CHAPTER 6

DIVERSITY AND DISTRIBUTION OF *THYLAMYS* (DIDELPHIDAE) IN SOUTH AMERICA, WITH EMPHASIS ON SPECIES FROM THE WESTERN SIDE OF THE ANDES

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Marsupials of the genus *Thylamys* Gray 1843 (Didelphimorphia: Didelphidae) include small mouse opossums with distinctive morphological traits, mainly distributed on dry open and semi-arid biomes of southern South America. Similar to other Neotropical mammals, its species diversity and distribution are poorly documented. *Thylamys*, with *Didelphis elegans* Waterhouse 1839 as type species, was early on used as a subgenus of *Marmosa*, with a broader definition and including species now in the genera *Marmosops* and *Gracilinanus.* By the 1980s, it became clear that *Marmosa* was not a natural group, and *Thylamys* was raised to full genus and associated to the *elegans* group of Tate (1933). However, the situation for most taxa included in the genus remains obscure because good series are not available.

Peruvian specimens show a wide variation; however, they may represent to two different taxa instead of a single species as it is currently recognised: *Thylamys elegans.* Through comparison and evaluation of discrete morphological traits and morphometric analyses of the variation within and among Peruvian and Chilean populations, I assign Peruvian specimens to *tatei* and *pallidior.* By comparing *tatei* and *pallidior* to *elegans*, I show this taxon to be more restricted than previously thought.

Because *elegans* is the only valid known species from the west of the Andes, it is supposed that *tatei* and *pallidior* should have closer affinities to it. Although *elegans* and *tatei* are alike externally, *pallidior* shares more cranial characters with *tatei.* In addition, the latter two species do not show sexual dimorphism, which is evident in *elegans.* I recommend the use of *tatei* as a valid species, restricted to the western slopes of central Peru. Morphological comparisons included other taxa from the whole geographic range of the genus to update the diversity and distribution of the genus on western South America.

Morphological characters used to distinguish species proved so effective that I have used the same set of characters to group the species. Used in combination with their distributions, I group the seven recognised species in three geographic units, as a first approach to natural groups. I propose a biogeographic scenario to explain the colonisation of the western side of the Andes by the genus, typically found at temperate areas to the east of the Andes. Two different types of dispersal are supposed to have occurred in this migration, favoured by the climatic fluctuations and final uplift of the Andes during the Plio-Pleistocene.

INTRODUCTION

Mouse opossums of the genus *Thylamys* Gray 1843 (Didelphimorphia: Didelphidae) comprise small mouse opossums with nasals of nearly the same width throughout, a distinctive tricolour fur pattern, capacity to store fat in the tail (incrassation), and many other morphological traits in body proportions, skull and dentition (Tate 1933, Creighton 1984, Gardner and Creighton 1989, Hershkovitz 1992b). For a long time it was considered a synonym or subgenus of *Marmosa* (sensu Tate 1933), with a less precise and polyphyletic definition (see Gilmore 1941, Cabrera 1958, Kirsch and Calaby 1977, Marshall 1982, Reig et al. 1985, 1987). Since the monophyly of Tate's *elegans* group was confirmed (Creighton 1984), the name has been used as a full genus (Gardner and Creighton 1989, Gardner 1993).

The oldest fossil record comes from the early Pliocene (Montehermosan) of Buenos Aires, Argentina (Marshall 1982). Other records are from the late Pleistocene of Lagoa Santa, Brazil (Reig et al. 1987), but many of these seem to correspond to *Gracilinanus agilis* (see Hershkovitz 1992b). Only Marshall (1982) and Reig et al. (1985, 1987) have specifically mentioned fossils of *Thylamys*, but their composite definition of the genus does not allow knowing its exact geological range. The report by Palma (1997) based on those references could correspond either to *Gracilinanus* or to *Thylamys*.

Species of *Thylamys* are restricted to South America (Tate 1933, Gardner 1993), with most species limited to the southern portion. They prefer open and temperate areas, such as Pampas, deserts, Andean valleys, Monte desert, Chaco, and even Puna (Creighton 1985). Although there are several names applied to populations along its geographic range (see Cabrera 1958), five (Gardner 1993) to six species (Palma 1994) are now recognised as valid.

HISTORICAL BACKGROUND

The concepts and relationships of *Thylamys* Gray 1843

Formerly, *Thylamys* Gray 1843 was proposed as different from the extant genera *Didelphis*, *Marmosa*, or *Micoureus*, only to include *Didelphis elegans* Waterhouse 1839, which became type species of *Thylamys* by monotypy. Some authors (e.g. Allen and Chapman 1897, Allen 1912, Matschie 1916, Cabrera 1919) applied a broad definition when they considered *Thylamys* should include species currently listed as either *Marmosops* or *Gracilinanus*.

In the first revision of the genus *Marmosa*, Tate (1933) proposed five species groups (*cinerea*, *microtarsus*, *murina*, *noctivaga*, and *elegans*) based on morphological traits, and establishing possible relationships among them. Although he considered *Thylamys* a junior synonym of *Marmosa*, the taxon was not clearly associated to any group. Later, Gilmore (1941)

suggested the relevance of some characters to join the *elegans* group and the *microtarsus* section of the *microtarsus* group of Tate (1933) under a subgenus *Thylamys*. These characters were the presence of pectoral mammae, well-developed palatal vacuities, and annular pattern of tail scales. Cabrera (1958) used the name *Thylamys*, following Gilmore (1941), to define a subgenus of *Marmosa*, without regard to other groups of Tate (1933). Despite the uncertainty of Tate's groups, they remained in use as natural taxa equivalent to subgenera. Handley (1956), Petter (1968), and Pine (1981) described and assigned new species of *Marmosa* to those groups.

Marshall (1982) used the names *Thylamys* and *Micoureus* as valid genera in a list of extant and extinct marsupials of South America. Composition of each genus based on the studies by Reig, Kirsch and Marshall, published in 1985 and 1987. Reig et al. (1985, 1987) listed *Marmosa* (with *Marmosops* as subgenus), *Micoure[u]s*, and *Thylamys* (sensu Cabrera 1958) as valid taxa. They used the Tate's groups (1933) to define each genus. *Thylamys* corresponded to an update and amplification of the polyphyletic taxon used by Gilmore (1941) and Kirsch and Calaby (1977).

Creighton (1984) raised *Thylamys* to generic status, but restricted the genus to the *elegans* group of Tate (1933), and included seven species. Gardner and Creighton (1989) rose to full genera to the *noctivaga* group and the *microtarsus* section of the *microtarsus* group (Tate 1933), using the names *Marmosops* and *Gracilinanus*, respectively.

Several hypotheses of phylogenetic relationships have been proposed for the genera of Didelphidae, most of them based on morphological characters and using cladistic methodologies. Creighton (1984) found a closer affinity between *Thylamys* (Tate's *elegans* group) and *Lestodelphys*. From Reig et al. (1985, 1987) it is practically impossible to find true affinities for *Thylamys* because of their composite definition, which includes taxa currently in genera *Thylamys* (*sensu stricto*) and *Gracilinanus*.

Kirsch and Palma (1995) used molecular techniques to group *Thylamys* and *Lestodelphys* in the tribe Thylamyini, which along with *Marmosops* and *Gracilinanus* (tribe Marmosopsini) make up the Thylamyinae. Recently, Jansa and Voss (2000) also recognised this group by comparing gene sequences of all the extant genera of Didelphidae.

Rather than discuss the confidence of proposed phylogenies, it is necessary to establish a framework for the relationships of *Thylamys* (*sensu stricto*) within the Didelphidae. Creighton (1984), Kirsch and Palma (1995), and Jansa and Voss (2000) pointed to *Lestodelphys* as the sister-group of *Thylamys*. For the purposes of this paper, I use *Lestodelphys* to evaluate the character that may help to better define the genus *Thylamys*.

Taxa associated to *Thylamys*

The genus *Thylamys*, like many other small mammals of the Neotropics (e.g. *Cryptotis, Monodelphis*), is known from few samples coming from very separate localities. Species descriptions were typically based on incomplete series, with specimens representing only one of the sexes or a single age class (Osgood 1943, Handley 1956, Cabrera 1958).

Although there are morphological characters that appear to define *Thylamys* (Creighton 1984, Gardner and Creighton 1989, Hershkovitz 1992b), there are no taxonomic revisions for many taxa (see Palma 1994, 1995). It is a critical aspect since many of them could belong to species complexes (Creighton 1985, Palma 1997). Often, criteria used to recognise species are not useful for all taxa, or they show high intraspecific variation which prevents valid diagnoses either at the species or subspecies level.

Gray (1843) proposed the generic name *Thylamys* to include *Didelphis elegans* Waterhouse 1839, which becomes the type species by monotypy. However, *elegans* had already been removed from *Didelphis* and assigned to *Micoureus* Lesson 1842 (see Matschie 1916). *Thylamys* was in use either as a subgenus or a junior synonym of *Marmosa* Gray 1821. One of the early names associated with *elegans* was *marmota*, mainly based on the general size and skull shape, in addition to share the 'unique character of not having the nasals expanded posteriorly' (Thomas 1894).

A second species assigned to *Thylamys* was *T. carri*, from Trinidad Island (Allen and Chapman 1897). It expanded the genus to include all the forms 'without postorbital processes, and nasals not expanded posteriorly, but of nearly the same width throughout'. Allen (1900) used this character to describe *T. keaysi*, and to include later (1912) *Marmosa caucae* Thomas 1900. All of these species are currently listed under *Marmosops* (see Gardner 1993).

Thomas's main contribution to *Thylamys* knowledge was the revision of the various forms of *elegans* (1902) where he defined two main 'geographic groups'. In later works he added new species and subspecies (1912, 1921a and b, 1926). The Andean or *elegans* group included *elegans elegans, e. venusta, e. pallidior, e. cinderella*, and *e. sponsoria*. His Paraguayan or *marmota* group included *marmota, citella, bruchi, verax*, and *janetta*.

Like Allen and Chapman (1897), Matschie (1916) regarded *Thylamys* a subgenus of *Marmosa* and included some species now listed in *Marmosops*. Only six out of nine species listed by him are referred to the present concept of *Thylamys*. Cabrera (1919) mentioned the smooth interorbital region and nasals shape as typical of subgenus *Thylamys*. His concept of *elegans* included four current species. Species *carri* and *keaysi* are now

Table 1 Recognised species of *Thylamys* (*sensu stricto*) listed by Tate (1933), and their correspondence to the current use (Gardner 1993; Palma 1995, 1997).

Use of Tate (1933)	Current use
Genus *Marmosa*	
elegans group	Genus *Thylamys*
a) Section *elegans*	
elegans elegans	*Thylamys elegans elegans*
elegans coquimbensis	*Thylamys elegans coquimbensis*
elegans soricina	*Thylamys elegans soricinus*
marmota marmota (= *grisea*)	*Thylamys macrurus*
marmota verax	*Thylamys pusillus*
janetta	*Thylamys venustus*
pusilla	*Thylamys pusillus*
b) Section *venusta*	
venusta venusta	*Thylamys venustus venustus*
venusta cinderella	*Thylamys venustus cinderella*
venusta sponsoria	*Thylamys venustus cinderella*
pallidior	*Thylamys pallidior*
bruchi	*Thylamys pallidior*
velutina (= *pimelura*)	*Thylamys velutinus*
formosa (= *muscula*)	*Gracilinanus agilis*

under *Marmosops*, and two species of his subgenus *Marmosa* (*pusilla* and *velutina*) actually belong to *Thylamys*.

Tate (1933) made the first revision of all the species then included in *Marmosa* (s.l.), and grouped them in five natural groups equivalent to subgenera. The *elegans* group included two sections and nine species; all the taxa (except *formosa* and *muscula*) belong to *Thylamys* (Table 1). Although his *elegans* group is the base for present genus *Thylamys*, Tate (1933) did not mention any equivalence between them.

Osgood (1943) treated *Marmosa elegans* with detail. His analysis suggested that differences between taxa, even *pallidior*, are only of subspecific level. The variation within the *elegans* group was explained by geographic gradients, where existing gaps would be artifacts of sampling. He considered *soricina* a valid subspecies of *elegans*. Other subspecies were *coquimbensis, soricina, venusta* (synonym: *janetta*), *cinderella* (synonym: *sponsoria*), and *pallidior*. He suspected that *pusilla* and *marmota* were variations of the same kind.

Cabrera (1958) followed Gilmore (1941) in recognising *Thylamys* as a valid subgenus of *Marmosa*, and included 'the *elegans* group and the *microtarsus* section of *microtarsus* group of Tate [1933]'. He included 12 species, but just four could be assigned now to *Thylamys* (*sensu stricto*). A main departure from Osgood (1943) is the distinction of *pallidior* from *elegans*. His concept of

pusilla included subspecies *bruchi*, *pallidior*, and *pusilla* (*marmota* Thomas 1894 as a synonym). For *grisea* he included *marmota* Thomas 1902 as a junior synonym, and for *velutina*, the subspecies *formosa* and *velutina*.

Hershkovitz (1959) proposed the undetermined growth of opossums as the main cause for small and large 'adults'. Therefore, all the taxa within the *elegans* group (Tate 1933) should be conspecifics. The first described name in that group, *Marmosa pusilla* Desmarest 1805, would be the only valid species.

Kirsch and Calaby (1977) followed the arrangement in subgenera proposed by Cabrera (1958), with additions and corrections from later works. Noteworthy changes were the ubication of *Marmosa emiliae* in subgenus *Marmosa*, the recognition of two new species (*karimii* and *tatei*), and the use of *M.* (*Thylamys*) *formosa* as different from *velutina*. The first edition of the World's mammal catalogue (Honacki et al. 1982) recognised three subgenera within *Marmosa* (*Marmosa*, *Thylamys*, and *Stegomarmosa* [Pine 1972]), but did not mention which species would belong to which group. The main reference was Kirsch and Calaby (1977).

Marshall (1982) recognised *Marmosa* as a composite of several genera. Based on unpublished studies of Reig et al. (see below), Marshall differentiated *Thylamys* from *Marmosa*, but did not explain the composition of *Thylamys*, except by the use of common name 'small mouse opossums' (p. 254).

Creighton (1984) presented a detailed phylogenetic evaluation of the intergeneric relationships within subfamily Didelphinae (s.l.), including a formal treatment for the groups of Tate (1933). Creighton proposed to differentiate the genus *Thylamys* from *Marmosa* (*sensu stricto*), and restricted the name to the *elegans* group with some changes based on revision of types and relevant specimens. After adding two recently described species, he listed *elegans*, *grisea*, *karimii*, *pallidior*, *pusilla*, *tatei*, and *velutina*.

Reig et al. (1985) presented the first phylogenetic hypothesis for the genera of Didelphidae, and showed that *Thylamys* (*sensu stricto*) was the closest to *Lestodelphys*. Included species were those proposed by Kirsch and Calaby (1977), with the addition of *lepida*, *emiliae*, and a fossil species. Reig et al. (1987) gave additional details on the employed methodology. This paper included a R.H. Pine's suggestion of recognising Tate's *elegans* group ('i.e. *elegans*, *formosus?*, *griseus*, *karimii*, *pusillus*, *tatei*, *velutinus*') as a natural group.

Gardner and Creighton (1989) recognised the soundness of Tate's (1933) supraspecific groups, as delimited by Creighton (1984). They validated the genera *Micoureus*, *Thylamys*, *Marmosops*, and created a new one for the *microtarsus* section: *Gracilinanus*. The list of species for *Thylamys* was more restricted than that of Creighton (1984), because of synonymy of *karimii* (to

velutinus) and *tatei* (to *elegans*). Gardner (1993) followed in full this proposal for the second edition of the catalogue of World's mammal species, listing five nominal species in *Thylamys*.

In the first revision of *Thylamys*, Palma (1994) distinguished the eastern (Bolivia and Argentina) populations of *elegans* (sensu lato) as *venustus*. His hypothesis of phylogenetic relationships shows a closer affinity of *elegans* (*sensu stricto*) to the clade *pallidior*–*pusillus*. Finally, he provided a biogeographic explanation for these patterns. Palma and Yates (1998) used a different set of characters, with allozyme and chromosomal data to re-evaluate the genus. Once again, *T. velutinus* was not included in the analyses. There were no clear conclusions about the affinities of *pallidior*, although *elegans* rather than *venustus* was suggested as its sister-group. However, there was support for a close relationship between *pusillus* and *macrurus*.

The genus *Thylamys* on the western side of the Andes

Here I present the case of Peruvian populations of *Thylamys* as an example of problems involved in the taxonomy and systematics of the genus. *Thylamys elegans* is recognised as the only species of this genus in Peru (Gardner 1993, Pacheco et al. 1995, Palma 1997). Palma (1997) mentioned this species also for Chile, and it could be the only valid species of *Thylamys* on the western side of the Andes.

Authorities disagree about the status of names in the synonymy of *elegans*. Recognition of these taxa relies on geographic range (see Tate 1933, Cabrera 1958) and differences in the colouration of fur (see Osgood 1943). Taxa *coquimbensis* and *soricina* were used as subspecies (Osgood 1943, Palma 1997), but *tatei* and *venusta* were listed as full species (Honacki et al. 1982, Palma 1994). Other authors (Handley 1956, Hershkovitz 1992b) have suggested that more than one species of *Thylamys* would be present on the west side of the Peruvian Andes. None of these authors mentioned any relationship between *elegans* and those species (i.e. *pallidior*, *tatei*).

Didelphis elegans Waterhouse 1839, was originally described from Valparaiso, on the central coast of Chile. Another species, *Didelphys soricina* Philippi 1894, came from Valdivia, southern Chile. The name *soricina* was not in use until Osgood (1943) removed it from the junior synonymy of *elegans* to subspecific status. Other valid names, already in existence but not used, or associated to *elegans*, were *Didelphis pusilla* and *Didelphys macrura*, both from Paraguay, and *Didelphys velutinus*, from Brazil. I will deliberately omit these three species from the following discussion, as they represent taxa geographically isolated from those on the western slope of the Andes (see Palma 1995). Although *pusilla* is sympatric with *venusta* and *pallidior* on northern Argentina and southern Bolivia, it relates only distantly to *venusta* (see Palma and Yates 1998), a lowland inhabitant of the eastern slope of southern Andes.

Thomas (1894) associated *griseus* (a junior synonym for *macrura*) to *elegans*, and eight years later (1902) described several subspecies of *elegans* (s.l.). All these new names had type localities on the Andean region of Bolivia (*pallidior* and *venusta*) and Argentina (*cinderella*). However, Thomas (1902) assigned one specimen from Lima, Peru, to *venusta*, without further details. Tate (1933) recorded the distribution of *venusta*, which considered a true species, with specimens from the highlands of Lima in the subspecies *venusta* (p. 225). Although Tate (1933) was uncertain about their precise identification, he stressed their presence as the northern end of the *elegans* group's distribution, presuming they would occupy a mountain stripe between central Peru and northern Chile (on the western slope of the Andes).

Osgood (1943) updated the distribution of the Chilean populations of *elegans*, including on this the subspecies *coquimbensis* and *soricinus*, along with *venusta*, *cinderella*, and *pallidior* on the eastern slope and the Puna of Bolivia and Argentina. He also mentioned specimens of *Marmosa* (*elegans* group) from southern Peru, which would represent a northern extension of *coquimbensis*. Zuñiga (1942) and Sanborn (1949) reported specimens of *Marmosa* sp. from the 'lomas' of Atocongo, Lima, extending the distribution of the *elegans* group to the central coast of Peru. However, they were never allocated to this group by any posterior work.

Description of *Marmosa tatei*, from Ancash, Peru, represented the northern extension of Tate's *elegans* group (Handley 1956), but there was no mention of the specimens from the Rimac valley. Cabrera (1958) relegated *venusta* as subspecies of *elegans*, including in this taxon the specimens from Lima, and suggesting that these opossums could be a new undescribed subspecies, or part of *M. elegans coquimbensis*. There were no references to *M. tatei*.

Pearson and Pearson (1978) reported *Marmosa elegans* from several habitats (lomas, desert scrub, mountain scrub, and queñual) along an altitudinal gradient (from 60 up to 3900 m) on southern Peru. Mann (1978) recognised *coquimbensis* as a subspecies of *elegans*, but synonymised *soricina* to *e. elegans*. Pine et al. (1979) disagreed with him, recognising specimens from Talca, south Chile, as *elegans soricina*, and others from Tarapacá and Atacama, northern Chile, as an undetermined subspecies of *elegans*. They also mentioned a series from Arequipa, in southern Peru, as very similar to *elegans coquimbensis*, but Hershkovitz (1992b) considered them as *Thylamys pallidior*.

Later, several authors considered *Marmosa tatei* as a valid species (Honacki et al. 1982, Streilein 1982, Creighton 1984) restricting it to the type locality, without any reference to the specimens from Lima (Tate 1933), Arequipa (Pine et al. 1979), or Tacna (Pearson and Pearson 1978). Gardner and Creighton (1989) did not mention *tatei* among recognised species of *Thylamys*, but later *tatei* was regarded as a junior synonym of *elegans* (Gardner 1993).

Recently, Palma (1994, 1995) raised *venusta* to the specific level, and reported specimens of *pallidior* from northern Chile (Tarapacá). In addition, he considered *tatei* as a junior synonym of *elegans*, and so all the Peruvian populations (Palma 1997).

Six specific names have been applied to the populations of *Thylamys* on the western slope: *elegans*, *soricina*, *venusta*, *coquimbensis*, *tatei*, and *pallidior*. Most recent authorities (Gardner 1993, Pacheco et al. 1995, Palma 1997) accepted *elegans* (s.l.) as the proper name for these populations. However, the name *pallidior* has been applied to populations from northern Chile (Palma 1995) and southern Peru (Hershkovitz 1992b), suggesting a migration of this species from the Puna of Chile and Bolivia. Previous studies of the genus have obscured its true diversity and, without clear morphological diagnoses, it is not possible to study their biogeographic patterns in South America.

Populations of *Thylamys* display a broad morphological variation along their distribution in Peru. These include samples from arid deserts, desert and mountain scrubs, between the sea level and 3200 m. The habitats are typical of those on the western slope of the Andes (see Cabrera and Willink 1980), and may be related to specific or subspecific variation. However, Pacheco et al. (1995) reported only one species of the genus *Thylamys*. My study aims primarily to assess the variation among the populations from Peru, and compare them with *T. elegans*, suggested by Pacheco et al. (1995) and Palma (1997) as present on western slopes of Peru and Chile. In addition, I will assess the diversity and distribution of the genus *Thylamys*, providing suitable morphological descriptions for species on the western slope of the Andes. I will provide a framework for future research about biogeography and systematics of the species, based on the information obtained from the review of type specimens and representative series.

MATERIALS AND METHODS

Specimens and institutions

Specimens I examined for this research are housed in collections of the following museums (identified throughout the chapter by their respective acronyms):

AMNH   American Museum of Natural History, New York, USA

BM(NH)   The Natural History Museum, London, UK

CBF   Colección Boliviana de Fauna, La Paz, Bolivia

FMNH   The Field Museum, Chicago, USA

MUSM   Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú

MVZ   Museum of Vertebrate Zoology, University of California, Berkeley, USA

NMNH   National Museum of Natural History, Smithsonian, Washington, DC, USA

Methods

Survey of morphological characters

In order to find useful characters to study the relationships within *Thylamys*, I used those considered in previous works on opossums (Gardner 1973, Pine 1981, Pine and Handley 1984, Creighton 1984, Reig et al. 1987, Hershkovitz 1992b), and others mentioned in original descriptions or revisions (Thomas 1902, Tate 1933).

The survey included specimens of both sexes, juveniles and adults, for most taxa within *Thylamys*, and one of *Lestodelphys*. Seventy-four (74) specimens were from Peru, 62 from Chile, and 70 from the Puna or the eastern slope of Bolivia, Argentina, Paraguay, and Brazil, representing twelve *Thylamys* taxa. I will describe each relevant taxon, identify those present on the western side of the Andes, and establish sound morphological characters to define them.

I included type specimens for five taxa previously considered as present on the western side of the Andes, and topotypes for other taxa. I reviewed the holotype and paratype of *tatei*, as well as a series of *soricinus* from Talca, south Chile, at the NMNH, and the type of *coquimbensis*, topotypes of *venusta* (sensu lato), and two specimens of *Lestodelphys* at the FMNH. V. Pacheco took notes of the holotypes of *elegans*, *pallidior*, *venusta*, and *janetta*, and topotypes of *macrurus* at the BM(NH).

Analysis of morphometric variation

I propose the use of 16 measurements for the morphometric study of specimens. They sample a variety of cranial and dental features (Fig. 1), which are informative of size differences between taxa, and allow the comparison with other works (Tate 1933, Pine 1981, Pine et al. 1985). All measurements were taken with digital calipers to the nearest 0.01 mm.

The measurements include: greatest skull length (GSL), condyloincisive length (CIL), palatal length (PL), greatest nasal length (GNL), zygomatic breadth (ZB), postzygomatic width (PZW), postorbital constriction (POC), breadth across bullae (BAB), width of single bulla (WSB), inclusive bulla-petrosal length (BPL), maxillary toothrow (MTR), width at M4-M4 (M4W), M2–M5 length (M2M5), mandibular ramus length (MRL), mandibular toothrow (LTR), m2–m5 length (m2m5).

To properly consider variation usually associated with differences at species level, I assess the variation within (sex and age) and between (geographic) populations of *Thylamys*. Sex and age variation are common sources of heterogeneity for mammals (Pine et al. 1985, Pacheco and Patterson 1992), and should not be considered for defining species.

Age was determined by using a sequence based on tooth replacement (Tribe 1990). The so-called deciduous premolars of Tribe (1990) are true molars (M1) displaced by the larger, late developing third premolar (PM3). However, as Archer (1978) and Hershkovitz (1992a) explained, all the functional adult marsupial teeth are first generation, so there are no replacement teeth. Thus, the fully erupted molar series correspond to the second to fifth molars (M2, M3, M4, and M5). Using this denomination, the sequence of Tribe (1990) is as follows:

Age class 1   M1 functional, M2 erupting.

Age class 2   M1 and M2 functional, M3 erupting

Age class 3   M1–M3 are functional, M4 erupting

Age class 4   M2–M4 functional, and
M1 retained, M5 erupting (typical pattern)
PM3 and M5 erupting (intermediate pattern)

Age class 5   M2–M5 functional, M1 retained or PM3 erupting

Age class 6   PM3 half to fully erupted, M5 shows little wear

Age class 7   PM3 functional, M5 considerably worn

I consider individuals of age classes 1 to 4 as juveniles, and those of class 6, as adults. Specimens in classes 5 and 7, correspond to young and old adults, respectively. Although there are no similar studies for *Thylamys*, age differences are more conspicuous between males than females of *Monodelphis* (Pine et al. 1985). The same study revealed an 'extreme sexual dimorphism' favouring males of *M. dimidiata*, and probably, by extension, to the Didelphidae (sensu lato). Palma (1997) showed sexual dimorphism in size for *T. elegans*, with males larger than females in 10 out of 12 measurements.

Because sample sizes for most of the localities were too small, analyses required combining them according to geographic proximity, to include specimens from most age classes and both sexes (see Hall 1943, Pacheco and Patterson 1992). Ten taxonomic units were identified from Peru and Chile (Table 2), representing 102 specimens from 36 western localities.

Once the nongeographic variation is evaluated, each sex or age class could be used as comparative units to study geographic variation (see Hall 1943, Pine et al. 1985). Nongeographic variation was assessed by two-way ANOVA tests. I estimated the components of variance (age, sex, interaction, and residual) for each variable. The ANOVA tests were employed only at the larger taxonomic units, before the analysis of geographic variation.

If a significative variation due to age is found, only adults (age class 6) should be included for the analyses of sexual dimorphism. An additional one-way ANOVA was used to assess the variation by sex only. According to the results of this analysis,
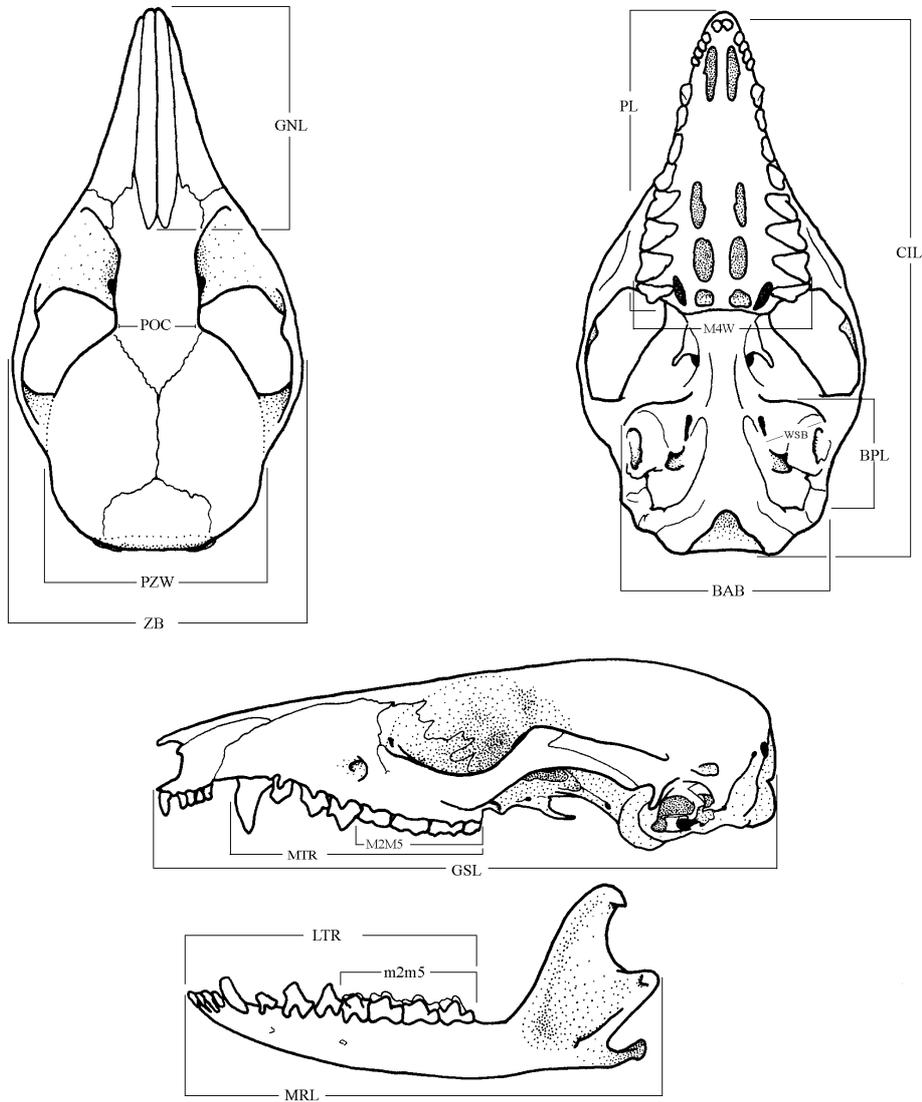
Figure 1 A variety of cranial and dental features used for for the morphometric study of specimens

sexes will be treated separately or pooled for geographic analyses. One-way ANOVA's assessed geographic variation within each taxon, and evaluated differences between taxa. All the statistical analyses were performed on SPSS 7.5 (Statistical Package for the Social Sciences) for Windows.

MORPHOLOGICAL DESCRIPTION OF *THYLAMYS*

The genus *Thylamys* corresponds to the *elegans* group of Tate (1933), and generic definitions by Creighton (1984), Gardner and Creighton (1989), and Hershkovitz (1992b). It is more restricted than the subgenus of Cabrera (1958) or the genus of Reig et al. (1985, 1987). *Thylamys* comprises small to moderate

body-sized species, total length less than 310 mm, and ears larger than those in other Marmosinae of similar size.

Dorsal pelage is greyish-brown, darker on the dorsal midline and lighter to the flanks, with ventral pelage white to buffy or grey, making up a tricolour fur pattern (Tate 1933, Creighton 1984). On the back, fur is longer and silky with bases and more than 3/4 of its length dark grey-slate. This pattern also extends over the crown, passes the ears bases, and reaches the area in between the eyes in some species. A patch of the mid-dorsal fur covers the shoulders.

Ventral pelage is highly variable. It may be cream-buffy, whitish, or pure white, extending to all the venter (e.g. *T. macrurus*)

Table 2 Taxonomic units used for study of morphometric variation in *Thylamys* of Peru and Chile. N = number of individuals, f and m are adult females and males (respectively).

Taxonomic unit	N	f	m
Huaraz	10	06	04
Lachay	07	02	03
Central Lima	10	03	01
Central Highlands	05	02	02
Parinacochas	16	01	03
Southern Highlands	18	04	08
Southern Lomas	06	02	02
Valparaiso	20	05	10
Aconcagua	06	01	02
Tierras Blancas	04	02	02

or just to a medial band (*T. elegans*). This colouration might be almost grey for some species (e.g. *T. venustus*), because of the extensive grey-slate bases of the hairs. Hairs may be self coloured, pure white (*T. pallidior*), or grey-based with white-cream tips (*T. elegans*). Delimitation between ventral and dorsal-lateral fur may be sharp, but for some species results in a transitional strip of greyish hairs.

There are no detailed references about presence and number of vibrissae, on head or extremities (see Brown 1971, Brown and Yalden 1973) for *Thylamys* or other Marmosinae. A little variation among specimens was observed. Distribution of vibrissae for *Thylamys* taxa includes (by each body side): 2 superciliary, 5 to 8 genal, 3 submental, 2 interramal, 1 antebrachial, 1 anconeal, and 3 to 4 carpal.

The tail is short, just surpassing 50 to 55% of the total length in most species, except for *velutinus* where it is almost 45% (Petter 1968, Palma 1995, Vieira and Palma 1996). Fat storage (incrassation) is known only for this genus and *Lestodelphys* (Creighton 1984), and it is perhaps related to their survival on highly seasonal habitats (Morton 1980). Tail is covered by small scales, with an annular arrangement (>35/cm). Each scale has three hairs of similar length (2,5-3,5 scales) on its posterior border, giving to the tail a hairy appearance. It may be bicoloured, because of pigmented tips of dorsal hairs, or monocoloured, although it could be affected by incrassation. It is slightly prehensile, using just the tip to grasp thin objects.

A pouch is absent and mammae are arranged in the abdominal region. In addition, there are two pairs of pectoral teats, with a basic formula of 7-1-7 = 15, and occasionally 9-1-9 = 19 (Tate 1933, Creighton 1984, Hershkovitz 1992b) in *Thylamys*. On the contrary, *Lestodelphys* may have up to 15 mammae (Hershkovitz 1992b).

Feet are comparatively small, as well as toes (Creighton 1984), both are densely covered by white or white-cream hairs, increasing the appearance of a small size. Ungual tufts are well developed, reaching the claw tips. However, specimens of *velutinus* in the NMNH lacked these hairs. Thenar and hypothenar pads are not fused with interdigitals (Creighton 1984).

Thylamys is characterised by the shape of the nasals, which are just slightly expanded at the maxilla-frontal suture (Tate 1933, Creighton 1984, Hershkovitz 1992b). Although the nasals may be considered not expanded for some species (i.e. *elegans*), they are variable among species. The nasals may or not narrow after that suture, producing four different patterns by the combination of both characteristics (see below).

Supraorbital processes are not well developed on most species (Tate 1933), although *macrurus* and *janetta*, and old individuals of *pusillus, pallidior* and *venustus* (s.l.) might show some degree of beading. Width of the postorbital constriction is variable. Supraorbital processes continue parallel or diverging over brain-case, but converge in a sagittal crest in *macrurus*.

The palate is highly fenestrated because of presence of palatine or posteromedial vacuities (Hershkovitz 1992b), enlargement of posterolateral ones, and the occasional development of mesolateral ones in some species (Creighton 1984, Tate 1933). A fenestrated palate is said to characterise *Thylamys* (Gilmore 1941, Cabrera 1958, Reig et al. 1985), however the condition is shared with *Gracilinanus*. Although specimens of *pallidior* presented enlarged vacuities, there are no bases to diagnose any species of *Thylamys* based on the development of some particular fenestra. Premaxillae are rounded (Redford and Eisenberg 1992).

Auditory or tympanic bulla is large and well developed, round shaped, with a slender anteromedial extension of its wall to the alisphenoid floor (Tate 1933, Creighton 1984, Hershkovitz 1992b). Distance between bullae is less than 1.5 times the width of a single bulla, which was considered diagnostic by some authors (Creighton 1984). Presence of a slender anteromedial process bulla-alisphenoid (Tate 1933, Creighton 1984, Hershkovitz 1992b) is another characteristic of *Thylamys*, which is shared with *Lestodelphys*. The slender and narrowed shape of basicranial bridge was suggested by Tate (1933) as typical of his *elegans* group. However, it has a variable shape among *Thylamys* species, therefore lacking taxonomic significance.

Dentition is similar to other Marmosinae, but third upper premolar (PM3) is equal or larger than second one (PM2), in height and length (Tate 1933, Creighton 1984, Hershkovitz 1992b). Molars in general and first upper three in particular, show great compression in length and increase of width. Paracone of second molar (M2) slightly displaced towards the lingual border (Tate 1933). Lower canines are pointed with a well-developed cusp.
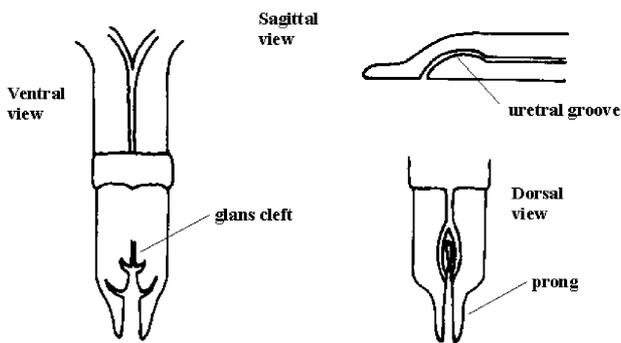
Figure 2 The most distinctive characteristic in the penis of *Thylamys pallidior* is its short glans cleft, determining shorter halves

For Peruvian and Chilean specimens of *Thylamys* I found a range of 20 to 21 caudal vertebrae. Hershkovitz (1992b) reported 21 vertebrae for a single specimen of *elegans*. In other marmosine genera, number of caudal vertebrae ranged between 22 and 27, apparently related to arboreal habits.

Szalay (1982) and Hershkovitz (1992a) discussed the significance of articular pattern of ankle joint bones for the phylogeny of marsupials. Hershkovitz (1992a) recognised these two patterns and showed both to occur among Didelphimorphia; even they could define natural groups. The separate pattern was reported for astragalus and calcaneus of *Thylamys elegans* and *T. pallidior*. Available specimens confirm this pattern, at least for the astragalus, in *T. pallidior* from Peru, and *T. venustus* from Bolivia.

Although studies of glans penis morphology are just preliminary, they have shown significant variation of taxonomic use to generic level (Reig et al. 1987, Hershkovitz 1992b, Martinelli and Nogueira 1997). In mature individuals, the penis is bifid, with urethral groove extending over internal side of each half allowing its urinary and ejaculatory functions (Hershkovitz 1992b). The most distinctive characteristic in the penis of *Thylamys pallidior* is its short glans cleft, determining shorter halves (Fig. 2). But, short length of glans (6–7 mm), subterminal ending of the urethra, and halves with pointed tips are similar to those of *Gracilinanus* and *Marmosops* (see Martinelli and Nogueira 1997). There is a skin fold on the inner side of each half that could be homologous to that of *Marmosops incanus*, but without more evidence than drawings of Martinelli and Nogueira (1997), I considered this feature particular to *Thylamys*.

The chromosome diploid number for *Thylamys* is 2N=14, which is common with other murine opossums (Palma and Yates 1996, 1998). Sex chromosome variation, as well as mosaicism, has been reported (Palma and Yates 1998).

Variation of morphological characters
Although most of the previously described traits are characteristics for *Thylamys*, some of them showed a variation that could

be used with taxonomic purposes. For each character, I describe related anatomical structures, its condition in the studied taxa and *Lestodelphys*, and discuss its use in previous references.

Externals
(01) Colouration of dorsal fur (medial and lateral bands)
The dorsal pattern of colouration on the back, with two dorsal bands, has been considered diagnostic for *Thylamys* (Tate 1933, Hershkovitz 1992b). The mid-dorsal band is very conspicuous, due its darker colouration and width, in *elegans, coquimbensis, soricinus, venustus, sponsoria, cinderella, janetta, pallidior, tatei, macrurus,* and *pusillus*. In *velutinus,* the contrast relative to the lateral bands (of back) is not too clear. The mid-dorsal bands of *sponsoria, soricinus,* and *tatei,* are darker, and with longer hairs. In *Lestodelphys,* the mid-dorsal band is also dark and conspicuous.

(02) Eye-rings
Blackish eye-rings are well developed and projected toward the nose in most species of *Thylamys,* except *velutinus, pusillus,* and *macrurus*. In those species, eye-rings are limited to the area around the eyes. Well-developed and projected eye-rings are present in *Lestodelphys*.

(03) Colour of ventral fur
Ventral fur exhibits a large variation in three of its traits: hair colouration, length and width extension of the mid band. Thomas (1902) used this variation to describe a number of *elegans* subspecies. Ventral hairs are lighter than those on dorsal and lateral bands, ranging from pure white to cream-buffy. Most of these hairs are self-coloured, from the base to the tips. However, in *pallidior* and *coquimbensis,* the hairs are pure snow-white. They are cream-white to whitish in *elegans, tatei, janetta, pusillus, macrurus,* and *velutinus,* but cream-buffy in *soricinus, venustus, cinderella,* and *sponsoria*. Hairs are snow-white in *Lestodelphys*.

(04) Length extension of lighter ventral band
The ventral hairs form a lighter band on the underparts of *Thylamys,* which has a variable extension (Thomas 1902, Osgood 1943). It might extend from the chin to the chest, as occurs in *soricinus, venustus, cinderella,* and *sponsoria,* or to the anus, through the belly, as in *elegans, coquimbensis, janetta, pallidior, tatei, pusillus, macrurus,* and *velutinus*. A band of pure white hairs extends from the chin to the anus in *Lestodelphys*.

(05) Width of the intermediate greyish bands
The presence and width of intermediate greyish bands, determined the width of the lighter ventral band (Tate 1933, Osgood 1943). Intermediate bands include hairs of grey-slate to blackish bases, with grey to cream-buffy tips. In *coquimbensis, pallidior, janetta, pusillus, macrurus,* and *velutinus,* these are very narrow (less than 5 mm each side), so the lighter ventral band extends
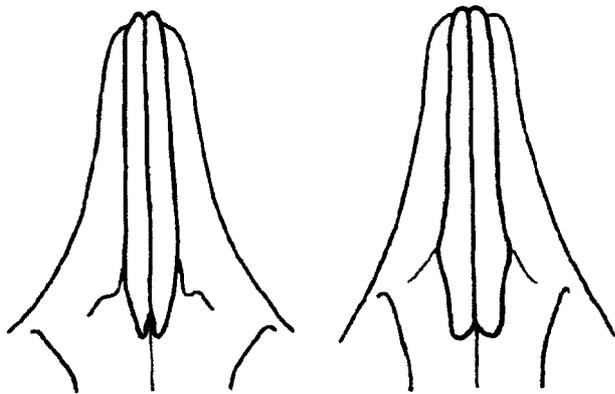
Figure 3 Nasals shape in Thylamys. Left: the nasal width at the maxilla-frontal suture, which may be almost parallel sided, as occurs in *elegans*, *coquimbensis*, *soricinus*, *venustus*, *cinderella*, and *sponsoria*. Right: a more conspicuous expansio, as for *pallidior*, *tatei*, *janetta*, *macrurus*, *pusillus*, and *velutinus*.

to the borders of venter. For other taxa, like *elegans*, *soricinus*, *venustus*, *cinderella*, *sponsoria*, and *tatei*, intermediate bands are wider (7–10 mm), resulting in a narrow ventral band. Ventrally, *Lestodelphys* shows narrow greyish bands.

(06) Relative size of the tail

Among *Thylamys* taxa, there is a little variation in the relative size of the tail, although only *velutinus* has a tail shorter than head and body length. All other taxa have tails longer than the head and body length. A short (and robust) tail is also present in *Lestodelphys*.

(07) Colour of distal end of the tail

Tail colouration in *Thylamys* is typically greyish to brownish on the dorsum, and lighter (white to whitish) on the ventral side, with variations of tone because of colour of tail scale hairs on each side. Nevertheless, *macrurus* and *tatei* present a deviation of this pattern. In *macrurus*, the distal third of the tail is particoloured; for *tatei*, the tip is whitish. Incrassation may affect the typical tail colouration. A whitish tail tip is also present in *Lestodelphys*.

Skull and dentition

(08) Shape of nasals at the maxilla-frontal suture

Nasals shape in *Thylamys* has been used as diagnostic, because of its scarce variation among taxa (Thomas 1894, Allen and Chapman 1897, Hershkovitz 1992b). However, there are two characters related to this shape. One is the nasal width at the maxilla-frontal suture, which may be almost parallel-sided, as occurs in *elegans*, *coquimbensis*, *soricinus*, *venustus*, *cinderella*, and *sponsoria*. However, for *pallidior*, *tatei*, *janetta*, *macrurus*, *pusillus*, and *velutinus*, the expansion is more conspicuous (Fig. 3). Nasals are conspicuously expanded in *Lestodelphys*.

(09) Shape of nasals behind the maxilla-frontal suture

A second character is the narrowing of the nasals just behind this suture, which is more evident by comparing to the nasal width at the suture. A light but conspicuous narrowing of nasals is present in *elegans*, *coquimbensis*, *pallidior*, *tatei*, and *velutinus*. Nasals of almost the same width are presents in *soricinus*, *venustus*, *cinderella*, *sponsoria*, *janetta*, *macrurus*, and *pusillus* (Fig. 4). In *Lestodelphys*, the nasals narrow behind the maxilla-frontal suture.

(10) Frontal-parietal processes

Creighton (1984) suggested a reduced development of the lateral edges of frontals in *Thylamys*, producing rounded superior borders. However, specimens of *janetta*, *macrurus*, and *velutinus* present conspicuous, squared to sharpened edges, which could occur also in other species (see Tate 1933). Old adults (age class VII) presented slightly beaded borders too, as evident in *pusillus*, *venustus*, *cinderella*, *sponsoria*, *pallidior*, and *tatei*. Processes are lacking even among old adults of *elegans*, *coquimbensis*, and *soricinus*. These processes show a light development in *Lestodelphys*.

(11) Development of stylar cusps on the upper molars

Development of a stylar cusp on the second and third upper molars may be used to group some taxa, as they are present only in *macrurus* and *pusillus*. No other *Thylamys* present these cusps. Development of this stylar cusp modifies the shape of the ectoflexus (the labial margin of molars), so it appears serrated in *macrurus* and *pusillus*. The stylar cusp of the anterior upper molars is also developed in *Lestodelphys*.

RECOGNISED SPECIES AND DISTRIBUTION OF *THYLAMYS*

The observed variation in discrete characters allows recognising seven species within *Thylamys*, as well as several of the subspecies mentioned by Tate (1933), Cabrera (1958) and Gardner (1993).
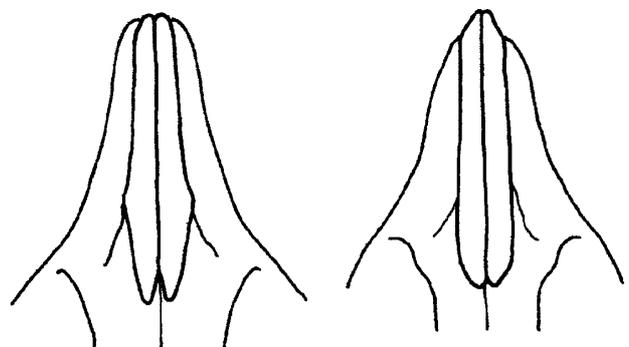

Figure 4 Left: a light but conspicuous narrowing of nasals is present in *elegans*, *coquimbensis*, *pallidior*, *tatei*, and *velutinus*. Right: nasals of almost the same width are present in *soricinus*, *venustus*, *cinderella*, *sponsoria*, *janetta*, *macrurus*, and *pusillus*.

Table 3 Diagnostic traits of five species of *Thylamys*, from the sampled variation in eight morphological characters (see the text for details)

	pusillus	*venustus*	*elegans*	*pallidior*	*tatei*
Blackish eye-rings	Not well developed	Developed and extended	Developed and extended	Developed and extended	Developed and extended
Ventral colouration	White cream to whitish	Cream-buffy	White cream to whitish	Snow white	White cream to whitish
Ventral lighter band	From the chin to the anus	From the chin to the breast	From the chin to the anus	From the chin to the anus	From the chin to the anus
Width of greyish ventral bands	Less than 4 mm at each side	More than 5 mm at each side	More than 5 mm at each side	Less than 4 mm at each side	More than 5 mm at each side
Shape of nasals at the suture	Slightly expanded	Parallel sided	Parallel sided	Slightly expanded	Slightly expanded
Nasals width behind suture	Almost not narrowed	Almost not narrowed	Conspicuously narrowed	Conspicuously narrowed	Conspicuously narrowed
Supraorbital processes	Slightly beaded to squared	Slightly beaded to squared	Rounded borders	Age related development	Age related development
Stylar cusp C	Developed	Absent	Absent	Absent	Absent

This composition matches closely with the *elegans* group (Tate 1933), with the inclusion of *bruchi*, *verax*, and *marmota* as synonyms of *pallidior*, *pusillus*, and *macrurus*, respectively (see Gardner 1993), and the exclusion of *formosa* (see Gardner and Creighton 1989). The species *venusta* was included as subspecies or synonym of *elegans* by Cabrera (1958) and Gardner (1993). However, it was recognised as a valid species by Palma (1994).

Additional to the six species recognised by Palma (1994), *Marmosa tatei* Handley 1956 shows a particular combination of characters (Table 3) that along its geographical isolation in Peru allow to specifically distinguishing it from *elegans*. Although listed as full species by Honacki et al. (1982), *tatei* was included in *elegans* by Gardner (1993) and Palma (1997). These authors used *elegans* as the only valid name for populations on the western side of the Andes, so including to *coquimbensis*, *soricinus* and *tatei* as subspecies (or synonyms).

According this variation, populations from Peru should be referred to *Thylamys tatei* and *T. pallidior*, and those of Chile to *T. elegans* and *T. pallidior*. As detailed in Table 3, none of the species present in Peru may be confused with *elegans*. Two subspecies of *elegans* are recognised: *coquimbensis* and *soricinus*, both are identifiable based on a particular set of characters that differentiate them from *elegans elegans*. These subspecies are externally similar to *pallidior* and *venustus*, respectively. However, both present the typical parallel-sided nasals of *elegans*, with some degree of variation, and rounded supraorbital borders.

Recognition of *pallidior* in southern and central Peru implies for this species the longest latitudinal distribution among *Thylamys* taxa. It goes from the Patagonia (Birney et al. 1996) of Argentina, to the central western slope of Peru, maybe following the

Andean range. Use of *venustus* as a full species by Palma (1994, 1995) did restrict *elegans* to central Chile, on the western slope of the southern Andes. Meanwhile, *tatei* is found at a small area between Lima and Ancash departments on the western slope of north Peru (Fig. 5).

Sympatry between species of *Thylamys* is not extensive or documented. From this revision, it appears that most of them are specialised on certain habitats, but they may extend also to contiguous regions (see Cabrera and Willink 1980). On the western side of the Andes, *pallidior* would be sympatric with *elegans coquimbensis* in northern Chile, and parapatric with marginal populations of *tatei* in northern Peru (Fig. 5). Subspecies of *elegans* occur parapatrically along a latitudinal gradient on central and northern Chile, with *soricinus* on the southern and *coquimbensis* on the northern end (see Mann 1978, Palma 1997).

Other species in the genus are commonly found at the southern part of South America (see below), onto the eastern slope of the Andes. They prefer dry and open habitats, like the Chaco and Pampas (Tate 1933), but also in mountain and desert scrub, or even the yungas. Two species are inhabitants of tropical areas (see Palma 1995, Vieira and Palma 1996): *macrurus* is the only species adapted to the subtropical moist forests of Paraguay, and *velutinus* occurs in the semi-arid habitats of the Cerrado and Caatinga of Brazil (Fig. 5).

Although the status of the name *Thylamys* is stable, as a masculine or neuter noun (Monjeau et al. 1994), the situation is confused among its species. Creighton (1984) listed the names *grisea*, *pusilla*, and *velutina*, which did not agree with the gender of the genus. Gardner (1993) changed the last one to *velutinus*. Following the Code of Zoological Nomenclature (ICZN 1999)
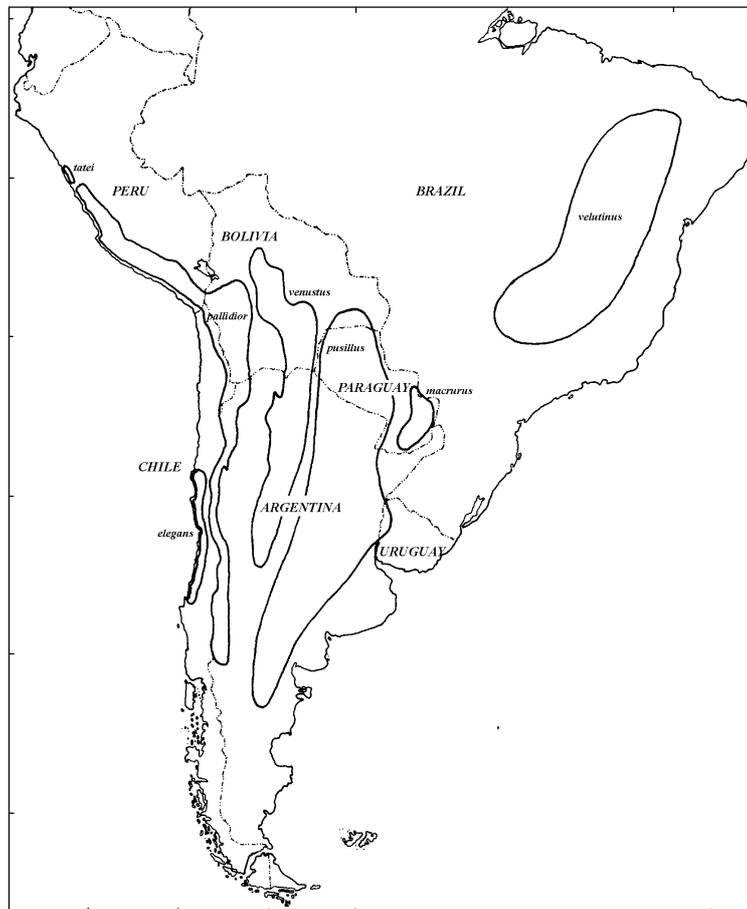
Figure 5 Distribution among Thylamys taxa

in regard to species-group names, if they are adjectives they should agree in gender with the genus (Art. 31.2). This is the case of names (already changed): *velutinus, pusillus, macrurus, venustus, cinderellus, sponsorius,* and *soricinus.* The rule does not apply for *janetta,* which has not been used as an adjective. It is considered as a name in apposition, and does not need to be changed (Art. 31.2.2). Other specific names, such as *elegans, pallidior, coquimbensis,* and *tatei,* are neuter or formed from personal names (Art. 31.1), and remain unchanged.

Species groups in *Thylamys*

In order to obtain a useful framework to further studies of *Thylamys* species, I group them using their morphological characters (Tables 3 and 4) and geographic distribution (Fig. 5) in three units. These are proposed as equivalent to natural (i.e. monophyletic) groups. Two of them are distributed to the eastern side of the Andes, and the last one (the Andean group) includes all the taxa occurring to the western side of the Andes, although one species (*venustus*) is found only to the east.

Because of my emphasis on species of the Andean region, full details are not given for all the species, but information on names in synonymy is included.

The Brazilian group
Thylamys velutinus
Didelphys velutina Wagner 1842

Archiv für Naturgeschichte, 8: 360

Didelphis pimelura Reinhardt 1849 (Lagoa Santa: Brazil)

Marmosa karimii Petter 1968 (Pernambuco: Brazil)

Type locality: Ipanema, Sao Paulo, Brazil

Description: Medial dorsal band inconspicuous, fur long (>7 mm), greyish, mouse-like; eye-rings not well developed; underparts cream-white, very short hairs; narrow (3 mm) intermediate greyish band. Tail shorter than head and body length (almost 0.75 HB), it is the only species in the genus with this

Table 4 Diagnostic traits of *Lestodelphys* and four species of *Thylamys,* from the sampled variation in nine morphological characters (see the text for details)

	Lestodelphys	*velutinus*	*macrurus*	*pusillus*	*venustus*
Blackish eye-rings	Developed and extended	Not well developed	Not well developed	Not well developed	Developed and extended
Ventral colouration	Snow white	White cream to whitish	White cream to whitish	White cream to whitish	Cream-buffy
Ventral lighter band	From the chin to the anus	From the chin to the anus	From the chin to the anus	From the chin to the anus	From the chin to the breast
Width of greyish ventral bands	Less than 4 mm at each side	Less than 4 mm at each side	Less than 4 mm at each side	Less than 4 mm at each side	More than 5 mm at each side
Relative length of tail	Shorter than head and body	Shorter than head and body	Longer than head and body	Longer than head and body	Longer than head and body
Shape of nasals at the suture	Conspicuously expanded	Slightly expanded	Slightly expanded	Slightly expanded	Parallel sided
Nasals width behind suture	Conspicuously narrowed	Conspicuously narrowed	Almost not narrowed	Almost not narrowed	Almost not narrowed
Supraorbital processes	Slightly beaded to squared	Squared to sharpened	Squared to sharpened	Slightly beaded to squared	Slightly beaded to squared
Stylar cusp C	Developed	Absent	Developed	Developed	Absent

characteristic. Petter (1968) reported incrassation for *M. karimii* in captivity. Tail slightly bicolour. Small feet (12 mm); toes without ungual tuft. Wide nasals little expanded at the maxilla-frontal suture. Then, nasals narrowing to the same width than anterior to the suture. Supraorbital processes well developed in adults, as conspicuous beaded borders, but not projected as lateral edges. Zygomatic arches well expanded. Cusp C not developed, ectoflexus is notch-shaped.

Distribution: Central and Southeast Brazil (Gardner 1993, Palma 1995), including eastern semi-arid habitats of Cerrado and Caatinga (Vieira and Palma 1996).

Specimens reviewed: NMNH 393536-8, from Matto Grosso, Brazil, identified as *Marmosa karimii* by Pine et al. (1970).

Remarks: This is the most distinctive species within *Thylamys*. Preliminary analysis points to an early or basal origin (see below).

The Paraguayan group
The included species are geographically delimited to the west and east of the Paraguay River (Mayr 1982, Creighton 1985, Palma 1995). They occupy the Chaco, and other dry biomes of the western side of the river, as well as the subtropical moist forests to the east (Cabrera and Willink 1980, Palma 1995). Fur colour pattern of underparts is distinctive: short, self-coloured cream-white or whitish hairs, clearly delimited from lateral bands. Other characteristics are: strong and stout skull, presence of stylar cusp C on upper molars, and submetacentric X chromosomes (Palma and Yates 1998). Analyses by Kirsch and

Palma (1995) and, Palma and Yates (1998) considered *pusillus* and *macrurus* as closer taxa within *Thylamys*.

Thylamys pusillus
Didelphis pusilla Desmarest 1804

Tabl. Méth. Hist. Nat., in Nouv. Dict. Hist. Nat., 24: 19

Marmosa marmota Thomas 1896

Marmosa citella Thomas 1912 (Corrientes: Argentina)

Marmosa verax Thomas 1921 (Concepción: Paraguay)

Type locality: San Ignacio, Misiones, Paraguay

Description: Dorsal colouration with a well-defined mouse grey medial band, dark bases, short fur; eye-rings poorly defined. Venter cream-white, sharply delimited of dorsal fur. Tail longer than HB length; it is slightly bicolour, fuscous above. Feet covered by short white hairs. Nasals slightly expanded at the maxilla-frontal suture, then narrowing to converge at their posterior end. Well-developed supraorbital processes only in a few adults, probably related to age. Zygomatic arches greatly expanded, giving to the skull a distinctive profile on dorsal view. Medial stylar cusp (C) present on upper molars, very conspicuous on M2 and M3; the ectoflexus on these teeth is serrated.

Distribution: West Paraguay (Chaco), southeast Bolivia, and north to south of Argentina. It would occupy the Chaco of Paraguay, Argentina, and Bolivia (Myers 1982, Anderson 1997), the mountain and desert scrubs, the Patagonia of Argentina

(Birney et al. 1996), and the Pampa of Argentina and Uruguay (Redford and Eisemberg 1992, González and Saralegui 1996).

Specimens reviewed: FMNH 54369,63862, and NMNH 390027-33, from Paraguay, and CBF 012 from Bolivia.

Remarks: Because its small size, some authors (Tate 1933, Cabrera 1958, Petter 1968) suggested a closer affinities of it to *velutinus* and *pallidior*. There is no type specimen for the taxon *pusillus*, its description was based on le micouré nain of Felix D'Azara.

Thylamys macrurus
Didelphys macrura Olfers 1818

in W.L. Eschwege, Journal von Brasilien, Neue Bibliotek Reisen., 15: 205

Didelphis grisea Desmarest 1827

Marmosa marmota Thomas 1912

Type locality: Tapua, Presidente Hayes, Paraguay

Description: Dorsal colouration similar to *pusillus*; eye-rings marked but not extended to the nose; lateral band lighter than medial one, appears grizzled; underparts cream-whitish over all the venter. Tail longer than head and body length. Tail bicoloured and particoloured, white spots on distal third. Large feet with long toes; claws well developed. Slender nasals, just little expanded at the maxilla-frontal suture. After it, nasals narrowing almost to their original width. Supraorbital processes developed as conspicuous sharp borders, projecting to converge as a low sagittal crest. Zygomatic arches well expanded, more than *pusillus*, with stronger bones. Cusp C on first two upper molars, ectoflexus is serrated.

Distribution: Restricted to the east of Paraguay River, but it may be present also in South Brazil (see Gardner 1993). It is the only species adapted to subtropical moist forests (Palma 1995). A single record of the Bolivian Chaco (Anderson 1997) is dubious.

Specimens reviewed: FMNH 26760, and BMNH 3.4.7.21, 99.11.17.1.

Remarks: The largest and stoutest species of the genus. Its taxonomic history is confused because misuse of *Didelphys marmota* a *nomen nudum* made available twice by Thomas (1896, 1912) to refer to actual *pusillus* and *macrurus*. Tate (1933) and Cabrera (1958) used different meanings for this species. Names *macrurus* and *griseus* were both based on le micouré à queue longue of F. D'Azara, so there are no type specimens associated to these species names.

The Andean group
This is the group of greater species richness, and the most uniform in characteristics of its species. Many of them were used as

synonym or subspecies of *elegans* in previous works (Thomas 1902, Osgood 1943, Gardner 1993). Studies by Kirsch and Palma (1995), and Palma and Yates (1998) gave support for further relationships between these taxa. Palma (pers. comm.) suggests basal position for *venustus*. Here, diversification is proposed as occurred due to the vegetational fluctuations during the last uplift of the Andes, in the Plio-Pleistocene.

Because of the morphological resemblance between all taxa in this group, I will provide a detailed description just for *elegans* (*sensu stricto*), for each remaining species the descriptions give the most relevant differences with respect to this one. Variation among subspecies is described in the account of each species.

Thylamys elegans
Didelphis elegans Waterhouse 1839

Zool. H.M.S. 'Beagle', Mammalia, p. 95

Didelphis soricina Philippi 1894 (Valdivia: Chile)

Marmosa elegans coquimbensis Tate 1931 (Coquimbo: Chile)

Type locality: Valparaiso, Valparaiso, Chile.

Description: A medium-sized species; wide and conspicuous medial band, greyish or grey-brownish, long (>8 mm) and silky dorsal fur; well-developed eye-rings that extend toward the nose. Lateral bands lighter than dorsal, mouse grey. Underparts from chin to anus, with a narrow band in middle, whitish to cream-whitish, self-coloured hairs. Grey-based hairs with cream-white tips, forming a band wider than 7 mm on each side of belly. Tail only slightly longer than head and body; and seasonally incrassated up to 10 mm of diameter at base. It is bicoloured, grey on dorsum and whitish below. Foot and toes covered by short white hairs. Nasals almost parallel-sided, not expanded at the maxilla-frontal suture. They narrow after they pass the suture, converging on their posterior ends. Nasals look parallel on dorsal view of skull. Supraorbital processes not developed, rounded; without evidence of sagittal crest. Zygomatic arch not very expanded, skull profile elongated. No evidence of cusp C on upper molars, the ectoflexus has a typical notch shape.

Distribution: I consider *elegans* as restricted to the Pacific slope of Chilean Andes, between 32° and 388°S. According to Mann (1978) and Palma (1995), subspecies *soricinus* is found to the south, and *coquimbensis* to the north of this distribution.

Specimens reviewed: BMNH 53.8.29.18 (type of *elegans*), NMNH 269806 (topotype of *elegans*), 541583-6, 541592, FMNH 22330-8, 22666-9, 23302 (type of *coquimbensis*), 23855-6, 23858-60, 23866, 23871-5, 24064, 24395, 119485-7. Also NMNH 541587-91, representing *soricinus*.

Remarks: Specific name *elegans* was suggested to include a complex of Andean taxa, which had been referred as individual

species on recent studies. Based on analyses of morphological characters (Table 3) and morphometric variation, I validate *tatei* as different from *elegans*. Taxon *coquimbensis* is only associated with the type specimen, without additional specimens it could be a *nomen dubious*. This specimen is very similar in size and fur colouration to *pallidior*, although the skull is typical of *elegans*, with narrow and little expanded nasals. Subspecies *soricinus* is geographically isolated in southern Chile. Mann (1978) stated the longer fur and darker dorsal colouration were response to the weather of southern Chile. Ventral pelage is more similar to *venustus* (see below). However, the skull is also typical as described for *elegans*, with little expanded but wider nasals and without beaded supraorbital processes.

Thylamys venustus

Marmosa elegans venusta Thomas 1902

Ann. Mag. Nat. Hist., ser. 7, 10: 161

Marmosa elegans cinderella Thomas 1902 (Tucumán: Argentina)

Marmosa elegans sponsoria Thomas 1921 (Jujuy: Argentina)

Marmosa janetta Thomas 1926 (Tarija: Bolivia)

Type locality: Parotani, Cochabamba, Bolivia.

Description: A medium-sized species, similar to *elegans*. Medial band grey-brownish is conspicuously darker than grey-yellowish of lateral bands. Wide blackish eye-rings. Ventral pelage appears tawny-grey, with plumbeous bases and cream tips, except the cream-buffy chest and throat. Tail longer than HB length, incrassated; and distinctly bicoloured, dark fuscous above and whitish below. Foot and digits not densely covered by whitish hairs. Nasals almost parallel throughout, not expanded or narrowed, but they are wider than in *elegans*. The type and topotype specimens have rounded interorbital region, but some old adult specimens present marked edges, even as lateral processes. The cusp C is absent and the ectoflexus looks like a notch.

Distribution: Cochabamba, Bolivia, to Neuquen, Argentina (Gardner 1993, as *elegans*). It was known as the montane representative of *elegans* on eastern Andes, although includes both low and high habitats. In Bolivia, *venustus* is found at lower montane forests and other drier montane habitats, but in Argentina it also occupies moist habitats to the south.

Specimens reviewed: BMNH 2.1.1.120 (type of *venusta*), FMNH 21553 (topotype of *venusta*), 21554;CBF 002-3, and NMNH 290899-900, from Bolivia. FMNH 22352-4 and 41266 (as *sponsoria*), 35014-5 (as *cinderella*), 29168, 30199-203 (as *venustus*), and NMNH 259257-8, from Argentina. In addition, BMNH 26.1.1.167 (type), FMNH 29169, 29170 (topotype), 50972-3, and NMNH 390570, 391293-4, are representing *janetta* from Bolivia.

Remarks: Described as subspecies of *elegans* (Thomas 1902), then raised to species status by Tate (1933). Palma (1994, 1995) supported its status as a different species based in phylogenetic molecular analyses. It would be the basal species within the Andean group (Palma and Yates 1998). Names *cinderella* and *sponsoria* were described as subspecies of *elegans*, but they are a single taxon (Thomas 1921c, Cabrera 1958) and a subspecies of *venustus*. Subspecies *cinderella* would be the lowland and southern representative of *venustus* in Argentina.

The taxon *janetta* is here recognised as a valid subspecies from wet areas of Tarija and Santa Cruz, Bolivia. This is the stoutest subspecies of *venustus*, its ventral pelage is cream-white with plumbeous bases, and general appearance is grey-whitish more than tawny-grey.

Thylamys pallidior

Marmosa elegans pallidior Thomas, 1902

Ann. Mag. Nat. Hist., ser. 7, 10: 161

Type locality: Challapata, Oruro, Bolivia

Description: One of the smallest species in the genus, with long (>11 mm) and silky dorsal pelage, silvery with dark grey bases on medial band; eye-rings blackish. Lateral bands not well defined, greyish with white or cinnamon tips, especially at posterior flank. Face conspicuously paler than dorsal or lateral colouration. Venter pure white throughout, long hairs; intermediate band of grey-based hairs not conspicuous. Tail slightly longer than head and body length, clearly bicolour even when incrassated, dark above. Very small feet (<15 mm) and digits densely covered with short white hairs. Skull elongated, small and delicate. Nasals little expanded at maxilla-frontal suture, then narrow, increasing the contrast. Supraorbital processes not beaded, rounded borders, but variable with age. Molars without cusp C, ectoflexus like a notch.

Distribution: East Argentina, south and east Bolivia (Gardner 1993), and extended to north Chile (Palma 1995) and western slope of Peruvian Andes. The species displays the broadest range of the genus, going from southern Argentina to central Peru, living in deserts, desert and mountain scrubs, and even reaching the Puna. Its wide altitudinal distribution goes from 8000 to 12,000 feet (2400 to 3800 m) on the Andes of Bolivia (Puna) and Argentina, but also reaches the sea level at coastal Peru.

Specimens reviewed: BMNH 2.2.2.116 (type of *pallidior*), CBF 006, 3258-9, FMNH 54255, and NMNH 121157, 271431, from Bolivia. FMNH 41397-8 and NMNH 236331-2 from Argentina. NMNH 391773-7, 54180-2, 541593-600 from Chile. FMNH 24141, 51003-7, 53155, 107398, MUSM 066, 070, 094, 983, 1302, 1749-51, 4754, 5806-14, 5953, 7018, 8374-5, 10722, 10737, 13091-2, 13097, 13104, 16085-

7, and MVZ 116614-5, 119913-5, 137584-5, 136248-50, 137896, 145531, 173937-9, from Peru.

Remarks: Some specimens from central highland of Peru showed variation in the extension of white on venter, with wide grey-based bands bordering a pure white stripe. Tate (1933) also noted this variation when mentioned the specimens from Peru (under *venusta venusta*). Although they were darker dorsally, did not show significant morphometric differences with typical *pallidior* (see below). Other specimens, especially very old males, showed beading of supraorbital processes and incipient sagittal crest; otherwise, they agreed with *pallidior*.

Thylamys tatei

Marmosa tatei Handley, 1956

J. Wash. Acad. Sci., 46: 402

Type locality: Chasquitambo, Bolognesi, Ancash.

Description: A species very similar to *elegans*, but with shorter (8 mm) and darker fur, greyish to grey-slate on medial band; eye-rings blackish. Lateral bands are greyish with cinnamon tones, but not too conspicuous as those of *pallidior*. Venter cream-whitish on medial band, wider at breast and narrow over most of belly, bordered by broad bands of grey-based hairs with cream tips. Tail just slightly longer than HB length, tip whitish for almost 10–15% of tail length. Feet and digits covered by short white hairs. Skull elongated, larger than *pallidior* or *elegans*. Nasals expanded at maxilla–frontal suture and then narrow, some like *pallidior*. Supraorbital processes not beaded in the series of Pariacoto, Ancash, but the type has marked edges, almost convergent on braincase. Molars without stylar cusp C, as typical for the group.

Distribution: This endemic species is just known from Ancash department (Handley 1956), and Lachay, north Lima, in central Peru. Its elevational range goes from 300 m (lomas de Lachay, Lima) to 3000 m (Huaraz, Ancash), including dry habitats such as deserts, lomas, and mountain scrubs of the western slope of the central Andes.

Specimens reviewed: NMNH 302915 (type), 302916 (paratype), FMNH 81443, MUSM 10738, MVZ 135503-12, and others collected by O. Ramírez (University C. Heredia, Lima).

Remarks: Creighton (1984) and Reig et al. (1987) recognised this taxon as a full species, but Gardner (1993) and Palma (1997) listed it as a synonym or subspecies of *elegans*.

ANALYSES OF MORPHOMETRIC VARIATION

Non-geographic variation

The analyses of non-geographic variation were carried out for three units of Peru, one of *tatei* (Huaraz) and two of *pallidior* (Parinacochas and Sierra Sur), and one of Chilean *elegans* (Val-

paraiso). These units had the largest available series, including juveniles and adults of both sexes. The ANOVA showed the effect of age and sex on the morphometric variation of *pallidior* and *elegans*. Seven and 13 variables, respectively, showed significant variation with age, with average variation over 35% and 59%. Variables most influenced by age were those referred to length of the skull. Sex variation was very low for both species, between 10 and 13%.

Because of the reduced size of these samples, a new ANOVA tested the variation between sexes of adult (age class VI) individuals. The taxonomic units were lumped according to the taxa they represent, to analyse their variation due to age. This variation was significant only for one variable (WSB) in *tatei*, none in *pallidior*, but 11 in *elegans*. Males were larger than females in every case. Three of the non-significant variables for *elegans* were dental measurements (M4W, M2M5, m2m5).

Geographic variation

Due to sexual dimorphism in earlier analyses, adult males and females of *tatei* and *pallidior* were pooled, but sexes were treated separately for *elegans*, in the analysis of variation within taxa. For the between taxa analysis, each sex was compared separately.

Among taxonomic units representing *Thylamys tatei*, only one variable (POC) differed geographically (Table 5). This small general variation may be due to the proximity of these units, less than 120 km apart. For *T. pallidior*, with a larger geographic range (Fig. 5), the units were very homogeneous, with no variation for any variable (Table 5). Finally, males of *T. elegans* showed a larger variation than that found in females, with 13 and five variables (respectively) showing significant differences. This result is worthy because that variation would occur over less than 700 km (Fig. 5).

In order to test the correspondence between taxonomic differentiation and geographic variation, a new ANOVA was carried out. From the results shown in Table 5, it is evident that the variation is equally evident among both males and females of the three species. Only one variable (POC and ZB, respectively) did not show significant variation (Table 5). Post hoc tests (Tukey, Duncan, and Scheffe) grouped to *tatei* and *elegans* as a homogeneous subgroup with larger means than *pallidior*. It is evident that the three species are distinguishable on morphological (Table 3) and morphometric (Table 5) grounds.

BIOGEOGRAPHY

The seven recognised species of *Thylamys* are grouped in three geographic units, proposed as a first approach to natural groups. However, relationships between these units are not conclusive at present. Previous hypotheses (Creighton 1985; Palma 1995) were built on an incomplete knowledge of

Table 5 Results of the analysis of geographic variation within and between taxa, for adults (age class VI) only. Differences are significatives for P < 0.05. See the text for details.

| | *tatei* | *pallidior* | *elegans* | *elegans* | Inter-taxa | |
	mm-ff	mm-ff	*mm*	*ff*	mm	ff
BAB	0.889	0.894	**0.007**	0.168	**0.000**	**0.000**
BPL	0.790	0.487	**0.033**	0.226	**0.000**	**0.001**
CIL	0.885	0.440	**0.001**	0.070	**0.000**	**0.004**
GNL	0.424	0.554	**0.021**	0.283	**0.000**	**0.000**
GSL	0.720	0.404	**0.001**	0.136	**0.000**	**0.002**
LTR	0.636	0.272	**0.001**	**0.024**	**0.000**	**0.000**
m2m5	0.484	0.144	0.053	0.063	**0.000**	**0.000**
M2M5	0.671	0.164	0.129	0.059	**0.000**	**0.000**
M4W	0.382	0.275	**0.001**	**0.000**	**0.000**	**0.000**
MRL	0.820	0.414	**0.009**	**0.045**	**0.000**	**0.004**
PL	0.513	0.440	**0.005**	0.258	**0.000**	**0.001**
POC	**0.032**	0.089	**0.037**	0.266	0.111	**0.000**
PZW	0.238	0.747	0.081	**0.010**	**0.000**	**0.009**
WSB	0.827	0.162	**0.020**	0.272	**0.036**	**0.027**
ZB	0.520	0.663	**0.011**	**0.036**	**0.000**	0.084

taxonomy and even distributions. In spite of the several taxa proposed to be found on the western slope of the Andes, no one study covered this area.

Most of the biogeographic hypotheses considered *Thylamys* as a genus of subtropical distribution, with the Chaco being the main barrier to taxa ditribution. Thomas (1902) pointed to geographic groups (Andean and Paraguayan) distinguishable by development of supraorbital borders, and distributed at both sides of the Chaco. Creighton (1985) proposed a temperate origin for *pusillus*, with later dispersal to the Andean region and to the subtropical Chaco. In the scenario suggested by Palma (1995), *venustus* would be the most basal taxon, from which all the other taxa originated. New analyses by Palma and Yates (1998) found a closer affinity between *pusillus* and *macrurus*, but did not resolve the relationship between *pallidior*, *elegans*, and *venustus*.

The present separation of *Thylamys* in geographic groups and updated information about distribution of the taxa allow the proposal of a preliminary hypothesis of relationships between species, and a biogeographic scenario for their origin. The following hypothesis is based on morphological similarity as evidence of recent ancestry, but also on previous phylogenies of the genus *Thylamys* (see Palma 1995, Palma and Yates 1998).

Although species of the Paraguayan group share many traits, they differ from each other in geographic ranges. The subtropical Chaco and the temperate regions of southern South America are occupied by *pusillus*, while *macrurus* appears restricted to the

subtropical forests to the east of the Paraguay River. Because of its particular characteristics, *Thylamys velutinus* appears as an early divergent taxon, also inhabiting very different habitats (Cerrado and Caatinga forests) on the eastern side of the genus distribution. According to previous hypotheses of tropical lowland ancestry for present taxa of dry, open areas (see Palma 1995), *macrurus* could originate *velutinus* and *pusillus*, by dispersal to the north-east and west, respectively. Both of these events would have occurred during climatic fluctuations of Plio-Pleistocene (5 Mya), but not necessarily at the same time.

From the evaluation of morphological characters, there is a closer similarity between *macrurus* and *pusillus* (Table 4), which would be indicative of a more recent differentiation of these taxa, as compared to the possible isolation of *velutinus*. Palma and Yates (1998) explained this differentiation by changes in habitat, soil, and topography at each side of the river (see Myers 1982), instead of a vicariant effect of the river. Accordingly, *pusillus* should be a successful disperser of this group, but the opportunity to colonise the Andes was reserved for the ancestor of the Andean group, a taxon allied perhaps to *venustus* (see Palma and Yates 1998).

The successful colonisation of highlands could occur when the Andes got their present elevation, during the last two million years (Pleistocene, Simpson 1978). Populations of *venustus* (or an ancestor), residents of open biomes, could be brought passively by the final uplift of the proto-Andes to higher, more temperate habitats. Consequent adaptation and diversification of these populations in highland habitats favoured a later coloni-

sation of lowlands (see Marquet 1994). Ancestors of *elegans* and *pallidior* could be originated by this way. Both habitats, the desert scrub and the Puna, correspond to the semi-arid, temperate conditions of the proposed center of origin for this group (see Potts and Behrensmeyer 1992).

Dispersal of *elegans* and *pallidior* should be more recent (late Pleistocene). Going through the mesic valleys that penetrate the arid coastal desert, *elegans* reached the central part of Chile, being limited to the north by the Atacama desert (see Marquet 1994). On the other hand, *pallidior* succeed in its latitudinal dispersal through the Andean range, actually ranging from 10 to 40 south (Fig. 5). Some cranial characters suggest a closer relationship between *pallidior* and *tatei* (Table 3), and the origin of the latter would be result of a recent isolation of marginal populations of *pallidior*. Altitudinal migration of *pallidior*, from Andean valleys to the desert coast, could be related to the arid conditions of the Holocene. This would be the origin of its intervening populations in the south and central desert of Peru.

SUMMARY AND PROSPECTS

The diversity of small mouse opossums of the genus *Thylamys* has been revised in this chapter. The genus presents a very scattered distribution over its range, with boundaries of species and geographic ranges poorly known. Here I have defined, characterised, and identified two different taxa in Peru, where only one (*T. elegans*) was usually recognised. Based on a set of characters, seven species of *Thylamys* are morphologically and geographically defined.

I group these taxa based on shared morphological characteristics and distribution. Three groups are identified, and a preliminary proposal of biogeographic relationships is given. High variation in most of morphological characters commonly used to identify species prevented evaluation of the whole range of their distributions. Recent molecular analyses by E. Palma (pers. comm.) partially support this hypothesis of relationships, and provide a useful framework for discussion. Inclusion of *velutinus* in these analyses should confirm its relationships to the Paraguayan group, as proposed here. Further molecular analyses, at the population level, should give us a more precise approach to the long history of diversification, colonisation, and extinction of the Andean group, as represented by *elegans* (and its subspecies), *pallidior*, and *tatei*.

ACKNOWLEDGEMENTS

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