature that resumes the compiling tradition started by Cabrera (1958), the works by Eisenberg (1989), Redford & Eisenberg (1992), and Eisenberg & Redford (1999) stand out, citing, still under *Marmosa*, (1) *T. bruchi* (with a distribution in San Luis and La Pampa [but with a single locality on the distribution map (Fig. 2.8, p. 25)]); (2) *T. elegans* (including the form *T. venustus*, and inhabiting most of Chile and the Yungas of Jujuy, Salta, and Tucumán); and (3) *T. pusilla* (including *T. citella*, *T. fenestrae*, *T. pallidior*, with a wide distribution ranging from western Paraguay, southwestern Bolivia, and, in Argentina, from Salta and Jujuy to Chubut, including southwestern Buenos Aires, Mendoza, Córdoba, and Santiago del Estero). Gardner (1993) further confuses the genus' taxonomy, recognizing only five species of *Thylamys*, three of which would inhabit Argentina: *T. elegans* (including as synonyms the forms *cinderella*, *coquimbensis*, *janetta*, *soricina*, *sponsoria*, *tatei*, and *venusta*); *T. pallidior* (including as synonyms the forms *bruchi*, *fenestrae*, and *pulchella*); and *T. pusilla* (including as synonyms the forms *citella*, *karimii*, *marmota*, *nana*, and *verax*). There is no basis for this grouping in his publication.

In a series of works aimed a describing the mammals of northwestern Argentina, Mares *et al*. (1981, 1989, 1996, 1997), Bárquez *et al*. (1991), Braun & Díaz (1999), Díaz *et al*. (1997, 2000), and Díaz & Bárquez (2007) provide species lists,

keys and taxonomic accounts for the provinces of Salta, Tucumán, Catamarca and Jujuy. For Salta Province, Mares *et al*. (1981) recognized *Marmosa elegans* (currently known as *T. venustus*) y *Marmosa pusilla* (currently known as *T. pallidior*), the former from moist forests of the north, the latter "mostly widespread throughout the arid parts of Salta", but they mentioned three individuals captured near Cachi, in the western portion of the province. The same species were recognized by Mares *et al*. (1989), but *M. pusilla* here was used for both specimens from the high western areas of the province (Precordillera and Puna environments) referrable to *T. pallidior*, and eastern Chacoan areas referrable to *T. pulchellus*. *T. venustus* (mentioned as *M. elegans*) was identified by its yellowish ventral fur, and living in the Yungas. Díaz *et al*. (1997) recognized *T. pallidior*, *T. pusillus*, and *T. venustus* for the province, a number expanded in Diaz *et al*. (2000) with the inclusion of *T. cinderella*, *T. sponsoria*, and *T.* sp., following the arrangement of Flores *et al*. (2000). They also mentioned the problematic identification of *T. pallidior* and *T. pusilla* (currently known as *T. pulchellus*) and restricted the distribution of the former to the west, and the latter to the Chaco ecosystems in the east. For Tucumán Province, Bárquez *et al*. (1991) recognized *T. elegans* and *T. pusillus*, the first form can be referred to the *T. venustus* complex, the second one to the species living in the Monte ecoregion, and arid environments of altitudes up to 3500 m (*i.e., T. pallidior*), and to the species living in Chacoan environments (*i.e., T. pulchellus*). For the latter, they (erroneously) mentioned an extensive distribution in Argentina from Neuquén and Río Negro provinces northward, with the exception of Corrientes and Misiones provinces. This distribution clearly involved the forms *T. bruchi* and *T. citellus*, as well as *T. pallidior* and *T. pulchellus*. The entire map of Tucumán Province is shaded with the presence of the form they referred to *T. pusillus*. What they referred to as *T. elegans* (currently known as *T. venustus*) is broadly distributed in most of the center, excluding what they described in page 145 as thorn forest Chaco along the east of the province, and montane bunchgrass, mesquite woodlands and Puna, in the northwest and extreme southwest of the province. Mares *et al*. (1996) recognized *Thylamys elegans* and *T. pallidior*, but use *elegans* in the sense of Waterhouse. Specimens described as *T. pallidior* from several localities (*i.e.,* El Bracho, El Cadillal, Las Mesadas, and San Pedro de Colalao) could be assigned to *T. pulchellus*, since they are distributed in the Dry Chaco ecoregion, or its transition with the Yungas. They mentioned the capture of *T. venustus* and *T. pallidior* (probably *T. pulchellus*) in sympatry at El Cadillal, north of Tucumán city. For Catamarca Province, Mares *et al*. (1997) recognized *T. elegans* and *T. pallidior*, and (erroneously) synonymized *elegans* with Waterhouse (see below). Their mention of *T. elegans* includes the southernmost record for *T. venustus* in Argentina. The use of *T. pallidior* is somewhat problematic in this geographic context, because some specimens were captured near Chumbicha (Chaco ecoregion), which could be assigned to either *T. bruchi* or *T. pulchellus*, and others from Minas Capillitas at an altitude of 3200 m, which can be assigned to *T. pallidior*. In a later work, Braun & Díaz (1999) included *T. pallidior* and *T. venustus* in the province, and mentioned that specimens identified by Mares *et al*. (1997) as *T. elegans* should be considered as *T. venustus*. For Jujuy Province, Díaz (2000) recognized three species: *T. pallidior*, *T. cinderella* and *T. sponsorius*, the first species inhabiting the Puna, the second one in both the Yungas and Chaco, and the third one in the Yungas. The latter two species were separated by the presence of smooth or pointed supraorbital processes, a character showing high intraspecific variability, and dubious for species identification (see authors below). In a later publication Díaz & Bárquez (2007) recognized four species of *Thylamys* for Jujuy: *T. cinderella*, *T. sponsorius*, *T. pallidior*, and *Thylamys* sp. They follow Palma (1994, 1995b) and Palma & Yates (1998) recognizing *T. elegans* as restricted to Chile, and *T. venustus* as the form from northwestern Argentina. However, they only recognized *T. cinderella* and *T. sponsorius* as part of the *T. venustus* group. They described *T. cinderella* as found in Chacoan vegetation, with some records in the transitional forests with the Yungas ("but always near the Chaco or arid areas"), *T. sponsorious* mostly occurring in Yungas, with a few specimens captured in Prepuna and Chaco environments, and *T. pallidior* from the High Andean, Puna, and Prepuna regions in Jujuy Province. The unnamed species (*Thylamys* sp.) was recorded at Cerro Calilegua, El Duraznillo, 3000 m, in a region of "alder (*Alnus*) forests with some specimens of queñoa trees (*Polylepis*), according to Olrog (1979) and Heinonen & Bosso (1994)". Although the identity of this specimen was not checked, it is close to the records from Santa Bárbara for *T. venustus* found in the literature.

Palma (1994, 1995a,b), Palma & Yates (1996, 1998), Meynard *et al*. (2002), and Palma *et al*. (2002) recognized only three species for Argentina: *T. pallidior*, *T. pusilla*, and *T. venusta*. Their distribution scheme ignores the Patagonian populations of *T. pallidior* (from Neuquén to Chubut); as well as the presence of the genus in southwestern Buenos Aires, Entre Ríos, Córdoba, Corrientes, Chaco, and Formosa (Tate, 1933; Cabrera, 1958; Reig *et al*., 1977; Birney *et al*., 1996; Brown, 2004).

Flores *et al*. (2000) recognized six species for northwestern Argentina: *T. cinderella*, *T. pallidior*, *T. pusillus*, *T. sponsorius*, *T. venustus*, and an unnamed species taxon. The most relevant results of their work allowed, on the one hand, to recognize the specific rank of two subspecies proposed by Thomas (1902a, 1921c), and traditionally considered within *T. elegans* (Cabrera, 1958) or *T. venustus* (Tate, 1933; see below); on the other hand, to consider *T. pulchellus* within *T. pusillus*, restricting this taxon to a distribution exclusively of the Chacoan biome. The unnamed species taxon includes seven subadult specimens, whose cranial features correspond to those of adult specimens of *T. venustus* (in part), and its distribution overlaps with that of *T. cinderella* and *T. sponsorius*.

Campos *et al*. (2001) described the use of food resources by small and medium-sized mammals in the Monte Desert biome (Argentina), and mention *T. pusillus* as an omnivorous species. Although the species inhabiting the Monte in Argentina is usually referred to as *T. pallidior*, this shows the ambiguous use of the name *T. pusillus* throughout the current history of *Thylamys* throughout its distribution, and especially in Argentina. The same occurs with a study from the same area (Ñacuñan Biosphere Reserve, Mendoza) by Díaz *et al*. (2001), who studied the water balance of this species and refer to it as *T. pusillus*. It might be interesting to point out, however, that Albanese *et al*. (2011), Albanese & Ojeda (2012), and Albanese *et al*. (2012) considered these populations as *T. pallidior*, and that Albanese *et al*. (2021) mention this species as *T. bruchi* in a study of delayed male mortality and semelparity, adding to the name confusion.

Solari (2003) presented an analysis of the diversity and distribution of the genus *Thylamys* in South America. For Argentina, he recognized three species (*T. pallidior*, *T. pusillus*, and *T. venustus*), taking *T. citellus* as a synonym of *T. pusillus*; his analysis did not include *T. bruchi*, *T. fenestrae*, and *T. pulchellus*. His distribution scheme is inaccurate, citing *T. pusillus* for Patagonia and extending the distribution range of *T. venustus* to central Argentina, where there are no suitable ecosystems for this species. The most important contribution of his work is the separation of the species into three groups that he considers monophyletic: one Andean (including *T. elegans*, *T. pallidior*, *T. venustus*, and *T. tatei*), one Brazilian (including *T. velutinus* (and *T. karimii* as a junior synonym, but see Carmignotto & Monfort, 2006), and one Chacoan (including *T. macrurus* and *T. pusillus*).

Braun *et al*. (2005) presented a phylogenetic analysis of the genus based on cytochrome-*b*, and considered only four species for Argentina: *T. cinderella*, *T. pallidior*, *T. pusillus*, and *T. venustus*. The authors synonymized *T. pulchellus* with *T. pusillus* based on the distribution of these taxa, although not based on molecular characters or morphologic traits. They separated *T. pallidior* into two subspecies, with a boundary at the Argentina-Bolivia border, which lacks biogeographic and morphologic support. Indeed, the Puna, where this species inhabits, shows a continuous ecosystemic unity from northwestern Argentina to southwestern Perú (see, *e.g*., Morrone, 2001; Olson *et al*., 2001). The proposed name for the northern subspecies was *T. pallidior pallidior*, and for the southern subspecies was *T. pallidior bruchi*.

Flores *et al*. (2007) updated the information on the systematics (taxonomy), distribution, and natural history of marsupials from Argentina, and presented a new taxonomic arrangement for *Thylamys* (and other genera). They recognized *T. cinderella*, *T. pallidior*, *T. pusillus*, *T. sponsorius*, and *T. venustus* as valid species, with *bruchi* as part of *pallidior* (not mentioned specifically, but Alto Pencoso, the type locality of *T. bruchi* is included in the localities of *T. pallidior*), and known records of *T. citellus* and *T. pulchellus* were included within *T. pusillus*. The inclusion of three forms from the Yungas Ecoregion followed the arrangement proposed by Flores *et al*. (2000), which is considered to be two species (*i.e., T. sponsorius* and *T. venustus*; Giarla *et al*., 2010; Palma *et al*., 2014) or one (*i.e., T. venustus*; Martin, 2008).

Creighton & Gardner (2008) recognized 10 species in the genus *Thylamys*, with *T. cinderella*, *T. pallidior*, *T. pusillus*, *T. sponsorius*, and *T. venustus* for Argentina. They provided a key to identify the species of *Thylamys* (mostly based on external characters), apparently following the arrangements of Flores *et al*. (2000), Braun

et al. (2005), and other sources. They included *T. bruchi* and *T. fenestrae* in the synonymy of *T. pallidior*, and (erroneously) included localities in central Chile as part of its distribution (these records are in the distribution area of *T. elegans*). They included *T. citellus* and *T. pulchellus* in *T. pusillus*, and also mentioned that *T. pusillus* reaches Mendoza Province, but their map (#49, page 111) only shows records as far south as northern Corrientes and northern Santiago del Estero provinces. The three species living in the Yungas ecoregion (*T. cinderella*, *T. sponsorius*, and *T. venustus*) overlap in most of their distribution maps, but they pointed out that the first species occurs in northern Argentina, the second species occurs in Salta, Jujuy, and Tucumán provinces, and the third species occurs in Salta Province. Their final comments mentioned an unclear taxonomy for these forms: "However, the amount and extent of that variation are too poorly known to warrant division into subspecies at this moment. The species needs revision."

Martin (2008) recognized six species of *Thylamys* occurring in Argentina (*T. bruchi*, *T. citellus*, *T. fenestrae*, *T. pallidior*, *T. pulchellus*, and *T. venustus*), and to consistently argue with this scheme, presented a new diagnosis for each taxon. In this work, comparisons were made between the closest species and the previously synonymized forms. Thus, *T. bruchi* and *T. fenestrae* were compared with *T. pallidior*, and *T. citellus* with *T. pulchellus*. Also, geographic localities (with coordinates) were given for each recognized form. The characteristics of each species were discussed concerning the other taxa, and tables with external, cranio-mandibular, and dental measurements for each species were presented. A complete diagnosis was also provided for the form *venustus*, which includes the forms *cinderella* and *sponsorius* as synonyms, which are considered a single species, a species-complex or separate forms (see Flores *et al*., 2000; Giarla *et al*., 2010). Also, the clinal variation of *T. pallidior* was discussed in full, including specimens from Bolivia to its southernmost localities in southern Argentina, and the sexual dimorphism in deciduous premolars. Unfortunately, none of the following works acknowledged the results of this work.

Carvalho *et al*. (2009) generated a phylogenetic analysis of *Thylamys*, to establish the relationships of *T. karimii* and all other previously analyzed species. They recognized *T. cinderella*, *T. pallidior*, *T. pusillus*, and *T. venustus* for Argentina. They suggested five species groups for the genus: Andean, Brazilian, Chacoan, Paraguayan, and Yungas. From Argentina, the Andean group includes *T. pallidior*, the Chacoan *T. pusillus*, and the Yungas *T. cinderella* and *T. venustus*. These authors do not recognize *T. bruchi*, *T. citellus* or *T. pulchellus* as part of the species in *Thylamys*.

Flores (2009) studied the postcranial skeleton of didelphid marsupials, and included four species of 10 he recognized for the genus: *T. macrurus*, *T. pallidior*, *T. pusillus*, and *T. venustus*, of which two specimens assigned to *T. pusillus* can be assigned to *T. pulchellus* (CML 3198, CML 3573). The postcranial evidence supports the monophyly of *Thylamys*, and its sister relationship to *Lestodelphys*.

Martin (2009) revalidated the form *fenestrae* (Marelli, 1931) for specimens in the Pampa and Espinal ecoregions (*sensu* Olson *et al*. 2001), morphologically and morphometrically separating this species from *T. pallidior*, and comparing it with *T. citellus*. This study was the first (and only) to include specimens from southern Córdoba Province, and throughout the Espinal ecoregion. The validity of *T. fenestrae* was questioned by Giarla *et al*. (2010) and Palma *et al*. (2014), but only based on genetic data, who included this species in *T. pallidior* (see below).

Teta *et al*. (2009) studied the species of *Thylamys* from northeastern and central Argentina, assessing the validity of *Thylamys pusillus* (Desmarest, 1804). Based on genetic, morphologic, and morphometric data, they recognized *T. citellus* (Thomas, 1912) for Entre Ríos and Corrientes provinces, and *T. pulchellus* (Cabrera, 1934) for the Argentine Dry Chaco ecoregion, restricting *T. pusillus* to the Bolivian and Paraguayan Chaco, and northern Formosa Province. Without acknowledging Martin (2008), they provide emended diagnosis for *T. citellus* and *T. pulchellus*, and data on each species distribution.

Voss & Jansa (2009) analyzed the phylogenetic relationships of didelphid marsupials which supported the monophyly of *Thylamys* based on parsimony, likelihood, and Bayesian analyzes, and recognized the following forms: *cinderella* Thomas, 1902a (including *sponsorius* Thomas, 1921); *elegans* Waterhouse, 1839 (including *coquimbensis* Tate, 1931; and *soricinus* Philippi, 1894); *karimii* Petter, 1968; *macrurus* Olfers, 1818 (including *griseus* Desmarest, 1827); *pallidior* Thomas, 1902b; *pusillus* Desmarest, 1804 (including *bruchi* Thomas, 1921; *citellus* Thomas, 1912; *nanus* Olfers, 1818; and *verax* Thomas,

1921); *tatei* Handley, 1957; *velutinus* A. Wagner, 1842 (including *pimelurus* Reinhardt, 1849-1950); and *venustus* Thomas, 1902a (including *janetta* Thomas, 1926a). Of these species, four occur in Argentina (*cinderella*, *pallidior*, *pusillus*, and *venustus*), and the authors "tentatively recognize" *bruchi* and *citellus* as synonyms of *T. pusillus* (the first one following Voss *et al*., 2009; see below), and mention that *pulchellus* and *fenestrae* "might be synonyms of *T. pusillus* and *T. pallidior*, respectively, but we have not seen the holotypes, and published information about these nominal taxa is insufficient to support any definite conclusions about them". As stated throughout many of the previous works, they concluded that "many other species-level issues in this genus remain problematic despite much recent taxonomic work (*e.g.,* Palma *et al*., 2002; Solari, 2003; Braun *et al*., 2005; Carmignotto & Monfort, 2006).", without mentioning the most recent works of Martin (2008, 2009) and Teta *et al*. (2009), which provided descriptions of taxa within their synonymized classification.

Voss *et al*. (2009) studied the opossums described by Felix de Azara, which include references to two species of *Thylamys*: *T. macrurus* and *T. pusillus*, for which they designated neotypes. The first species was assigned a correspondence with Azara's "*colilargo*", or "*micouré quatrième, ou micouré à queue longue*"; the second one with the "*enano*", or "*micouré sixième, ou micouré nain*" (Voss *et al*., 2009). Throughout his years in South America, Felix de Azara traveled through eastern and northeastern Argentina (*e.g.,* Buenos Aires, Santa Fe, Corrientes, and Misiones provinces), eastern Paraguay (*e.g.,* Asunción, and the eastern departments of Ñeembucú, Misiones, Itapuá, Caazapá, Paraguarí, Central, Cordillera, Caaguazú, and Guairá), and Uruguay (Mones & Klappenbach, 1997; Contreras, 2011). Despite that Azara did not travel to western Paraguay (at least not officially), and that the specimens of "*el enano*" were sold to him by "indians from San Ignacio Güazú" (Azara, 1801; p. 304), Voss *et al*. (2009) assigned this form to the *Thylamys* living in western Paraguay (Dry Chaco ecoregion), instead of the form we know to inhabit Argentine Mesopotamia (Entre Ríos, Corrientes, and Misiones provinces), *Thylamys citellus*. Throughout its history, the name *pusillus* has been used inconsistently to describe species of *Thylamys* from Argentina or even Paraguay by different authors (see above), with a dubious or mistaken consideration of their geographic provenance. However wrong the designation of Voss *et al*. (2009) might be, and to avoid further confusion, we will restrict *T. pusillus* to a form living in western Paraguay and eastern Bolivia, but with an unclear distribution in Argentina (see above Martin, 2008 and Teta *et al*., 2009). We should bear in mind, however, that this species has nothing to do with Azara's "*enano*", and represents a completely different biologic entity.

Giarla *et al*. (2010) arguably presented the most complete synthesis of the genus *Thylamys* so far, using nuclear genes and morphology. They separated *Thylamys* in two subgenera (*Xerodelphys* and *Thylamys*), and recognized four species for Argentina (all within subgenus *Thylamys*), including *T. pallidior*, *T. pusillus*, *T. sponsorius*, and *T. venustus*. Unfortunately, their study of specimens from Argentina was limited, and they disregarded the works of Martin (2008, 2009) and Teta *et al*. (2009). The forms *bruchi*, *citellus*, and *pulchellus* were considered a synonyms of *T. pusillus*, despite the many craniodental and morphometric differences which clearly separate them. The authors separated *T. pallidior* in the *elegans* group (which include *T. elegans* and *T. tatei*, not present in Argentina), and *T. sponsorius* and *T. venustus* in the *venustus* group, and provided ample discussion on their synonyms and morphologic characterizations.

Formoso *et al*. (2011) described the distribution of *T. pallidior* and *L. halli* in Patagonia, showing differences in their general distribution, and 20 localities of sympatry (based on remains recovered from owl pellets), but mention they found "no conclusive evidence of syntopy by trapping at any site".

Albanese *et al*. (2012) studied the diet of *Thylamys* in Ñacuñan Biosphere Reserve (Mendoza Province) based on a large fecal sample, with arthropods as the most important items (> 68 %), and showed constant proportions throughout the year, despite the resource variability and seasonality of the Monte habitat. From a taxonomic point of view, they used the name *T. pallidior* for the species previously defined as *T. pusillus* (see Campos *et al*., 2001; Díaz *et al*., 2001), and later as *T. bruchi* (see below).

Giarla *et al*. (2013) tested the evolutionary history within *T. pallidior*, *T. sponsorius*, and *T. venustus*, and results of their mtDNA haplotype analysis confirmed the existence of allopatric and genetically isolated lineages for two groups within *T. pallidior*, two within *T. sponsorius*, and three within *T. venustus*. Although no formal separation was presented, they mentioned

names are available for the different lineages they identified: *T. pallidior* and *T. fenestrae* for the first species, *T. janetta* and *T. sponsorius* for the second species, and *T. cinderella* and *T. venustus* for the third species, for which two haplotypes are combined in *T. cinderella*.

Palma *et al*. (2014) studied the phylogenetic relationships of *Thylamys* with samples from different localities throughout the genus' distribution, evaluated the phylogenetic structure within *T. pallidior* (and *T. elegans* from Chile), the validity of *T. sponsorius* and *T. cinderella* (and *T. tatei* from Perú), and the haplogroups recognized within *T. pusillus*. For the species in Argentina, they recovered a clade including *T. sponsorius* and *T. venustus*, a Chacoan clade which included *Thylamys pusillus* (in the sense of Voss *et al*., 2009) and *T. pulchellus* and *T. citellus*, and an Andean clade that included *T. pallidior*. The latter was separated in two groups: one in the Andean Altiplano and transversal valleys in the Atacama Desert of northern Chile, and a second one ranging to southern Argentina but with an unclear northern limit. Unfortunately, no specimens assigned to *T. bruchi* were included in their analysis. However, specimens geographically coincident with the southern distribution of *T. fenestrae* (Martin, 2009) were included, and recovered as part of *T. pallidior s.l.* Although no morphologic or morphometric analyzes were made by these authors, they mentioned *fenestrae* as an available name for subspecific treatment. They also calibrated a molecular clock in which they hypothesized an origin of the clade at 24 Ma.

Astúa (2015) recognized 11 species within *Thylamys*, six of them for Argentina: *T. citellus*, *T. pallidior*, *T. pulchellus*, *T. pusillus*, *T. sponsorius*, and *T. venustus*. Information on the taxonomy, morphology (as descriptive notes), distribution, ecology and conservation were presented for each species, when available. In his review, *T. fenestrae* was recognized as a synonym of *T. pallidior*, but *T. bruchi* is not mentioned at all. The three species considered by Giarla *et al*. (2010) as part of the *pusillus* species group are considered as valid species, with their distribution apparently following the scheme of Teta *et al*. (2009) (*e.g., T. citellus* living in Entre Ríos and Corrientes provinces; *T. pulchellus* living in Chaco, Santiago del Estero, Catamarca, and San Juan provinces; and *T. pusillus* includes the province of Formosa in central northern Argentina). The species inhabiting the Yungas ecoregion partially overlap, but *T. sponsorius* is wrongly shown east of *T. venustus*, which is not coincident with the species known distribution.

Nowak (2018) included seven species for Argentina: *T. cinderella*, *T. citellus*, *T. pallidior*, *T. pulchellus*, *T. pusillus*, *T. sponsorius*, and *T. venustus*. The author discussed the position of *T. bruchi*, *T. cinderella*, *T. fenestrae* based on previous works, described the genus generalities (*e.g.,* anatomy, breeding, distribution), and species' conservation status based on International Union for the Conservation of Nature (IUCN) assessments.

Teta *et al*. (2018) presented a revised checklist of mammals from Argentina, and although they claimed to use Voss & Jansa (2009) for marsupial taxonomy, they included *T. bruchi*, *T. citellus, T. pallidior*, *T. sponsorius*, and *T. venustus* in the genus *Thylamys*. As noted above, Voss & Jansa (2009) considered *T. bruchi* and *T. citellus* part of the synonymy of *T. pusillus*. Teta *et al*. (2009) considered *T. pulchellus* as part of *T. bruchi*.

The most recent assessment of Argentine mammals (Secretaría de Ambiente and Desarrollo Sustentable & Sociedad Argentina para el Estudio de los Mamíferos, 2019) recognized six species of *Thylamys*: *T. bruchi*, *T. citellus*, *T. pallidior*, *T. pulchellus*, *T. sponsorius*, and *T. venustus* (Albanese & Martin, 2019a,b; Martin, 2019a,b,c; Martin *et al*., 2019). Their distribution is shown in Fig. 1. In these assessments, *T. bruchi* was recognized as different from *T. pallidior* based on its morphology and unpublished molecular analysis (Albanese & Martin, 2019a); *T. citellus* and *T. pulchellus* were recognized as valid species separated from *T. pusillus* (Martin *et al*., 2019; Martin, 2019a).

Astúa *et al*. (2023) recognized 11 species within *Thylamys*, five of them living in Argentina: *T. bruchi*, *T. citellus*, *T. pallidior*, *T. sponsorius*, and *T. venustus*. Without much discussion, they synoymized *T. pulchellus* with *T. bruchi*, two distinct forms from central Argentina. They also mentioned that the names *T. pallidior* and *T. fenestrae* are available for binomial or trinomial usage for the two groups recognized by Giarla *et al*. (2010) and Palma *et al*. (2014).

Bonvicino *et al*. (2023) studied the diversification of South American marsupials, presented a map with the maximum likelihood topology of *Thylamys*, and recognized five species for Argentina: *T. citellus*, *T. pallidior*, *T. pulchellus*, *T. sponsorius*, and *T. venustus*. They mentioned its origin from peripheral isolates of the ancestral lineage in the Andes (*sensu* Palma *et al*., 2002), and confirmed their monophyly and arrange-

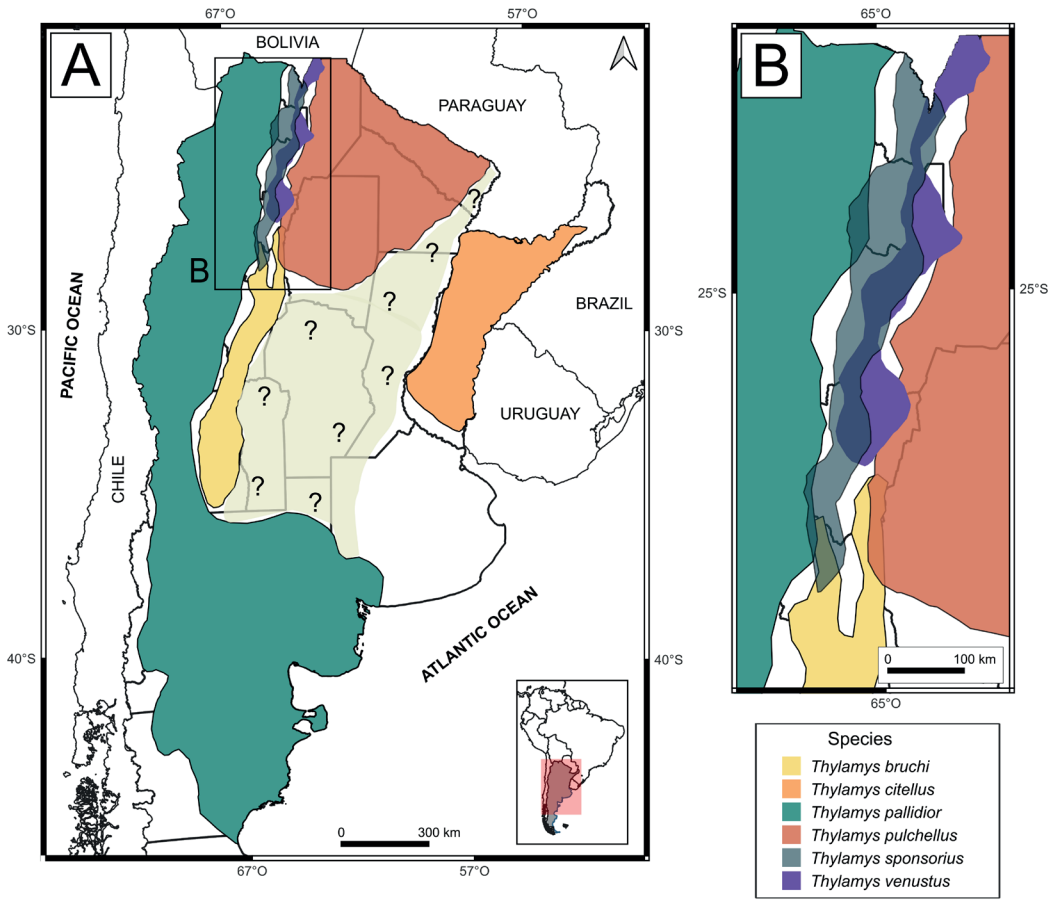

Fig. 1. (A) Distibution of *Thylamys* species in Argentina, based onthe latest assessment by Secretaría de Ambiente y Desarrollo Sustentable and Sociedad Argentina para el Estudio de los Mamíferos (2019); (B) overlap between species in northwestern Argentina. Question marks (?) indicate areas where the identity of the species present is unknown.

ment "consistent with previous studies", providing an estimate for the origin of *Thylamys* ca. 17 Ma, questioning the interpretation of Jansa *et al*. (2013), who placed the radiation of this genus in the Pliocene.

Martin *et al*. (2022) studied the richness and conservation status of marsupials from Argentina, and considered 6 species of *Thylamys* following Secretaría de Ambiente and Desarrollo Sustentable & Sociedad Argentina para el Estudio de los Mamíferos (2019): *T. bruchi*, *T. citellus*, *T. pallidior*, *T. pulchellus*, *T. sponsorius*, and *T. venustus*. They also discussed the distribution of each species within the different ecoregions of Argentina.

Voss (2022) included the following species for Argentina: *T. pallidior*, *T. pusillus* (including *T. bruchi*, *T. citellus*, and *T. pulchellus*), *T. sponsorius*, and *T. venustus*. He also discussed each species type material, synonyms, distribution, and added remarks/comments where suitable.

Martin & Carmignotto (2024) examined the recent taxonomic revisions and conservation priorities for New World marsupials, based on the IUCN Red List assessments and the most recent literature. They included 12 species of *Thylamys*, seven of them from Argentina: *T. cinderella* (a current synonym of *T. sponsorius*), *T. citellus*, *T. fenetrae* (a current synonym of *T. pallidior*), *T. pallidior*, *T. pulchellus*, *T. pusillus*, and *T. venustus*.

Based on the above review, the number of species of *Thylamys* recognized for Argentina during the last 25 years is summarized in Table 1. Despite many works, there is still no consensus on the identity and number of accepted species.

Table 1. Species of *Thylamys* identified for Argentina during the last 25 years, based on reviews or studies including all the country's richness (excluding works dealing with a selected group or a single species; *e.g.,* Martin 2009; Teta *et al.* 2009; Albanese 2010). CMA, Categorización de los Mamíferos de Argentina (Secretaría de Ambiente y Desarrollo Sustentable de la Nación y Sociedad Argentina para el Estudio de los Mamíferos (2019); n = number of species recognized.

		T. bruchi	*T. cinderella*	*T. citellus*	*T. fenestrae*	*T. pallidior*	*T. pulchellus*	*T. pusillus*	*T. sponsorius*	*T. venustus*
Flores *et al*. (2000)	n = 5		X			X		X	X	X
Solari (2003)	n = 3					X		X		X
Braun *et al*. (2005)	n = 4		X			X		X		X
Gardner (2005)	n = 5		X			X		X	X	X
Flores *et al*. (2007)	n = 5		X			X		X	X	X
Creighton & Gardner (2008)	n = 5		X			X		X	X	X
Martin (2008)	n = 6	X		X	X	X	X			X
Voss & Jansa (2009)	n = 4		X			X		X		X
Giarla *et al*. (2010)	n = 4					X		X	X	X
Palma *et al*. (2014)	n = 6			X		X	X	X	X	X
Astúa (2015)	n = 6			X		X	X	X	X	X
Nowak (2018)	n = 7		X	X		X	X	X	X	X
CMA (2019)	n = 6	X		X		X	X		X	X
Voss (2022)	n = 4					X		X	X	X
Astúa *et al.* (2023)	n = 6	X		X		X		X	X	X
Bonvicino *et al*. (2023)	n = 8	X	X	X		X	X	X	X	X
Martin & Carmignotto (2024)	n = 7		X	X	X	X	X	X		X

Table 2. Morphologic comparison between species of *Thylamys* from Argentina.

	bruchi	*citellus*	*pallidior*	*pulchellus*	*venustus*[1]
Ventral coloration	white, self colored	creamy white, self colored	white with lateral grey-based hairs	white to creamy white, self colored	grey base, yellow tips
Supraorbital processes	absent	present	absent	present	variable
Cranium in lateral view (Fig. 6)	triangular	boved	triangular	boved	triangular
Rostrum in ventral view (Fig. 4)	narrow/pointy	broad	narrow/pointy	broad	narrow/pointy
Maxillary *fenestrae* (Fig. 4)	present	present	absent	present	present
Area between *bullae* (Fig. 4)	narrow	broad	narrow	broad	broad
Angle of the coronoid process of the mandible (Fig. 8)	slightly obtuse	obtuse (> 100º)	slightly obtuse	obtuse (> 100º)	slightly obtuse
Stylar cusp C (Fig. 9)	present	present	absent	present	absent (sometimes present in M1-M2)
Ectoflexus development	poorly developed	poorly developed	well developed	poorly developed	well developed in M2-M3
Anterobasal cingulum	well-developed	poorly developed, very reduced	well-developed	not well-developed	poorly developed

[1] this species includes *T. sponsorius*

Following is an emended diagnosis and a chresonymy (a summary of occurrences or usages of any given scientific name or set of names; Smith & Smith, 1972) for the species I recognize for Argentina, a map showing their distribution with main overlap areas and those without confirmed records (Fig. 1), and a table describing their main morphologic differences (Table 2). Cranial anatomy follows Voss & Jansa (2003), dental nomenclature follows Goin (2003); upper and lower teeth are indicated by uppercase and lowercase letters, respectively; eruption patterns follow Luckett (1993).

Institutional abbreviations. British Museum of Natural History (BMNH), London, United Kingdom. Museo de La Plata (MLP), La Plata, Buenos Aires, Argentina.

The genus *Thylamys* in Argentina: Taxonomy

MAMMALIA Linnaeus, 1758
METATHERIA Huxley, 1880
MARSUPIALIA, Illiger 1811
DIDELPHIMORPHIA Gill, 1872
DIDELPHIDAE Gray, 1821
THYLAMYINAE Reig, Kirsch & Marshall, 1987
Thylamys Gray, 1843

Thylamys bruchi (Thomas, 1921)

Fig. 2A

Marmosa bruchi Thomas, 1921b: 519
Thylamys pusillus – Campos *et al*., 2001: 142–146; Díaz *et al*., 2001: 323–329; Tabeni & Ojeda 2003: 715–726; Corbalán & Ojeda 2004: 5–14; Creighton & Gardner, 2008: 112; Carvalho *et al*., 2009: 419–425; Voss & Jansa, 2009: 138; Giarla *et al*., 2010: 39; Voss, 2022: 55.
Thylamys pallidior – Braun *et al*., 2005: 154; Flores *et al*., 2007: 34 (part, localities); Albanese, 2010: 1–216; Albanese *et al*., 2011: 1270–1277; Albanese *et al*., 2012: 185–188; Albanese *et al*., 2012: 237–243.
Thylamys bruchi – Martin, 2008: 127; Teta *et al*., 2009: 193; Teta *et al*., 2018: 172; Albanese & Martin, 2019a; Albanese *et al*. 2021: 258–269; Astúa *et al*., 2023: 144; Bonvicino *et al*., 2023: 664; Martin *et al*., 2022: 4.

Holotype. BMNH 21.4.21.8, subadult male (with P3 still erupting); skin and cranium with associated mandibles (collected by Dr. Carlos Bruch).

Type locality. Alto Pencoso, San Luis Province, Argentina.

Geographic distribution. Low areas in San Luis, San Juan, Mendoza, La Rioja, Catamarca, and Tucumán provinces (Fig. 1).

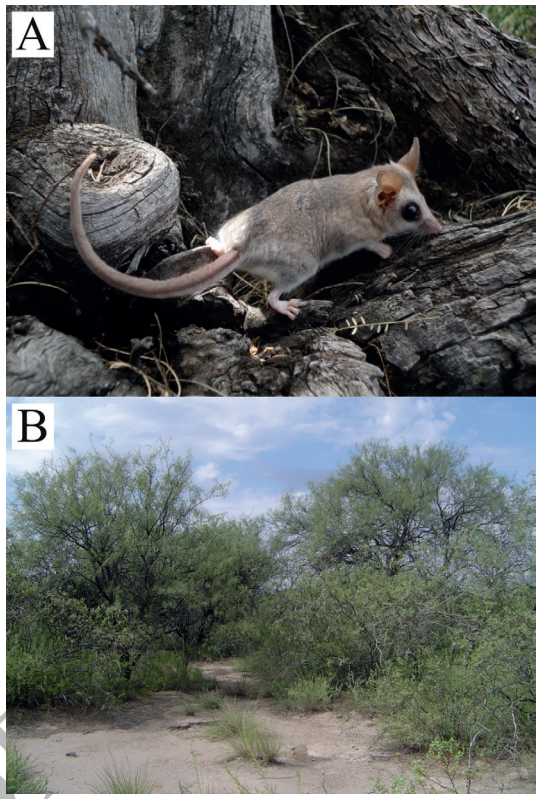

Fig. 2. *Thylamys bruchi* (Thomas, 1921) (A) and its environment (B) in Reserva de Biosfera Ñacuñan, eastern Mendoza Province. Photographs courtesy of Soledad Albanese ©.

Common name. Dry Chaco fat–tailed opossum.

Spanish common name. Marmosa coliguresa del chaco seco, comadrejita enana común, marmosa chaqueña.

Differential diagnosis. One of the smallest species of the genus, with the tail slightly longer than the combined length of the head and body. The dorsal coloration is brownish, tricolored, and the ventral coloration is whitish with hairs of a single color ("self-colored"; Tate, 1933). The feet are proportionally very small and covered with whitish hairs. The skull is small and delicate in appearance; the face is short but narrow and the interorbital region is wide; the nasals are parallel to each other and do not abruptly widen at the naso-frontal-maxillary suture (unlike *T. pulchellus*); they also do not narrow posteriorly to this suture (as in *T. pallidior*); the palate shows the presence of maxillary *fenestrae* (absent in *T. pallidior*); in the orbital region, through the sphe-

norbital fissure, a column between the presphenoid and basisphenoid is observed. In the dentary, the ascending (coronoid) process forms an angle with respect to the horizontal branch, in a pattern intermediate between those of *T. pallidior* and *T. citellus*. The upper molar row is shorter than that of *T. pallidior*, with less lingual development of the molars, which are more square-shaped, almost as long as they are wide (*i.e.,* not so compressed antero-posteriorly); the M4 is less compressed antero-posteriorly and has less labiolingual development; the ectoflexus is much less marked in all the molars than in *T. pallidior*; the M3 shows a well-developed StC, clearly separable from StB and StD (absent in *T. pallidior*); the preprotocrista joins the anterobasal cingulum in all molars (in other species of *Thylamys*, the preprotocrista ends at the base of the paracone). The lower molar row is proportionally smaller than that of *T. pallidior* (with a difference of at least one molar over the total length); the anterobasal cingula are well-developed in all teeth (in *T. pallidior* they are also well-developed; in *T. pulchellus* they are not well-developed); the trigonid is laterally compressed (more than in *T. pallidior*); the hypoconulids are less prominent in m1–m3; the cingulum between the protoconid and hypoconid is well developed in m1–m3 (much more than in *T. pallidior*).

Comments. The species was described based on two subadult specimens (with the P3 in the process of eruption, not yet occupying their final position in the maxilla and mandible), and the specimens used in the original description were separated: one was sold to the British Museum of Natural History (United Kingdom) and the other is deposited in the mammal collection of the Museo de La Plata (Argentina). It was previously included as a synonym of *T. pallidior* or *T. pusillus* (*e.g.,* Flores *et al*., 2000; Giarla *et al*., 2010; Voss, 2022). Braun *et al*. (2005) considered the name valid for the subspecies of *T. pallidior* that would inhabit, according to their biogeographic scheme, western Argentina from the border with Bolivia to Patagonia. The characteristics mentioned above for this taxon (especially in dentition) make its association with *T. pallidior* inappropriate, maintaining its differentiated status.

Thylamys citellus (Thomas, 1912)

Fig. 3A

Didelphis pusilla Desmarest, 1817: 430 (Description based on Azara).

Didelphys pusilla – Desmarest, 1820: 261; Desmoulins, 1824: 493; *Didelphys pusilla* Waterhouse, 1846: 514 (Descriptions based on Azara).

Marmosa citella Thomas, 1912: 409.

Grymaeomys pusilla Matschie, 1916: 270.

Thylamys citella Matschie, 1916: 271; Cabrera, 1919: 40.

Marmosa pusilla Cabrera, 1919: 39.

Thylamys pusillus – Solari, 2003: 94; Braun *et al*., 2005: 154; Flores *et al*., 2007: 35 (part, localities); Creighton & Gardner, 2008: 114; Carvalho *et al*., 2009: 419–425; Voss & Jansa, 2009: 138; Voss *et al*., 2009: 420; Giarla *et al*., 2010: 39; Voss, 2022: 55.

Thylamys citellus – Martin, 2008: 129; Martin, 2009: 334–343; Teta *et al*., 2009: 187; Palma *et al*., 2014: 217–234; Astúa, 2015: 177; Nowak, 2018: 87; Teta *et al*., 2018: 172; Martin *et al*., 2019; Astúa *et al*., 2023: 144; Bonvicino *et al*., 2023: 664; Martin *et al*., 2022: 4; Martin & Carmignotto, 2024: 11.

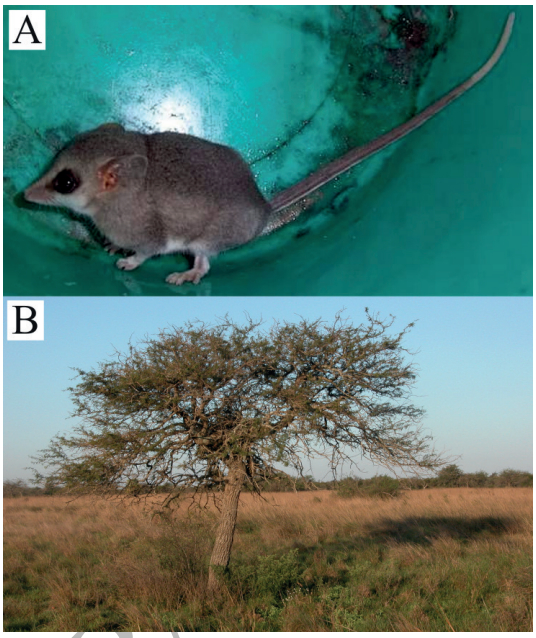

Fig. 3. *Thylamys citellus* (Thomas, 1912) (A) and its environment (B) in Corrientes Province. Photographs courtesy of Pablo Díaz © and Sebastián Cirignoli ©, respectively.

Holotype. BMNH 98.8.19.9, male, skin, and cranium with associated mandibles (collected by R. Perrens, No. 10, July 1885).

Type locality. Goya, Corrientes Province, Argentina.

Geographic distribution. Entre Ríos, Corrientes, and Misiones Provinces (Fig. 1).

Common name. Mesopotamian fat-tailed opossum.

Spanish common name. Marmosa coliguresa de la Mesopotamia

Differential diagnosis. A species with a globose skull with an oval appearance, a short rostrum, laterally expanded zygomatic arches, prominent supraorbital processes, and small crests on the frontals. In dorsal view, the nasals are widened at the naso-fronto-parietal junction, not narrowing abruptly as seen in *Gracilinanus* spp., but rather they widen and maintain this width; the nasals do not extend posteriorly to the facial expansion of the lacrimals. In lateral view, the skull lacks the triangular appearance with a pointed face observed in other species (*e.g., T. pallidior*), but rather has a domed appearance. The infraorbital foramina are narrow, not wide, and appear compressed against the skull (visible in both frontal and lateral views). The spine that is part of the zygomatic arch of the lacrimals extends to the boundary between M2–M3. The parietals extend anteriorly to the point of greatest anterior projection of the squamosal (unlike *T. pulchellus*, where the squamosal extends beyond the frontoparietal junction). The zygomatic arches are not very robust and are slightly arched at the jugal-squamosal junction (in *T. pallidior* and *T. venustus*, the sphenorbital fissure is distinguishable). In ventral view, the palate is relatively flat, less domed than in other species (*e.g., T. pulchellus*), and shows abundant fenestration, with maxillary fenestrae at the protocone of M1 (Fig. 4). The incisive fenestrae are long and wide (long and narrow in *T. pallidior* and *T. venustus*); the maxillopalatine fenestrae are long and relatively large; the palatine fenestrae are medium-sized and round. The posterolateral foramina are large, elongated, and extend anteriorly to the protocone of the M4. The interpterygoid bridge is robust and projects posteriorly (Fig. 4). The presphenoid widens markedly anterior to the suture with the basisphenoid (unlike in *T. pulchellus*, where this bone is narrow). The tympanic *bullae* are relatively swollen, large, and well-separated (Fig. 4), creating a broad basicranium (similar to that of *T. pulchellus,* but the latter shows greater anterior and ventral development of the alisphenoid). It differs from the *bullae* of *T. pallidior* by having greater vertical development and less anteroposterior development of the alisphenoid than in *T. pallidior*. The mandibles are relatively delicate (though not as much as in *T. pallidior*); the ascending (coronoid) process forms an open angle with the horizontal process, similar to that observed in *T. pulchellus* but more pronounced. In the upper dentition, the less pronounced anteroposterior compression of the molars, especially in M4, stands out (contrasting with the pattern observed in *T. pallidior*, but similar to that observed in *T. pulchellus*); and the presence of a prominent StC, distinguishable from StB and StD in M1–M3 (even in specimens with some dental wear). The metacone is the largest and highest cusp of the upper molars (except for the M4); a metaconule is present, giving rise to a crest that reaches the base of the metacone, and to a lingual one that continues the line of the tooth toward the base of the molar, forming a marked cingulum between the metacone and protocone (a character which is absent in *T. pulchellus*). The lower canines are moderately sized and vertically or subvertically oriented; the dp2 and p3 are subequal in occlusal (length) and labial (height) views. The molars have a reduced anterobasal cingulum (more so than in *T. venustus*); the trigonid is more compressed in m1, which progressively widens in the successive teeth; the talonid is laterally compressed but not anteroposteriorly reduced in m4 (unlike in *T. pallidior* and *T. pulchellus*); the entoconid is displaced anteriorly (more pronounced in m2–m3); and there is no labial cingulum between the protoconid and hypoconid (conspicuous in m2–m3 of *T. venustus*).

Comments. Tate (1933) was the only author to designate *Thylamys* specimens with a regional criterion, considering the geographic location of the areas prospected by Azara (1802) and the sites where he lived and moved. In his concept, the species *T. citellus*, described by Thomas (1912) for Mesopotamian Argentina (and eastern Paraguay), corresponds to Azara's "dwarf" or "*enano*" (but see comments to Voss *et al*., 2009). The holotype is not a juvenile (as noted by Tate), but an adult with all its dentition erupted. This taxon differs from the rest of the species in the genus due to the robustness of its skull; the presence of well-developed supraorbital crests, even in subadult specimens; the large size of the alisphenoid portion of the tympanic *bullae* (which, unlike in *T. pallidior*, are well-separated); and some dental traits described above. Its general characteristics bring it closer to the species *T. pulchellus*, but with much more pronounced features and a larger size. Its distribution would be limited to the west by the Paraná River, which would act as a substantial barrier to the species' dispersal into Chaco ecosystems, separating it from the form *T. pulchellus,* which inhabits the dry Chaco. Myers (1982) proposed that in eastern Paraguay, the homonymous river would separate terrestrial mammal fauna into two, one to the east and one to the west; a pattern that

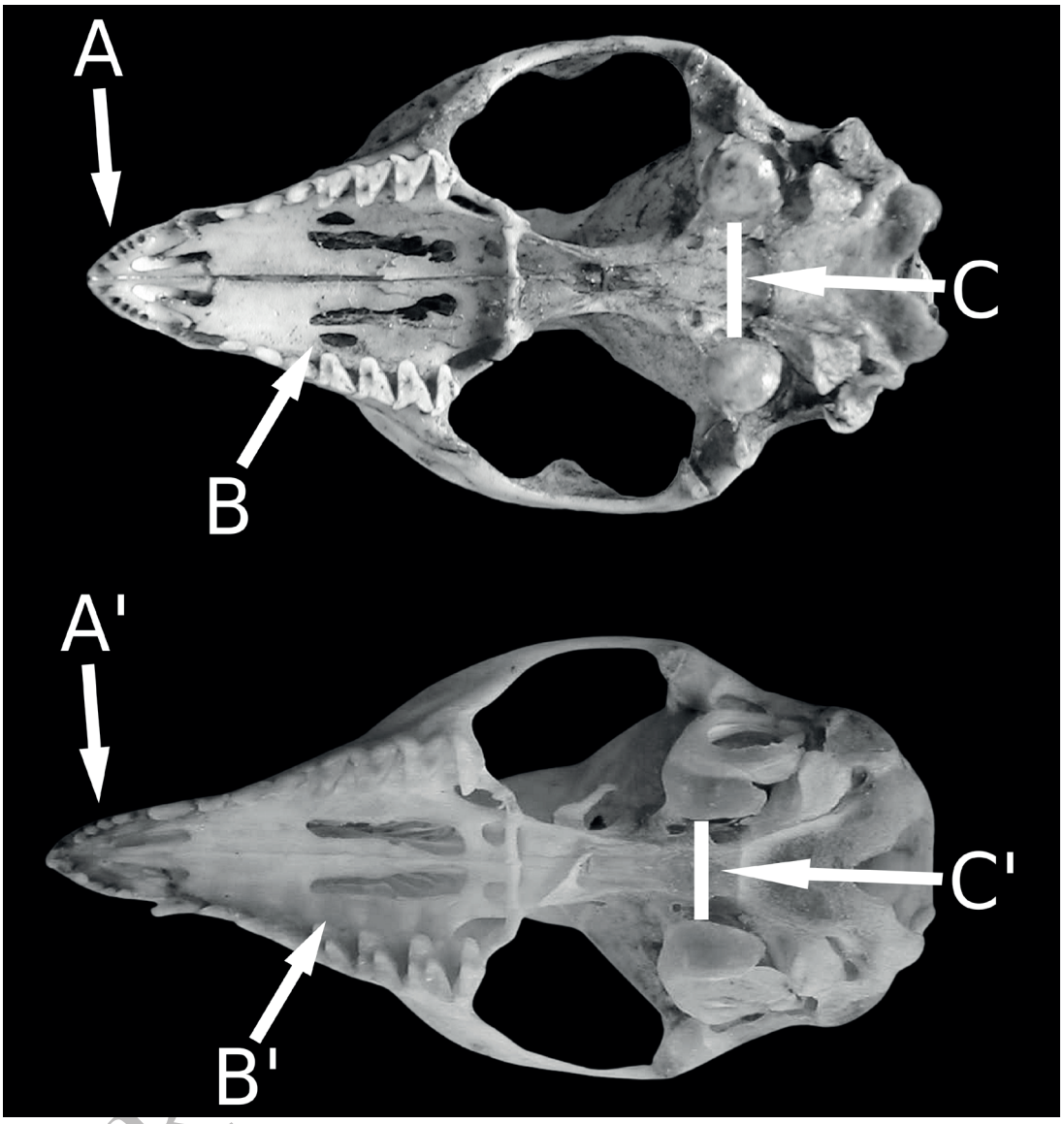

Fig. 4. Ventral views of the crania of *Thylamys citellus* (above) and *Thylamys pallidior* (below) showing differences in the rostrum (A, rounded; A', pointed), maxillary *fenestrae* (B, present; B', absent), and development of the alisphenoid *bullae* and interorbital region (C, broad; C', narrow). Specimens are not to scale.

would be increased in Argentina by the action of the Paraná River, with a greater flow and real channel than the Paraguay.

Thylamys pallidior **(Thomas, 1902a)**

Fig. 5A

Grymaeomys elegans Burmeister (not Waterhouse, 1839), 1856: 83 (part, figure and description of an animal from Mendoza Province, Argentina).

Didelphys elegans Burmeister (not Waterhouse, 1839), 1861: 412; Burmeister (not Waterhouse, 1839), 1879: 193.

Marmosa elegans Thomas, 1902a: 230 (not Waterhouse, 1839); Reig *et al*., 1977: 211; Massoia & Pardiñas, 1988a; Massoia & Vetrano, 1988.

Thylamys pallidior Matschie, 1916: 271; Contreras, 1979; Yensen & Tarifa, 1993: 51; Palma, 1995a: 2; Mares *et al*., 1996: 107 (part); Anderson, 1997: 164; Mares *et al*., 1997: 100 (part); Flores *et al*., 2000: 327 (part); Mares & Braun, 2000: 36 (part); Solari, 2003: 96 (part); Brown, 2004: 141; Braun *et al*., 2005: 148–156; Flores *et al*., 2007: 31; Creighton

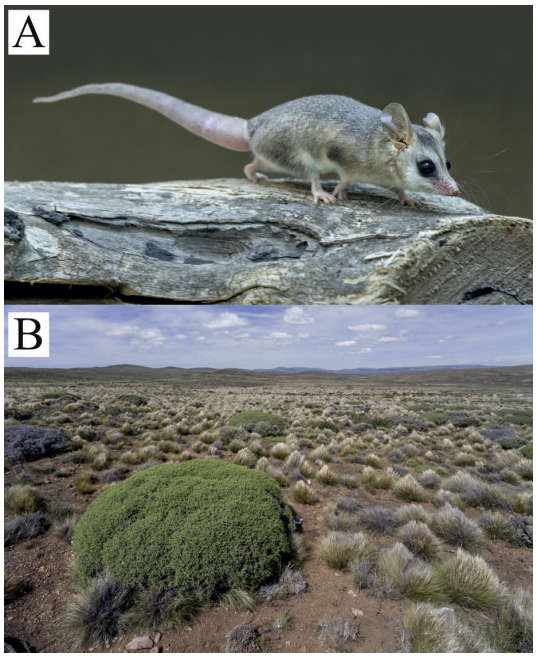

Fig. 5. *Thylamys pallidior* (Thomas, 1902) (A) and its environment (B) in Patagonia. Photographs courtesy of Darío Podestá ©.

& Gardner, 2008: 112; Martin, 2008: 133; Carvalho *et al*., 2009: 419–425; Flores, 2009: 7; Martin, 2009: 334–343; Voss & Jansa, 2009: 138; Giarla *et al*., 2010: 46; Formoso *et al*., 2011: 371–379; Giarla *et al*., 2013: 137–151; Palma *et al*., 2014: 217–234; Astúa, 2015: 176; Nowak, 2018: 87; Teta *et al*., 2018: 172; Albanese & Martin, 2019b; Astúa *et al*., 2023: 145; Bonvicino *et al*., 2023: 664; Martin *et al*., 2022: 4; Voss, 2022: 54; Martin & Carmignotto, 2024: 11.

Thylamys fenestrae – Martin, 2008: 131; Martin, 2009 –343.

Marmosa elegans fenestrae Marelli, 1931: 68.

Marmosa pallidior – Tate, 1933: 229; Yepes, 1936: 699.

Thylamys pusilla (Desmarest, 1804) – Mares & Braun, 2000: 38.

Thylamys pusillus (Desmarest, 1804) – Birney *et al*., 1996: 151; Solari, 2003: 94.

Thylamys elegans (not Waterhouse) – Massoia & Pastore, 1997; Massoia *et al*., 1997; Heinonen Fortabat & Chebez, 1997.

Marmosa elegans pallidior Thomas, 1902b: 159, 161; Thomas, 1913: 143; Thomas, 1919a: 118; Thomas, 1919b: 135; Thomas, 1921a: 422; Thomas, 1921e: 617; Thomas, 1926c: 195; Thomas, 1926d: 641; Thomas, 1927a: 657; Thomas, 1927b: 202; Mares *et al*., 1981: 165.

Marmosa pusilla bruchi Cabrera, 1958: 32; Crespo, 1974: 2; Daciuk, 1974: 23;

Marmosa pusilla pallidior Cabrera, 1958: 32; Olrog, 1959: 407; Olrog, 1979: 9.

Thylamys sp. Pardiñas *et al*., 2003: 89; Martin, 2003: 150; Nabte, 2004: 253; Udrizar and Pardiñas, 2006: 260.

Marmosa (Thylamys) pusilla pallidior Anderson *et al*., 1993: 18.

Thylamys bruchi Teta *et al*., 2009: 193.

Holotype. BMNH 2.2.2.116, young male, skin, cranium, and associated mandibles (collected by P.O. Simons, October 26, 1901).

Type locality. Challapata, east of lake Poopo, Cochabamba, Bolivia.

Geographic distribution. from the high Andes of Jujuy and Salta to southern Chubut, including western Tucumán, Catamarca, La Rioja, San Juan, Mendoza, central and southern Córdoba, Neuquén, La Pampa, western Buenos Aires, and Río Negro (Fig. 1).

Common name. Pallid fat-tailed opossum, white-bellied fat-tailed mouse opossum.

Spanish common name. Marmosa pálida, comadrejita común.

Differential diagnosis. Skull with an elongated and slender rostrum (Figs. 4, 7); parallel nasals that widen very little at the naso-fronto-maxillary suture; without supraorbital processes or sagittal crest; palate without maxillary fenestrae (Fig. 4); tympanic *bullae* with notable development of the alisphenoid (Fig. 4); small, procumbent, and curved canines; dP2/dp2 subequal to P3/p3; molars of moderate size, large in proportion to the skull size; notable anteroposterior compression in all molars, very marked in M4; well-developed ectoflexus, increasing in size from M1 to M3/m1 to m4; well-developed anterobasal cingulum. Sexual dimorphism in deciduous lower premolars (Martin, 2008).

Comments. The species shows the largest latitudinal distribution range of all the species in the genus, spanning about 3,250 km from north to south. Despite this extensive distribution, there is little intraspecific variability recorded in its characteristic traits (*e.g.*, well-developed tympanic *bullae*, pointed face, parallel nasals with little widening at the naso-fronto-maxillary suture, very developed anterobasal cingulum, to name just a few) (Martin, 2008). Braun *et al*. (2005) proposed the separation of the species into two subspecies, *T. pallidior pallidior* for the northern form, and *T. pallidior bruchi* for the southern form. As described above, *T. bruchi* constitutes a full species differentiated from *T. pallidior* based on morphologic traits. From a biogeographical perspective, the proposed division has little support, especially considering that the Puna ecosystem presents great unifor-

mity throughout its extent (see Morrone, 2001; Olson *et al*., 2001). Martin (2009) separated *T. fenestrae* from *T. pallidior* based on morphologic traits, but molecular analyzes recovered this species as part of *T. pallidior*. *T. fenestrae* has also been mentioned as a valid name for the southern subspecies of *T. pallidior* by Giarla *et al*. (2013) and Palma *et al*. (2014).

Thylamys pulchellus **(Cabrera, 1934)**
Fig. 6A

Marmosa janetta pulchella Cabrera, 1934: 126.
Thylamys pusillus – Braun *et al.*, 2005: 154; Flores *et al.*, 2007:35 (part, localities); Creighton & Gardner, 2008:114; Carvalho *et al.*, 2009:419–425; Flores, 2009; Voss & Jansa, 2009: 138; Giarla *et al.*, 2010: 39; Voss, 2022: 55.
Thylamys pulchellus – Martin, 2008: 136; Teta *et al.*, 2009: 193; Palma *et al.*, 2014: 217–234; Astúa, 2015: 177; Nowak, 2018: 87; Martin, 2019b; Asúta *et al.*, 2023; Bonvicino *et al.*, 2023: 664; Martin *et al.*, 2022: 4; Martin & Carmignotto, 2024: 11.
Thylamys bruchi – Astúa *et al.*, 2023: 144; Teta *et al.*, 2018: 165.

Holotype. MLP 21-X-35-32; adult female; skin, cranium, and associated mandibles (collected by Dr. Jorge Argañaraz).
Type locality. Robles, Santiago del Estero Province, Argentina.
Geographic distribution. Formosa, Chaco, Santiago del Estero, and eastern Salta, probably extending to northern Córdoba and Santa Fe provinces (Fig. 1).
Common name. Chacoan fat-tailed mouse opossum.
Spanish common name. Marmosa chaqueña; comadrejita enana común.
Differential diagnosis. Skull small, with a short face and large orbits, due to the presence of wide zygomatic arches. Supraorbital processes of moderate development (not as pronounced as in *T. citellus*); marked supraorbital crests, even in juvenile specimens, which project posteriorly in parallel without joining into a single sagittal crest. Nasals slightly narrowed at the beginning of their posterior third, projected posteriorly just barely past the posterior edge of the lacrimal (this trait is not observed in any other species of *Thylamys*). The frontals reach their greatest width at the level of the postorbital process; toward the back, these bones narrow, being surrounded by anterior processes of the parietals that form an "M"-shaped suture, more than in any other species of the genus. Poorly developed lambdoid crest; occipital condyles not very projected backward. In lateral view, the general shape of the skull is domed (Fig. 6), with the cranial roof curved backward (in other species of *Thylamys* this is more triangular and the posterior part of the skull does not show this pattern, except *T. citellus*). The dorsal spine of the premaxillaries extends very little backward (in *T. pallidior*, *T. citellus*, and *T. bruchi* this process is more extended posteriorly, with a broader premaxillary-maxillary contact area, and generally has a diagonal orientation with respect to the dental axis). The palate is vaulted, whereas in *T. citellus* it is rather flat. The premaxillary fenestrae are short, wide in their anterior portion and very narrow in their posterior part (in *T. pallidior* and *T. venustus* they are narrow and long; in *T. citellus* they are short and wide throughout their extent); maxillopalatine fenestrae of moderate size; a pair of small lateral fenestrae and relatively large posterolateral foramina, extending anteriorly to the protocone of M4. The interpterygoid bridge, unlike *T. citellus*, is not so extended posteriorly nor is it so robust. The *bullae* are large but well separated from each other, differing from *T. citellus* by the lesser development of the alisphenoid (see above). The paroccipital processes are of moderate development, similar to *T. pallidior*, but smaller than in *T. citellus*. The hor-

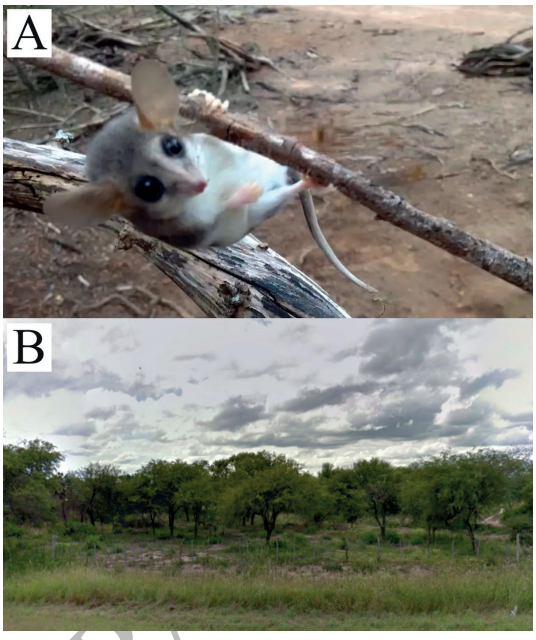

Fig. 6. *Thylamys pulchellus* (Cabrera, 1934) (A) and its environment (B) in eastern Salta. Photographs courtesy of Mariela Nieves ©.

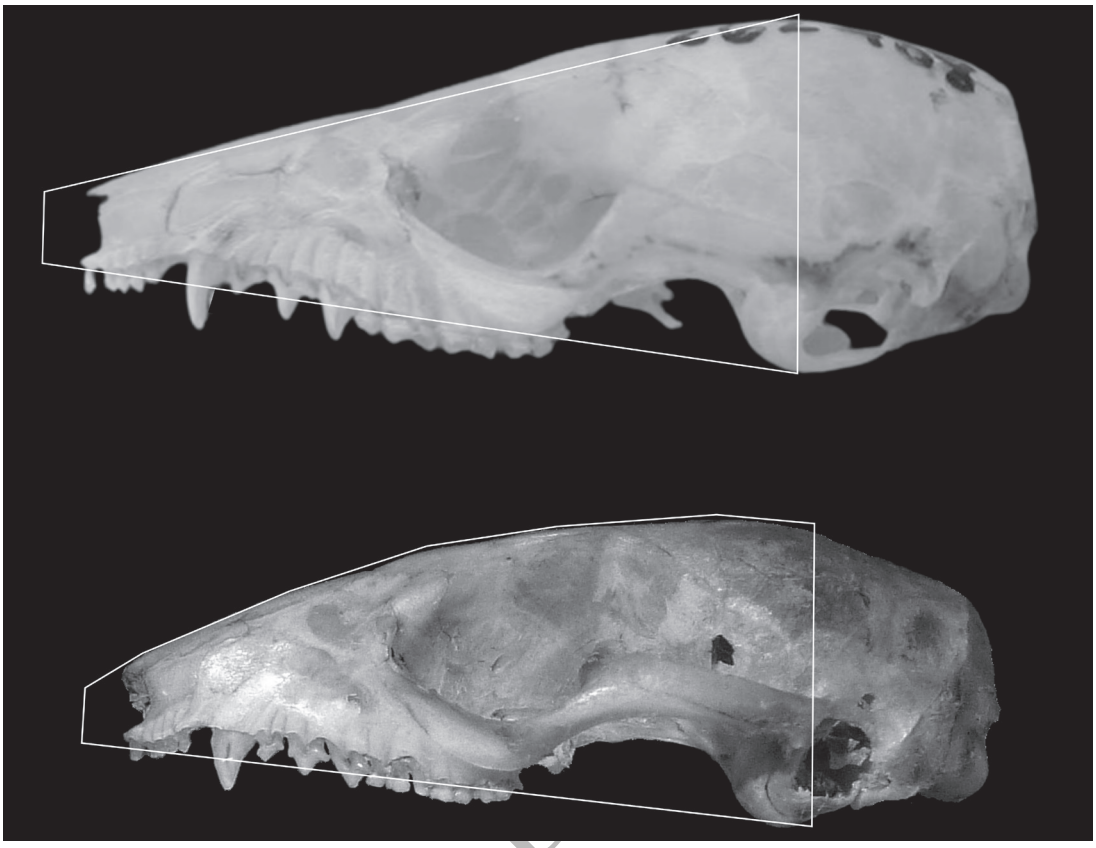

Fig. 7. Lateral view of the crania showing a triangular shape in *Thylamys pallidior* (above) and domed shape *Thylamys pulchellus* (below). The yellow line represents the upper leg of a triangle over the cranium of *T. pulchellus*. Specimens are not to scale.

izontal mandibular ramus is slender, reaching its greatest height below the m3–m4 boundary and then quickly narrows forward. The most notable feature of the ascending ramus is the inclination of its coronoid process (Fig. 8), which forms a very open angle with the alveolar plane of the horizontal ramus (similar to *T. citellus*). The M1–M4 length is the shortest of all *Thylamys* species from Argentina, a trait especially noticeable in relation to the overall skull size; the upper molars show the persistence of a StC (Fig. 9), and M4 is not very compressed anteroposteriorly. It can be distinguished from all other species of the genus by the great lateral compression of the canines and premolars. The upper incisors are very small, with I2–I5 being tubular, somewhat spatulate in the crown, and subequal in size, except for the last ones, with a crown barely wider than the rest. The scant relative development of I1 is more reminiscent of species of *Gracilinanus* spp. than of *Thylamys* spp. The upper canines have two crests, one anterior and one posterior, which are well developed, and no anterior or posterior cusps are apparent. The premolars have a well-developed posterior cusp; additionally, dP1–dP2 have a tiny anterior cusp. The upper molars are not compressed anteroposteriorly; StC persists at the level of the ectoflexus (Fig. 9). The lower canines are poorly developed and more reminiscent of those of *Gracilinanus* spp. than any species of the genus *Thylamys*. The three lower premolars have a subtriangular outline, laterally compressed, and with a moderately developed posterior talon. The molars are compact in appearance, with a compressed trigonid and a relatively wide talonid (unlike *T. citellus* where the talonids are more compressed). The hypoconids are not very prominent, and the entoconids and hypoconulids are only moderately developed. The talonid of m4 is relatively narrow and apparently not cuspidate.

Comments. This taxon was originally described as a subspecies of *T. janetta* (Cabrera, 1934), a form synonymized with *T. venustus* (Gardner,

Fig. 8. Lateral view of the mandibles of *Thylamys pallidior* (above) and *Thylamys citellus* (below) showing different angles between the ascending coronoid process and horizontal ramus. Specimens are not to scale.

1993; Braun *et al*., 2005) but with distinctive characteristics that have allowed its separation (Martin, pers. obs.). Subsequently, the species *T. pulchellus* was included within *T. bruchi* (*sensu* Cabrera, 1958) and *T. pusillus* (Flores *et al*., 2000; Giarla *et al*., 2010; Voss, 2022). Current work comparing *T. bruchi* with *T. pulchellus* separates these species based on morphologic characters, environmental variables, and other traits (Martin & Mignino, 2024).

Although *T. sponsorius* and *T. venustus* were separated by genetic data (Giarla *et al*., 2010; Palma *et al*., 2014), no discrete morphologic characters have been identified between these species (Giarla *et al*., 2010; Voss, 2022). Therefore, I present an emended morphologic diagnosis for *T. venustus* (the type species), and added some novel morphologic characters separating *T. sponsorius* and *T. venustus* (see comments), and with *T. janetta* (a species taxon included in the synonymy of *T. sponsorius* by Giarla *et al*., 2010).

***Thylamys venustus* (Thomas, 1902a)**

Fig. 10A

Marmosa elegans Thomas (not Waterhouse, 1839), 1898: 4; Thomas (not Waterhouse, 1839), 1900:

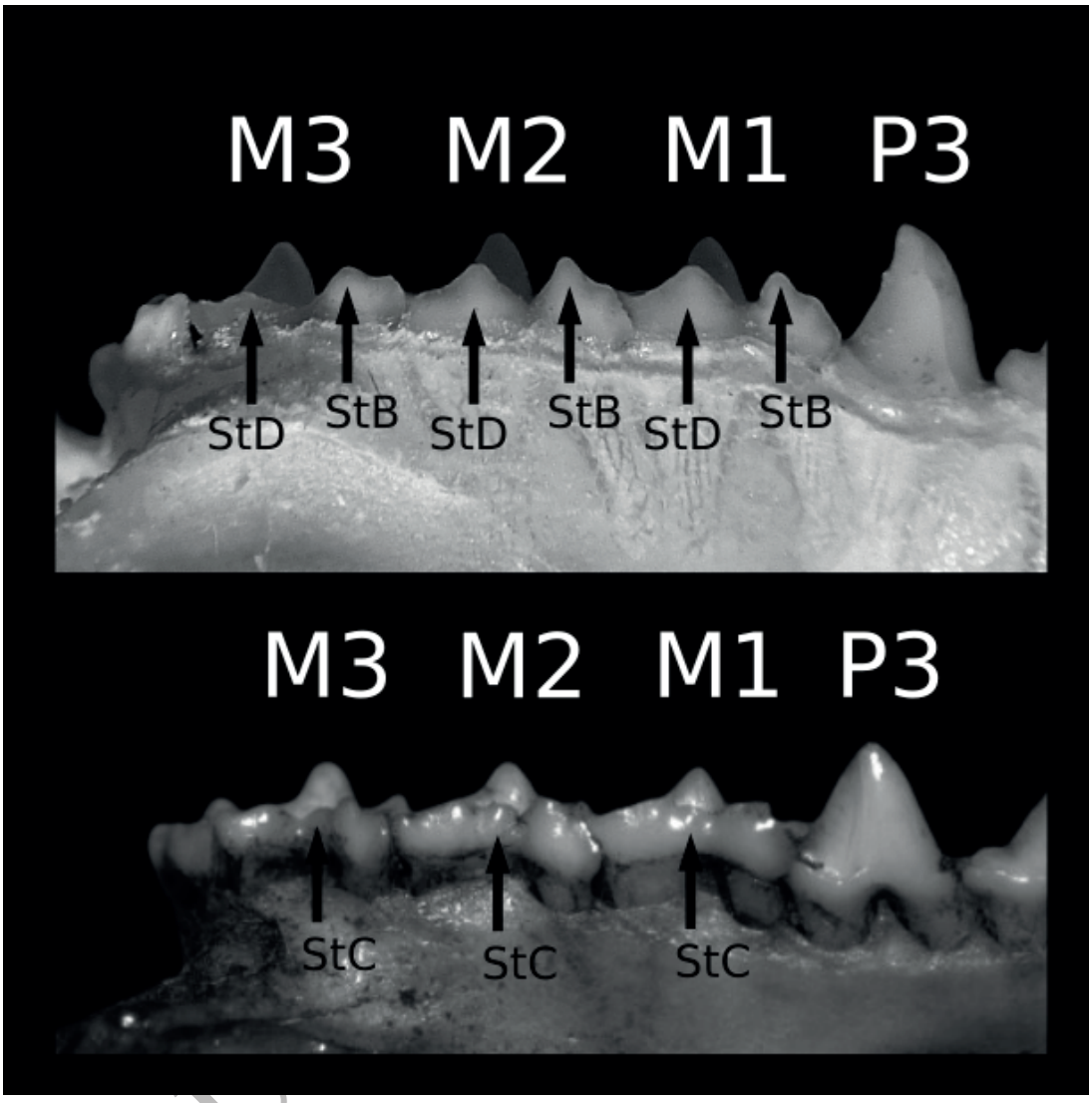

Fig. 9. Labial view of the upper toothrow showing the absence of stylar cusp C (StC) in the molars of *Thylamys pallidior* (above) and its presence in *Thylamys pulchellus* (below). Specimens are not to scale.

302; Thomas, 1902a: 230; Thomas, 1902b: 143.

Thylamys elegans – Heinonen & Bosso, 1994: 55; Mares *et al*., 1996: 106; Mares *et al*., 1997: 100; Capllonch *et al*., 1997: 53.

Marmosa elegans venusta Thomas, 1902a: 159–160; Osgood, 1916: 200; Olrog, 1959: 405; Mares *et al*., 1981: 165.

Marmosa (*Thylamys*) *elegans venusta* – Anderson *et al*., 1993: 17.

[*Thylamys*] *venusta* Matschie, 1916: 271.

Thylamys venusta Cabrera, 1958: 30.

Marmosa venusta venusta Tate, 1933: 225.

Thylamys venustus – Heinonen & Bosso, 1994: 55; Flores *et al*., 2000: 331; Anderson, 1997: 165; Mares & Braun, 2000: 39; Solari, 2003: 96; Braun *et al*., 2005: 153; Flores *et al*., 2007: 38; Creighton & Gardner, 2008: 116; Martin, 2008: 139; Carvalho *et al*., 2009: 419–425; Flores, 2009: 7; Voss & Jansa, 2009: 138; Giarla *et al*., 2010: 56; Giarla *et al*., 2013: 137–151; Palma *et al*., 2014: 217–234; Astúa, 2015: 179; Nowak, 2018: 87; Teta *et al*., 2018: 172; Martin, 2019d; Astúa *et al*., 2023: 147; Bonvicino *et al*. 2023; Martin *et al*., 2022: 4; Voss, 2022: 56; Martin & Carmignotto, 2024: 11.

Marmosa elegans cinderella Thomas, 1902a: 159, 161; Thomas, 1918: 193; Thomas, 1920: 196; Thomas, 1925: 582; Thomas, 1926b: 608; Olrog, 1959: 405.

Marmosa venusta cinderella Tate, 1933: 226.

[*Thylamys*] *cinderella* Matschie, 1916: 271.

Thylamys cinderella – Flores *et al*., 2000: 325.

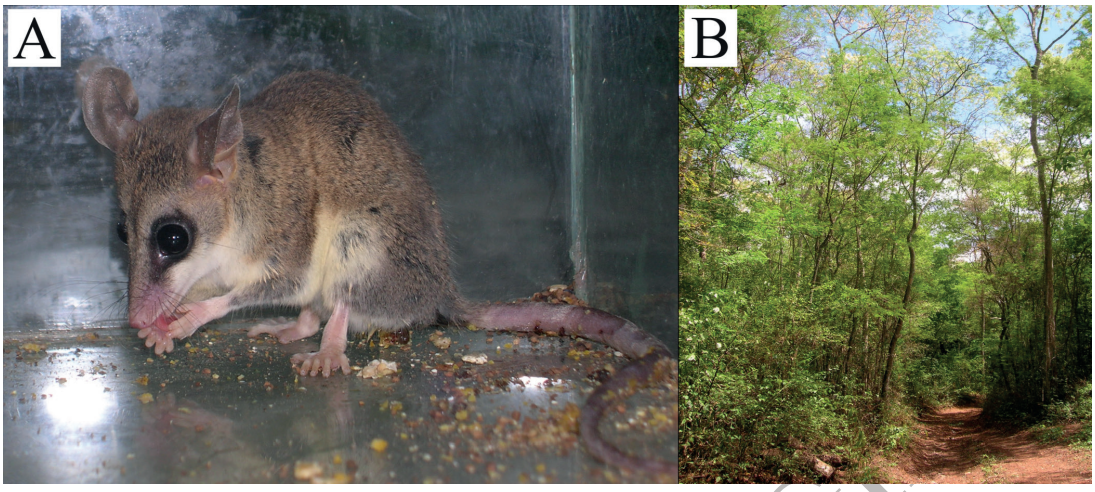

Fig. 10. *Thylamys venustus* (Thomas, 1902a) (A) and its environment (B) in eastern Salta Province. Photographs courtesy of Pablo Jayat ©.

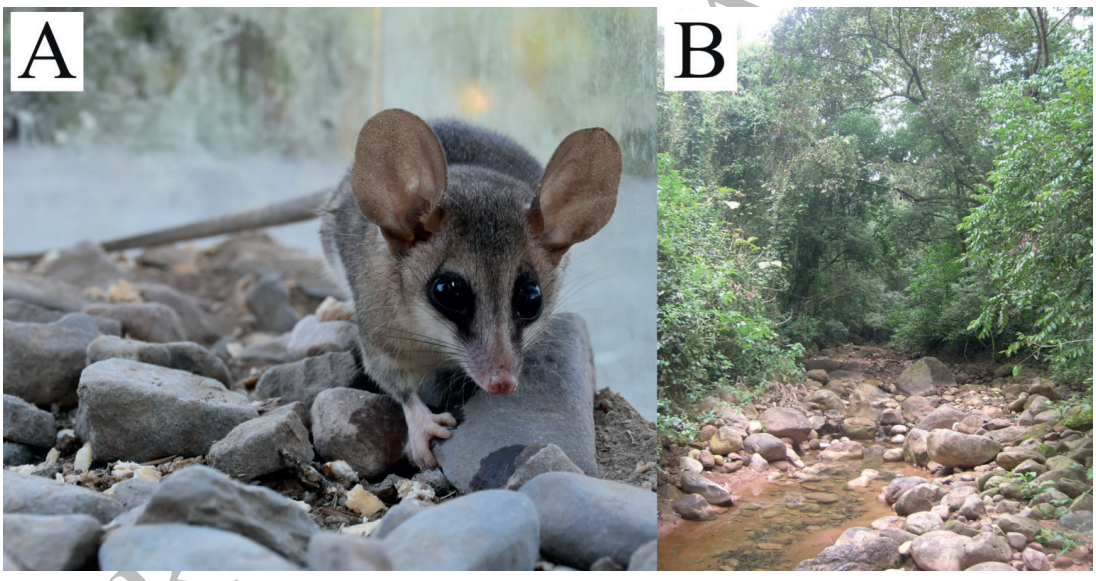

Fig. 11. *Thylamys sponsorius* (Thomas, 1921) (A) and its environment (B) in eastern Jujuy Province. Photographs courtesy of Pablo Jayat ©.

Marmosa elegans sponsoria Thomas, 1921c: 186.
Marmosa venusta sponsoria Tate, 1933: 228.
Thylamys sponsoria – Flores *et al*., 2000: 330.

Holotype. BMNH 2.1.1.120; adult female; skin, cranium, and associated mandibles (collected by Mr. Perry O. Simons).
Type locality. Parotani, Bolivia.
Geographic distribution. Salta, Jujuy, and Tucumán (Fig. 1).
Common name. Buff-belied fat-tailed mouse opossum.
Spanish common name. Marmosa elegante, comadrejita yungueña, marmosa yungueña, marmosa selvática.
Differential diagnosis. Similar in size to *T. elegans*, but with a dark brown to brown dorsal coloration, without the gray pattern found in *T. pallidior*. Ventral surface with hairs that have gray bases and yellowish tips (not whitish or cream-colored as in other species from Argentina). Skull and teeth similar in appearance to those of *T. elegans* but smaller. Alisphenoid bullae are smaller than in *T. pallidior*, well sepa-

rated from each other (with an average interbular distance of 4.2 mm). Upper and lower dental rows are similar in size to *T. elegans*, with the incisors increasing in size from I2 to I5, the latter being clearly larger than the rest. Canines are less procumbent than in *T. elegans* but not as vertical as in *T. pallidior*. The third upper premolar is larger in lateral view than the dP2, though subequal in occlusal view. The upper molars increase in size from M1 to M3, with M4 compressed anteroposteriorly but not mesiodistally. Lower canines are less procumbent than in *T. pallidior*. In occlusal view, dp2 is the largest premolar, with a well-developed talonid; in labial view, it is subequal to p3. Lower molars have a poorly developed anterobasal cingulum; the talonid of m4 is not compressed labiolingually and has well-developed cusps, similar to those of m1–m3; hypoconulids are twinned with the entoconid, not oriented posteriorly, and are medially displaced as in *T. pallidior*.

Comments. Flores *et al*. (2000) proposed the separation of the forms *T. cinderella* and *T. sponsorius* as valid species. Braun *et al*. (2005) only acknowledged the validity of *T. cinderella* and tentatively included *T. janetta* as a synonym of *T. venustus*. In a recent review based on morphologic and morphometric characters of the four forms associated with *T. venustus*, morphologic characteristics were recognized that separate *T. janetta* from *T. venustus* (and *T. sponsorius*). These traits are as follows: total length and head-body length greater than *T. venustus*, the tail exhibits the opposite pattern (shorter in *T. janetta*); presence of white ventral hairs throughout their length, unlike *T. venustus* where they are gray at the base and yellow at the tip; periocular rings thinner than in *T. venustus* (more similar to those of *Lestodelphys halli*); shorter and wider snout than in *T. venustus*; zygomatic arches more laterally expanded than in *T. venustus*; inter-pterygoid bridge more posteriorly expanded than in *T. venustus*; tympanic bullae smaller and more separated than in *T. venustus*; alisphenoid with less vertical and posterior development than in *T. venustus*; alisphenoid strut long, relatively transverse to the anteroposterior axis of the skull, giving it a broader and more posteriorly expanded appearance than in *T. venustus*; mandibular ramus more robust than in *T. venustus*; and dP1 smaller than in *T. venustus*. When examining specimens assigned to *T. cinderella* and *T. sponsorius*, both the measurements of external characters and those of cranial and dental characters fall within the intraspecific variability of the specimens originally assigned to *T. venustus*. None of the diagnostic characters used in Flores *et al*. (2000) (*e.g.,* skull length, zygomatic arches, supraorbital ridges and presence/absence of processes, rostrum length and width, development of lambdoidal crests, dentition size) allowed for the separation of the forms recognized as *T. cinderella* and *T. sponsorius*. Giarla *et al*. (2010) mention that they were unable to find morphologic discrete characteristics that allowed a proper separation between *T. sponsorius* de *T. venustus*. I identified subtle differences between the specimens they assigned to these two species: more developed alisphenoid in *T. sponsorius* than in *T. venustus*, where it is smaller and the bullae appear slightly more separated; smaller upper and lower molars in *T. venustus* than in *T. sponsorius*; more developed ectoflexus in *T. sponsorius*, with a curved crest joining StB and StD; m1 with a more laterally compressed trigonid, slightly more salient hypoconid and anteriorly displaced entoconid in *T. venustus*. Although these characteristics need further exploration, they might represent a recent and ongoing split between these forms.

Thylamys sponsorius (Thomas, 1921)

Fig. 11A

Thylamys sponsorius – Solari, 2003: 96 (part); Díaz & Bárquez, 2007: 431; Flores *et al*., 2007: 37; Creighton & Gardner, 2008: 115; Martin, 2008: 139 (part); Carvalho *et al*., 2009: 419–425; Voss & Jansa, 2009: 138; Giarla *et al*., 2010: 51; Giarla *et al*., 2013: 137–151; Palma *et al*., 2014: 217–234; Astúa, 2015: 178; Nowak, 2018: 87; Teta *et al*., 2018: 172; Martin, 2019c; Astúa *et al*., 2023: 146; Bonvicino *et al*., 2023: 664; Martin *et al*., 2022: 4; Voss, 2022: 55; Martin & Carmignotto, 2024: 11.

Thylamys cinderella – Braun *et al*., 2005: 153; Díaz & Bárquez, 2007: 429; Flores *et al*., 2007: 30 (part); Creighton & Gardner, 2008: 109 (part); Carvalho *et al*., 2009: 419–425; Voss & Jansa, 2009: 138; Nowak, 2018: 87; Bonvicino *et al*., 2023: 664.

Holotype. BMNH 21.1.1.85; adult male; skin and cranium with associated mandibles; collected by

Type locality. Sunchal, Sierra de Santa Bárbara, Jujuy Province, Argentina.

Geographic distribution. Salta, Jujuy, Tucumán, and Catamarca provinces (Fig. 1).

Common name. Buff-bellied fat-tailed mouse opossum, Argentine fat-tailed opossum.

Spanish common name. Marmosa común, comadrejita yungueña, marmosa coligruesa de Argentina.

Comments. See those of *T. venustus* above.

CONCLUSIONS

So, what is next for the genus *Thylamys* in Argentina? The main taxonomic issues that need to be addressed are: (1) Elucidate the validity and taxonomic relationships between *T. bruchi* and *T. pulchellus,* and their relationship with *T. pusillus*; (2) Determine the identity of *T. pallidior* throughout its range, including the possible separation of the forms *fenestrae* and *pallidior s.s.*; and (3) Elucidate the validity and morphologic differentiation between *T. sponsorius* and *T. venustus*, and their relationship and validity with the form *T. janetta* from Bolivia.

The main issues that need to be addressed regarding the distribution of *Thylamys* species recognized for Argentina are as follows: (1) Update the distribution maps of *T. bruchi*, *T. citellus*, *T. pulchellus* and *T. venustus s.l.*, and their overlapping ranges; (2) Confirm the presence of *T. citellus* for Misiones Province; (3) Elucidate the distribution of *T. pallidior s.l.*, and its presence in eastern Córdoba and southern Santa Fe provinces; and (4) Define areas of sympatry between species (*e.g., T. bruchi* and *T. pallidior*; *T. pulchellus*, and *T. venustus*).

It is clear that despite many years of research, the status of many of these forms remains controversial, especially in Argentina where most of the species are found. Limited morphologic and morphometric work has been done on the most poorly known species, and many revisionary studies have been based mostly on genetic analysis, excluding publicly available specimens from Argentine collections (*e.g.,* the type of *T. pulchellus*, topotype of *T. bruchi*, and type of *T. fenestrae* are at the Museum of La Plata). Much work remains to be done with this genus of mostly arid-adapted species, for which I hope this work serves as a basis for.

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