

Range expansion of two South American mouse opossums (*Thylamys*, Didelphidae) and their biogeographic implications

Ampliación de la distribución geográfica de dos comadrejas enanas de Sudamérica (*Thylamys*, Didelphidae) y sus implicancias biogeográficas

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ABSTRACT

The range expansion of two South American mouse opossums (*Thylamys*, Didelphidae) is reported. On the basis of morphological characters it is concluded that forms identified as *Marmosa karimii* from the Cerrado of Brazil (State of Mato Grosso), correspond to *Thylamys velutinus*, a taxon currently recognized for the Atlantic Rainforests of Brazil. Additionally, thylamyines collected in northern Chile (Province of Tarapacá) and previously reported as *Marmosa elegans*, represent *Thylamys pallidior*, a form previously thought to be restricted to the Andean Prepuna of Argentina and Bolivia. The occurrence of this Andean mouse opossum in areas of northern Chile represents a new didelphimorph marsupial for that country. The range expansions of both thylamyines are based on series of specimens collected in northern Chile and central Brazil deposited in the National Museum of Natural History, Smithsonian Institution USA. The range expansion is discussed in light of the historical biogeographic events that affected the southern part of South America during the Plio-Pleistocene, as well as the floristic relatedness of the semi-desertic biomes of the continent.

Key words: *Marmosa*, Andean altiplano, coastal desert, Cerrado, Atlantic rainforests.

RESUMEN

Se presenta la ampliación de la distribución geográfica de dos comadrejas enanas de Sudamérica (*Thylamys*, Marmosidae). A través de comparaciones morfológicas se concluye que formas reconocidas como *Marmosa karimii* del Cerrado de Brasil (Estado de Mato Grosso), corresponden a *Thylamys velutinus*, un taxon reconocido para el Bosque Atlántico. De igual forma, thylamyinos colectados en el norte de Chile (Provincia de Tarapacá) clasificados como *Marmosa elegans*, corresponden a *Thylamys pallidior*, forma restringida a la Prepuna Andina de Argentina y Bolivia. El reconocimiento de la comadreja enana Andina en áreas del norte de Chile representa la existencia de un nuevo marsupial didélfido para este último país. Estas conclusiones fueron el resultado de una revisión de especímenes colectados en el norte de Chile y centro de Brasil, depositados en el National Museum of Natural History, Smithsonian Institution, USA. La extensión del área de distribución de ambos thylamyinos se discute en base a eventos biogeográfico-históricos que afectaron la parte sur de Sudamérica durante el Plio-Pleistoceno, así como a las relaciones florísticas de los biomas semidesérticos del continente.

Palabras clave: *Marmosa*, altiplano Andino, desierto costero, Cerrado, bosque Atlántico.

INTRODUCTION

Mouse opossums have generally been regarded as all small-bodied and long-tailed didelphid marsupials from the Neotropical Region (*Marmosa* Gray, 1821, sensu lato). Tate (1933) recognized five species-groups in *Marmosa* that today approximate the genera *Marmosa* (sensu stricto), *Micoureus* (Lesson, 1842), *Marmosops* (Matschie, 1916), *Gracilinanus* (Gardner & Creighton,

1989), and *Thylamys* (Gray, 1843). According to Hershkovitz (1992) the first four taxa should be included in the subfamily Marmosinae, while *Thylamys* should constitute the monotypic Thylamyinae, both comprising the new family Marmosidae. Marmosine mouse opossums represent the most speciose assemblage within the didelphimorph marsupials, with 33 recognized species (Gardner 1993) distributed along an extensive latitudinal and altitudinal

gradient (Tate 1933). They range from central Mexico (*Marmosa mexicana*), southward to Argentinean Patagonia and the Coastal Desert of Chile (*Thylamys*). Altitudinally, mouse opossums are found at low areas (e.g., *Micoureus*), as well as altitudes as high as 3,500 m (*T. pallidior*).

While the majority of mouse opossums occur in tropical and semi-tropical forests of Central and South America, *Thylamys* (Tate's [1933] *elegans* group) is mainly an inhabitant of dry open biomes. Six species of *Thylamys* are currently recognized (Fig. 1; Gardner 1993, Palma 1994): *T. elegans* (Waterhouse, 1839) inhabits the Coastal Desert of Peru and Chile, and also is found over coastal areas as far south as 37° S in Chile; *T. venusta* (Thomas, 1902) occurs on the eastern slopes of the Andes (the "Monte Espinoso" of southeastern Bolivia and northern Argentina); *T. pusillus* (Desmarest, 1804) is found in the Chaco region of Argentina, Bolivia, and Paraguay, and in the Monte Desert of Argentina; *T. pallidior* (Thomas, 1902) inhabits the rocky slopes of the Andean Altiplano (Prepuna) in Argentina and Bolivia at elevations as high as 3,500 m; *T. macrura* (Olfers, 1818) ranges in the moist subtropical forests of eastern Paraguay and adjacent Brazil; and *T. velutinus* (Wagner, 1842) is found in the Atlantic Rainforests of southeastern Brazil.

As part of a larger study of *Thylamys*, I examined and identified mouse opossums collected in southern Brazil (Pine et al. 1970) and northern Chile (Pine et al. 1979), and based on these, I here report range expansions for one species of *Thylamys* to the pre-Andean and Coastal Desert areas of northern Chile (*T. pallidior*), and for another, to the Cerrado region of Brazil (*T. velutinus*). The range expansions of both taxa are discussed in light of the historical biogeography of southern South America and the paleoecological relatedness of the dry open biomes where thylamyines are found.

MATERIALS AND METHODS

Specimens examined

I examined specimens deposited in the National Museum of Natural History

(USNM), Smithsonian Institution, Washington D.C., identified as *Marmosa elegans* (Waterhouse, 1839), and as *M. karimi* Petter, 1968. The specimens were collected by Mel L. Schamberger in Chile (Pine et al. 1979), and by Ronald H. Pine in Brazil (Pine et al. 1970). I recorded standard external measurements, localities, and sex, from the skin labels, and noted characters in teeth skins and skulls. Standard external measurements of the USNM specimens were compared with those of *Thylamys pallidior*, *T. pusillus*, and *T. elegans* (Table 1) from Bolivia and Chile, deposited in the Museum of Southwestern Biology, University of New Mexico (MSB), in the American Museum of Natural History (AMNH), and in the Colección de Mamíferos of the Instituto de Ecología y Evolución, Universidad Austral de Chile (IEEUACH). Specimens examined and specific localities are:

Thylamys pallidior— Chile: Province of Atacama, Mina Altamira, Coastal Cordillera of Vallenar (USNM 391776, female; no measurements); Province of Tarapacá, 5 km S of Belén, 3,200 m (USNM 541600, male); 1 km W of Belén, 3,505 m (USNM 541596, male); Río Tignamar, 10 km SE of Tignamar, 3,505 m (USNM 541598, male); Chapiquiña, 3,200 m (USNM 541597 male, and USNM 541599 female); Zapahuirá, 7 km SE of Socorama [*sic*; probably corresponds to Socoroma], 3,100 m (USNM 541593 and USNM 541594, males); Esquiña, Camarones Valley (USNM 391777, no sex; no measurements).

Thylamys pallidior— Bolivia: Department of Chuquisaca, 68 km (by road) N of Camargo, 3,400 m, 20° 09' S, 65° 17' W (MSB 57003, AMNH 262406, AMNH 262407, males; AMNH 262406, female). Department of Tarija, Serranía Sama, 3,200 m, 21° 27' S, 64° 52' W (MSB NK 23533, female); 1 km E of Iscayachi, Río Tomayapo, 3,450 m, 21° 20' S, 64° 57' W (AMNH 262408, female).

Thylamys elegans— Chile: Province of Limarí, Fray Jorge National Park, 600 m (IEEUACH 2733, male; MSB NK 27569, MSB NK 27582, and MSB NK 27591, males; MSB NK 27583, female); Province of Elqui, Quebrada de Monárdez, 10 km (by

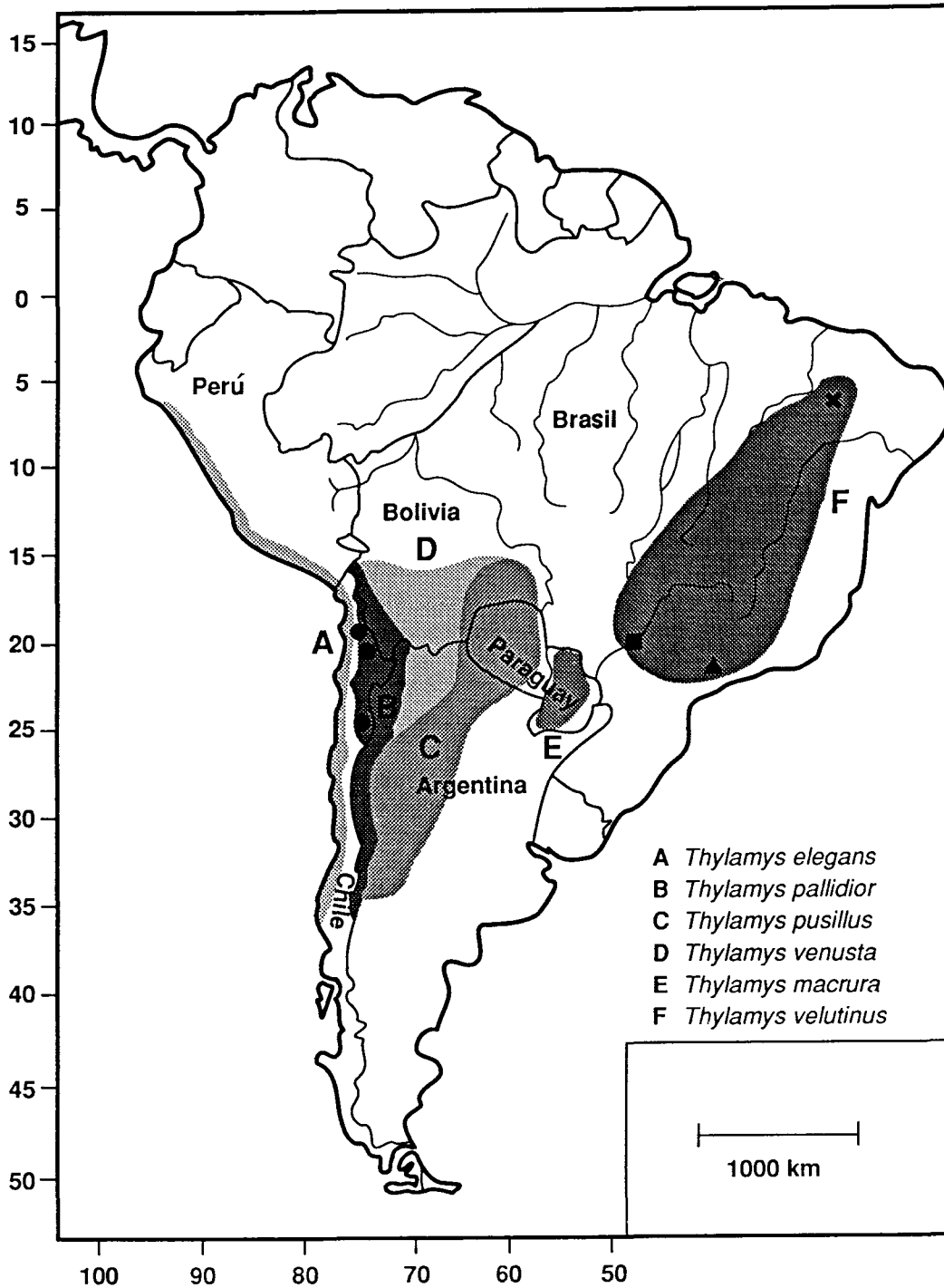


Fig. 1: Geographic ranges of thylamyines in South America. The dots within the range of *T. pallidior* represent the localities where this taxon was collected by ML Schamberger in Chile. The cross on the top of the range of *T. velutinus* represents the type locality of *M. karimii*, the triangle represents the type locality of *T. velutinus*, and the square shows the locality where Pine et al. collected additional forms that they assigned to *M. karimii*.

Distribución geográfica de thylamyinos en Sudamérica. Los puntos en el área de *T. pallidior* representan las localidades donde ML Schamberger colectó este taxon en Chile. La cruz en el rango de *T. velutinus* representa la localidad tipo de *M. karimii*; el triángulo representa la localidad tipo de *T. velutinus*, mientras que el cuadrado exhibe la localidad donde Pine et al. colectaron formas adicionales de *M. karimii*.

road) SE of La Serena (IEEUACH 2734 and IEEUACH 2735, males).

Thylamys velutinus— Brazil: State of Mato Grosso, 264 k N (by road) Xavantina, 12° 51' S, 31° 46' W, Serra do Roncador, 530 m (USNM 393536 and USNM 393537, males; USNM 393538, female).

Thylamys pusillus— Bolivia: Department of Chuquisaca, 3.8 km (by road) E of Carandaytí, 20° 46' S, 63° 03' W, 480 m (MSB 55846 and AMNH 261268 males). Department of Santa Cruz, 53 km (by road) E of Boyuibe, 20° 27' S, 62° 37' W, 600 m (MSB NK 23289 female, MSB NK 23330 male); Tita, 18° 25' S, 62° 10' W, 300 m (AMNH 260025). Department of Tarija, 5 km W of Estancia Bolívar, 400 m (MSB NK 25140 and MSB NK 25141, males); Estancia Bolívar, 21° 8' S, 62° 37' W, 400 m (MSB NK 23289, female).

RESULTS AND DISCUSSION

Thylamys elegans and *T. pallidior*

Tate (1933: 231) stated that *T. pallidior* had “a very wide range” comprising “eastern and southern Bolivia, all western Argentina, at least as far south as Neuquén and the Rio Negro [provinces]”. The type locality of *T. pallidior* is Challapata, east of Lake Poopo, Department of Oruro, Bolivia, 3.800 m (Tate

1933; he erroneously ascribed this locality to the Department of Cochabamba). Other marginal localities reported by Tate (1933) for this species are the Department of Tarija (Bolivia), and Mendoza and Neuquén provinces (Argentina; Tate 1933). I have captured *T. pallidior* at Camargo (Chuquisaca, 3.400 m), and Iscayachi and Serranía Sama (Tarija, 3.400 m), Bolivia. Table 1 summarizes body measurements taken from the skin labels of *Thylamys pallidior* from Bolivia and northern Chile, and from *T. elegans*.

Schamberger collected six males and a single female of “*Marmosa (Thylamys) elegans*” from different localities in Tarapacá Province, Chile (Pine et al. 1979). Pine et al. (1979: 341) gave no detailed description of these specimens, stating merely that they “are not as pale as *Marmosa elegans coquimbensis* [the northernmost subspecies of *elegans*] but are not as dark as *Marmosa elegans elegans* and until a revision of these mouse opossums is undertaken we prefer not to designate the population discussed here with a new or old trinomial”. Two additional specimens (for which no measurements were taken, USNM 391776 and 391777) are known from the Coastal Cordillera of Vallenar (Mina Altamira, Ataca Province), and from the Camarones Valley (Esquiña, Tarapacá Province) of northern Chile. Externally, the characters of all nine spec-

TABLE 1

Standard body measurements of marmosines from Chile and Brazil. HB = head and body length, TL = tail length, HF = hind foot length, and EL = ear length. Numbers above the parenthesis correspond to the mean of that variable, whereas numbers in parenthesis correspond to the standard deviation. n = sample size

Medidas corporales estándar de marmosinos de Chile y Brasil. HB = longitud del cuerpo, TL = longitud de la cola, HF = longitud de la pata con uña, y EL = longitud de la oreja. Los números sobre el paréntesis corresponden a la media de dicha variable, mientras que los números entre paréntesis corresponden a la desviación estándar. n = tamaño muestral

	<i>T. pallidior</i> (Bolivia) n = 8	<i>T. elegans</i> (Chile) n = 6	<i>M. elegans</i> (Schamberger's) n = 5	<i>M. karimii</i> (Pine 1970) n = 2	<i>M. karimii</i> (Petter 1968) n = 1	<i>T. pusillus</i> n = 5
HB	87.12 (7.02)	104.33 (7.31)	103.60 (8.68)	92.5 (6.5)	95.0 (—)	89.40 (4.31)
TL	114.25 (4.84)	118.57 (5.60)	102.60 (4.45)	70.00 (6.00)	72.0 (—)	111.00 (5.91)
HF	14.45 (0.69)	14.85 (0.83)	14.80 (1.32)	12.00 (0.00)	11.00 (—)	12.83 (0.68)
EL	22.62 (2.23)	25.85 (2.23)	25.20 (1.16)	18.00 (1.00)	19.00 (—)	20.83 (1.77)

imens agree with those of the Andean mouse opossum, *Thylamys pallidior*. This species is characterized by having long lax pelage (both ventrally and dorsally), white or creamy-white underparts with hairs usually gray-based (*T. elegans* has yellowish gray-based underparts), grayish color dorsally (with the characteristic dark stripe of thylamyines running along the body), pale brown color laterally, overall size smaller than in *T. elegans* (see Table 1), and pinnae larger than those of *T. elegans*. The skull of *T. pallidior* has a relatively shorter rostrum and larger auditory bullae when compared to other species of *Thylamys*.

Only minor differences can be detected when comparing the standard measurements of *T. pallidior* with those of *T. elegans* and of the forms collected by Schamberger (Table 1). However, average head plus body length of *T. pallidior* is less than in *T. elegans*. This feature has been used as a taxonomic character to differentiate *T. pallidior* from the other thylamyines (Tate 1933). *Thylamys elegans* from Chile and the specimens collected by Schamberger have similar values in length of the head and body, ear, and hind foot (Table 1), but *T. elegans* has a longer tail, longer pelage, and white underparts (Table 1). The subtle differences between *T. pallidior* and the specimens collected by Schamberger in northern Chile suggest that Chilean populations might represent a recognizable subspecies of *T. pallidior*. The finding of *T. pallidior* in Chile documents the occurrence of a new didelphimorph marsupial in this country, since *T. pallidior* is a "good" species closely related to *T. elegans* (Palma 1994).

Marmosa karimii and *Thylamys velutinus*

Pine et al. (1970) reported three mouse opossums (two males and one female) from the phytogeographic province of the Cerrado (Mato Grosso, Brazil). Pine et al. stated that these marmosines agreed best with the description given by Petter (1968) when naming *Marmosa (Thylamys) karimii* from the Brazilian Caatinga (Exú, Pernambuco; Fig. 1). Petter (1968), who had but a single specimen, depicted *M. karimii* as a small species, with the tail shorter than the body

and also very thick at its base, with pelage grayish dorsally and white ventrally, with short manus and pes, and with reduced canines. These characters agree with those given for *Thylamys velutinus*, characterized by its "Monodelphis-like" in appearance (Tate 1933), in its small size, short pelage (the original color remains problematical; Tate 1933), tail thick at its base and shorter than the body (usually less than 85 mm), and short hind feet (less than 14 mm; Tate 1933). These dimensions of *velutinus* and of specimens identified as *karimii* are similar (Table 1). The skull of *T. velutinus* is characterized by having very narrow nasals, small bullae (compared to those of *T. pallidior*), and short canines (Tate 1933).

Mares et al. (1981) reported additional specimens of *M. karimii* from Pernambuco, Brazil, that were also discussed by Streilein (1982) as part of an ecologic study on the small mammals of the Caatinga. Streilein (1982: 96) when describing the food habits of some captive individuals, stated that "flying insects were snatched in mid-flight and manipulated by the forefeet while the prehensile tail [emphasis added] and hind limbs supported the body". This observation clearly suggests that what Streilein (and Mares et al. 1981) recognized as *M. karimii*, is certainly not the form described by Petter, because true *M. karimii* lacks a prehensile tail.

Petter (1968), in comparing *M. karimii* with other marmosines concluded that *M. karimii* was related to *T. pallidior*. Earlier, Tate (1933) placed *velutinus* in the *pallidior* section, characterized by forms of small size, gray or white-bellied, and with a narrow interorbital region. However, Gardner (1993) placed *karimii* in synonymy with the Chacoan form *Thylamys pusillus*, although this latter species is characterized by having a much longer tail (Table 1) and a venter with hairs creamy-white throughout their length.

Given the agreement on anatomical and cranial characteristics of the Caatinga and Cerrado forms (*karimii*) with the Atlantic forest forms (*velutinus*), I conclude that the species identified by Petter (1968) as *Marmosa karimii*, is the same species that occurs in the Atlantic forests and the Cerrado of

Brazil, and to which the name *T. velutinus* applies. In fact, the type locality of *T. velutinus* (Ypanema, Sao Paulo, Brazil; Tate 1933), although geographically located in the Atlantic Rainforests is in close proximity to Cerrado habitats (Sarmiento 1983).

Historical biogeography

By the end of the Eocene the landscape of South America consisted of Neotropical forests that covered much of the region, with the exception of the southern part of the continent (Potts & Beherensmeyer 1992, Janis 1993). Known Miocene macrofloras consisted of humid forests in areas now covered with dry-adapted vegetation types, a pattern reinforced by the uplift of the Andes that promoted desertic environments (e.g., Altiplano, Patagonia; Potts & Beherensmeyer 1992). Palynological data have shown that Plio-Pleistocene times were characterized by a series of expansions and contractions of forests and savannas, caused by glacial and interglacial periods (Van der Hammen 1982). A general consequence of Late Tertiary events was the shrinking of forests and the subsequent expansion of open areas as grasslands and deserts (Potts & Beherensmeyer 1992). Given all these vegetational shifts in the landscape, it seems plausible that a fauna adapted to dry, open areas, such as *Thylamys*-type forms, could have originated from ancestral marmosines (e.g., ancestors to *Gracilinanus* and *Marmosops*) that were adapted to moist tropical forests. The oldest fossil records for *Thylamys* are from the Pliocene (Montehermoso) beds in Buenos Aires Province, Argentina (Reig et al. 1987).

Recent phylogenetic analyses on *Thylamys* (that did not include *T. velutinus*) based on allozyme data (26 loci), and sequences of a 600 bp region of the mitochondrial DNA (mtDNA) cytochrome *b* gene, have shown that *T. elegans* is the sister taxon of *T. pallidior* and *T. pusillus* (Palma 1994). In fact, the total evidence analysis (the combined allozyme and mt DNA data set; Kluge, 1989) showed that the ancestral forms that may have given rise to *T. elegans*, might also have given rise to the ancestors of *T. pallidior* and *T. pusillus* (Palma 1994, Fig.

2). The phylogenetic relationships between the Coastal Desert and the Andean taxon could be explained by the ecological affinities and geographic proximity between the Andean Puna and the Coastal Desert (Sarmiento 1975, Romero 1986). Therefore, the occurrence of *T. pallidior* on the Chilean side of the Cordillera, and further records of *T. pallidior* in Coastal desert areas of Chile, suggest that dispersal to the western Andes has been occurring in some populations of *T. pallidior*. Such events would account for the range expansion of *T. pallidior* to areas over the Chilean Pre-puna and the Coastal Desert of northern Chile.

Although a phylogenetic hypothesis that considers the relationships of *T. velutinus* with respect to the other thylamyines is not available, its relatedness can be inferred to the *pallidior-pusillus* clade (Tate 1933, Petter 1968, Gardner 1993). If the relationship between the *Thylamys* of the Brazilian Cerrado and the *pallidior-pusillus* clade is confirmed, it may be hypothesized that an ancestor to the latter clade dispersed from areas of the eastern Chaco Dominion (Solbrig 1976; e.g., Monte Desert, Chaco) to areas of the Cerrado. The shifts of savanna during the alternating dry and wet climatic phases of the Pleistocene might have triggered speciation in isolation, thus promoting the differentiation of *T. velutinus* in areas of the Brazilian Cerrado. Therefore, it seems possible that Brazilian *Thylamys* was primarily and inhabitant of the Cerrado, and that it reached more eastern areas in Brazil because of a continuity in vegetation (i.e., the transition of the Cerrado into the humid

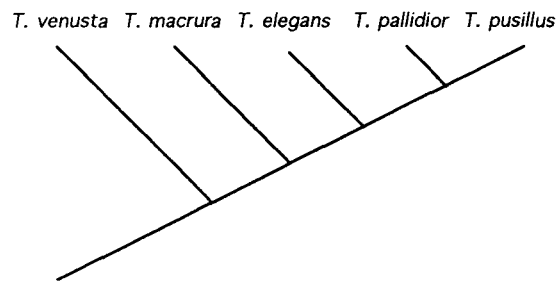


Fig. 2: Phylogenetic relationships of *Thylamys* based on allozymes and mitochondrial DNA data (Palma 1994).

Relaciones filogenéticas de *Thylamys* basadas en datos alozímicos y de DNA mitocondrial (Palma 1994).

forest areas of eastern Brazil is gradual), and the penetration of Cerrado-like vegetation in southeastern Brazil (Sarmiento 1983). On the other hand, the occurrence of *Thylamys* in the Caatinga may be explained by the floristic relatedness and geographic proximity of this biome and the Cerrado that have allowed them to share several vertebrate taxa (Mares et al. 1985).

The occurrence of thylamyines in the Cerrado and Caatinga provinces confirm *Thylamys* as a genus adapted to semi-arid biomes that developed traits adapted to a dry and cursorial way of life, such as a short and seasonally incrassated tail, and an enlarged bullae. The only known exception to *Thylamys* inhabiting semi-arid areas is the occurrence of a sylvan form in the subtropical moist forests of eastern Paraguay, *T. macrura*, which lacks and enlarged bullae, and may also not store fat in the tail during colder winter months.

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LITERATURE CITED

GARDNER AL (1993) Order Didelphimorphia. In: Wilson DE & DM Reeder (eds) Mammal species of the

world: a taxonomic and geographic reference: 15-23. Smithsonian Institution Press, Washington D.C.

- HERSHKOVITZ P (1992) The South American Gracile Mouse Opossums, genus *Gracilinanus* (Gardner & Creighton 1989): a taxonomic review with notes on general morphology and relationships. *Fieldiana, Zoology* 70: 1-56.
- JANIS CM (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics* 24: 467-500.
- KLUGE AJ (1989) A concern for evidence and phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* 38: 7-25.
- MARES MA, MR WILLIG, KE STREILEIN & TE LACHER (1981) The mammals of northeastern Brazil: a preliminary assessment. *Annals of the Carnegie Museum* 50: 81-137.
- MARES MA, MR WILLIG & TE LACHER (1985) The Brazilian Caatinga in South American zoogeography: tropical mammals in a dry region. *Journal of Biogeography* 12: 57-69.
- PALMA RE (1994) Historical relationships of South American mouse opossums (*Thylamys*, Didelphidae): evidence from molecular systematics and historical biogeography. PhD dissertation, University of New Mexico, Albuquerque, New Mexico, USA 112 pp.
- PETTER F (1968) Une sarigue nouvelle du nord-est du Bresil, *Marmosa karimii* sp. nov. (Marsupiaux, Didelphides). *Mammalia* 32: 313-316.
- PINE RH, IR BISHOP & RL JACKSON (1970) Preliminary list of mammals of the Xavantina/Cachimbo expedition (Central Brazil). *Transactions of the Royal Society of Tropical Medicine and Hygiene* 64: 668-670.
- PINE RH, SD MILLER & ML SCHAMBERGER (1979) Contributions to the mammalogy of Chile. *Mammalia* 43: 339-376.
- POTTS R & BEHRENSMEYER (1992) Late Cenozoic terrestrial ecosystems. In: Behrensmeier AK, JD Damuth, JD DiMichelle, R Potts, HD Sues & SL Wing (eds) *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*: 419-451. The University of Chicago Press, Chicago.
- REIG OA, JAW KIRSCH & LG MARSCHALL (1987) Systematic relationships of the living and Neocenoic American "opossum-like" marsupials (Suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In: Archer M (ed) *Possums and opossums: studies in evolution*: 1-89. Surrey Beatty and Sons and the Royal Society of New South Wales, New South Wales.
- ROMERO EJ (1986) Paleogene phytogeography and climatology of South America. *Annals of the Missouri Botanical Garden* 73: 449-461.
- SARMIENTO G (1975) The dry plant formations of South America and their floristic connections. *Journal of Biogeography* 2: 233-251.
- SARMIENTO G (1983) The savannas of tropical America. In: Bourliere F (ed) *Ecosystems of the world: tropical savannas*: 245-288. Elsevier Scientific Publications, volume 13, New York.
- STREILEIN KE (1982) Ecology of small mammals in the semiarid Brazilian Caatinga. I. Climate and faunal composition. *Annals of Carnegie Museum* 51: 79-107.

- SOLBRIG OT (1976) The origin and floristic affinities of the South American temperate desert and semidesert regions. In: Goodall DW (ed) Evolution of desert biota: 7-49. University of Texas Press, Texas.
- TATE GHH (1933) Systematic revision of the marsupial genus *Marmosa*, with a discussion of the adaptive radiation of the murine opossums (*Marmosa*). Bulletin of the American Museum of Natural History 66: 1-250.
- VAN DER HAMMEN T (1982) Paleocology of tropical South America. In: Prance GT (ed) Biological diversification in the tropics. Columbia University Press, New York.