

# On Paraguayan *Thrichomys* (Hystricognathi: Echimyidae): the distinctiveness of *Thrichomys fosteri* Thomas, 1903

Guillermo D'Elía<sup>1\*</sup>, and Philip Myers<sup>2</sup>

**Introduction:** *Thrichomys* is a genus of cursorial rodents of the family Echimyidae that is distributed across open tropical ecoregions in central and eastern South America. The understanding of species boundaries within the genus has changed dramatically during the last decade with the widespread usage of chromosomal and molecular data, resulting in an unstable taxonomy. One of the issues recently raised, on the basis of a study of specimens from south central Brazil (Mato Grosso do Sul State), is the distinctiveness at the species level of *T. fosteri* (with type locality in Paraguay), usually considered a synonym of *T. pachyurus*. Here we provide the first morphologic, karyotypic and molecular data for a series of Paraguayan specimens of *Thrichomys* aimed to resolve this taxonomic conundrum.

**Methodology:** Thirty one specimens collected at five Paraguayan localities were morphologically assessed. Descriptive statistics for 20 cranial measurements were calculated for a subset of specimens considered juveniles and for a subset of specimens considered to be adults. Seven specimens of *Thrichomys* from three Paraguayan localities were karyotyped using standard chromosome techniques. The genetic (*p*-distance) and phylogenetic (Bayesian inference) analyses were based on the first 801 base pairs of the cytochrome *b* gene of 15 Paraguayan specimens collected at one locality and 71 Brazilian specimens of *Thrichomys* that belong to about eight forms of species level.

**Results:** Paraguayan specimens examined closely match Thomas's (1903) description of *Thrichomys fosteri* in size and qualitative characters. All specimens have  $2n = 34$ ,  $FN = 64$ . The Paraguayan sample used for the genetic analysis shows no variation. Observed genetic variation between the Paraguayan haplotype and haplotypes from other populations ranges from 0.5 % to 8.5 %. The phylogenetic analysis show that Paraguayan haplotype falls within the clade ( $PP = 1$ ) formed by haplotypes of specimens from Mato Grosso do Sul, Brazil and referred by Nascimento *et al.* (2013) to *Thrichomys fosteri*.

**Discussion and conclusions:** Our data indicate that in fact Paraguayan populations of *Thrichomys* belong, together with those of the neighbouring Brazilian state of Mato Grosso do Sul, to a distinct species of *Thrichomys* to which the name *T. fosteri* applies. We expect that these data will contribute to a much needed comprehensive revision of the genus.

**Key words:** Eumysopinae, Hystricognathi, Octodontoidea, Paraguay, taxonomy

## Resumen

*Thrichomys* es un género de roedores cursoriales de la familia Echimyidae distribuido en las ecorregiones tropicales abiertas del centro y este de América del Sur. La comprensión de los límites de especies al interior de éste género ha cambiado radicalmente en la última

<sup>1</sup> Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile. Campus Isla Teja s/n, Valdivia, Chile. E-mail: guille.delia@gmail.com.

<sup>2</sup> University of Michigan Museum of Zoology, Ann Arbor. 1109 Geddes Av. MI 48109, USA. E-mail: pmyers@umich.edu.

\* Corresponding author

década con el uso intenso de datos cromosómicos y moleculares, lo que ha resultado en una taxonomía actual inestable. Uno de los temas recientemente cuestionados, en base al estudio de especímenes del centro sur de Brasil (estado de Mato Grosso de Sul) es la distinción a nivel de especie de *T. fosteri* (localidad típica en Paraguay), la que ha sido generalmente considerada como un sinónimo de *T. pachyurus*. En este estudio proveemos los primeros datos morfológicos, cariotípicos y moleculares de una serie de especímenes paraguayos de *Thrichomys* con el objetivo de poner a prueba dicha propuesta taxonómica. Los datos indican que las poblaciones paraguayas de *Thrichomys*, junto con aquellas del vecino estado brasilero de Mato Grosso do Sul, pertenecen a una especie distinta de *Thrichomys* a la que le corresponde el nombre *T. fosteri*. Esperamos que estos datos contribuyan a una necesaria revisión integral del género.

**Palabras clave:** Eumysopinae, Hystricognathi, Octodontoidea, Paraguay, taxonomía

## Introduction

The family Echimyidae is the most diverse family of New World hystricognaths. Echimyids are not only diverse taxonomically, but also in their life histories and ecomorphology; most forms are arboreal, but others are scansorial, fossorial, or semiaquatic (Emmons *et al.* in press). The taxonomic history of the family is complex and the classification of these forms is still unstable (Emmons *et al.* in press). Unresolved issues range from the number and limits of subfamilies (e.g., the monophyly of Echimyinae and Eumysopinae), to relationships among genera (some authors have suggested that the echimyid radiation was explosive and provides a putative example of adaptive radiation; e. g., Lara *et al.* 1996; Leite and Patton 2002), to species boundaries. In this last regard, the genus *Thrichomys* Trouessart, 1880 is no exception.

*Thrichomys* occurs in open vegetation biomes of tropical South America, including the Caatinga, Cerrado, Chaco, and Pantanal ecoregions of Bolivia, Brazil, and Paraguay. This genus has a complex nomenclatorial and taxonomic history. For example, its type species was designated just one decade ago (dos Reis and Pessôa 2004). Furthermore, *Thrichomys* was incorrectly associated by Thomas (1912) with *Cercomys* F. Cuvier and relegated to that genus for most of the 20<sup>th</sup> century. Further, despite the publication of several recent taxonomically oriented studies, the number and identity of the species of *Thrichomys* remains unclear.

Until the last decade, the genus was envisioned to comprise a single species, *T. apereoides* (Lund, 1839), with *Echimyus inermis* Pictet, 1843, *Isothrix pachyura* Wagner, 1845, *Thrichomys Fosteri* Thomas, 1903, and *Thrichomys laurentius* Thomas, 1904, considered either as full synonyms or as subspecies of *apereoides* (e. g. Moojen 1952; Cabrera 1961). However, studies published in the 1990s showed that the genus demonstrates considerable geographic structure in its morphological, karyotypic and genetic variation. As a result, Leal-Mesquita *et al.* (1993) and Lara *et al.* (1996) suggested that *Thrichomys* was composed of more than one species. This trend of findings continued during this century (e. g., Bandouk and dos Reis 1995; Bonvicino *et al.* 2002; dos Reis *et al.* 2002; Pessôa *et al.* 2004; Braggio and Bonvicino 2004; Borodin *et al.* 2006; Neves and Pessôa 2011; Nascimento *et al.* 2013) as available names were applied to groups of populations that showed distinct morphologies and/or karyotypes. Most recently,

Pessôa *et al.* (in press) recognized four species of *Thrichomys*: *T. apereoides*, *T. inermis*, *T. pachyurus* (including *fosteri*), and *T. laurentius*, but suggested that the relationship between *T. pachyurus* and *fosteri* required further elucidation.

Recently, Nascimento *et al.* (2013), in an extensive phylogeographic study based on cytochrome *b* gene sequences, found that haplotypes recovered from *Thrichomys* specimens collected in state of Mato Grosso do Sul, in south-central Brazil, form a clade at the same level as 7 other lineages already recognized at the species level, for which at least three have no available name. In addition, they reported that topotypes of *T. pachyurus* showed a diploid complement of  $2n = 30$ ,  $FN = 56$  that is distinct from the  $2n = 34$ ,  $FN = 64$  of specimens from Mato Grosso de Sul; the authors also mentioned that specimens collected 35 km north of the type locality of *T. fosteri* in neighbouring Paraguay have  $2n = 34$ . As a result, Nascimento *et al.* (2013) recognized a fifth species of *Thrichomys* distributed in Mato Grosso do Sul, Brazil and Paraguay, removing the taxon *Thrichomys fosteri* (type locality Sapucay, Paraguay; Thomas, 1903) from the synonymy of *T. pachyurus* and applying this name to the form from Mato Grosso do Sul and Paraguay. However, while karyotypes were available, no Paraguayan specimen was sequenced. The main goal of this study is to assess the genetic differentiation of Paraguayan specimens of *Thrichomys* from specimens of Brazilian populations of the genus; in particular those collected in the state of Mato Grosso do Sul. We aim to determine if the name *fosteri* applies to populations from Paraguay and Mato Grosso do Sul, Brazil as suggested by Nascimento *et al.* (2013). In addition, we provide morphological data for a large series of Paraguayan specimens of *Thrichomys*, including the first available set of measurements, with the expectation that these data will contribute to a much needed synthetic revision of the genus.

## Material and Methods

Paraguayan specimens of *Thrichomys* analyzed in this study (Appendix 1; Fig. 1) are housed at the following collections: University of Michigan Museum of Zoology (UMMZ), Ann Arbor, USA and Colección de Mamíferos, Universidad Austral de Chile (UACH), Valdivia, Chile.

Thirty one specimens collected at five Paraguayan localities (Appendix 1) were measured. Sex, external measurements, and weight were taken from specimen labels. The following 17 cranial measurements were recorded with a digital calliper, following Myers *et al.* (1990):

CIL, condylobasal length: distance from anterior edge of upper incisors to posterior face of occipital condyles.

IFL, incisive foramen length: greatest length of the incisive foramen.

MTRL, maxillary toothrow length: greatest length of the upper tooth row taken at the alveolus.

AW, alveolar width: width of the palate measured across the labial margins of the alveoli of right and left M1s.

DL, diastema length: from the posterior margin of the upper incisors to the anterior margin (root) of M1.

BOL, basioccipital length: length of basioccipital along the ventral midline of the cranium.

ZB, zygomatic breadth: greatest distance between the outside margins of the zygomatic arches.

IOC, interorbital constriction: least distance across the interorbital region.

MB, mastoid breadth: breadth of the braincase measured across the mastoid processes.

BB, breadth of braincase: greatest breadth of the braincase at a point just superior to the zygomatic root of the squamosal.

OCW, occipital condyle width: width between the lateral borders of the occipital condyles.

OL, orbital length: the greatest longitudinal distance across the inside of the orbit.

NL, length of the nasals: measured at the midline.

RL, length of the rostrum: diagonal distance from the anterior margin of the orbit to the anterior tip of the nasals.

RW1, rostral width: breadth of the rostrum across the nasolacrimal capsules.

RW2, mid rostral width: breadth of the rostrum measured at the top of the arc formed by the roots of the incisors as they pass posteriorly. This arc is visible as a raised curve along the rostral walls.

CD, cranial depth: depth of skull, measured by placing the skull on a glass slide, measuring the distance from the bottom of the slide to the top of the cranial vault, and subtracting the thickness of the slide.

In addition, we recorded the following three measurements:

BIF, breadth across incisive foramina: from the labial margin of the right foramen to the labial margin of the left.

GLS, greatest length of skull: from the posterior-most point of the occipital region to the tip of the nasals.

LPB, length of palatal bridge: distance from the posterior end of the incisive foramina to the anterior-most border of the mesopterygoid fossa.

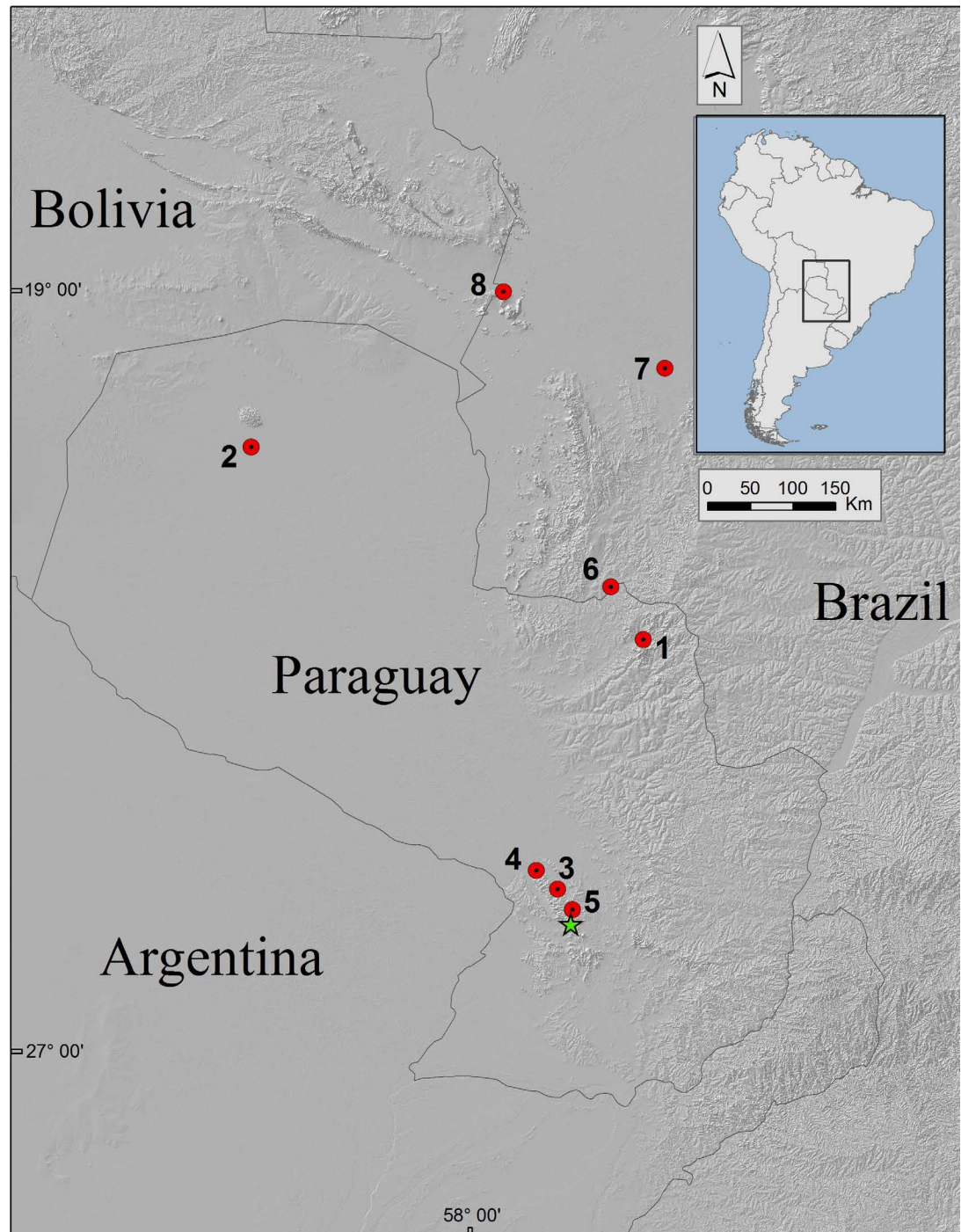
Descriptive statistics were calculated for a subset of specimens considered juveniles and for a subset of specimens considered to be adults (i.e, those with molars completely erupted and showing at least some wear).

Seven specimens of *Thrichomys* from three Paraguayan localities (1, Amambay: UMMZ 125551 female; 2, Chaco: UMMZ 125552 male, UMMZ 125618 female; 3, Cordillera: UMMZ 126046 male, UMMZ 126049 female, UMMZ 126050 female, UMMZ 126285 female; Fig. 1) were karyotyped using standard chromosome techniques.

The genetic and phylogenetic analyses were based on the first 801 base pairs of the cytochrome *b* gene. DNA sequences of 15 Paraguayan specimens collected at a single locality (Appendix 1) were gathered using the laboratory procedures outlined by Cañon *et al.* (2010) with primers MVZ 05 and MVZ 16, which delimit a fragment of 801 base pairs.

Amplicons were purified and sequenced at Macrogen (Seoul, Korea). Newly generated sequences were submitted to GenBank (accession numbers: KJ551913 - KJ551927). Paraguayan sequences were integrated with 71 *cyt b* sequences of *Thrichomys* that by November 15, 2013 were available in GenBank and that belong to about eight forms of species level (see Nascimento *et al.* 2013). Only one sequence of each haplotypic class ( $n = 57$ ) found in the *Thrichomys* sample was used in the phylogenetic analysis (Fig. 2). In addition, one sequence of each of the other living genera that together with

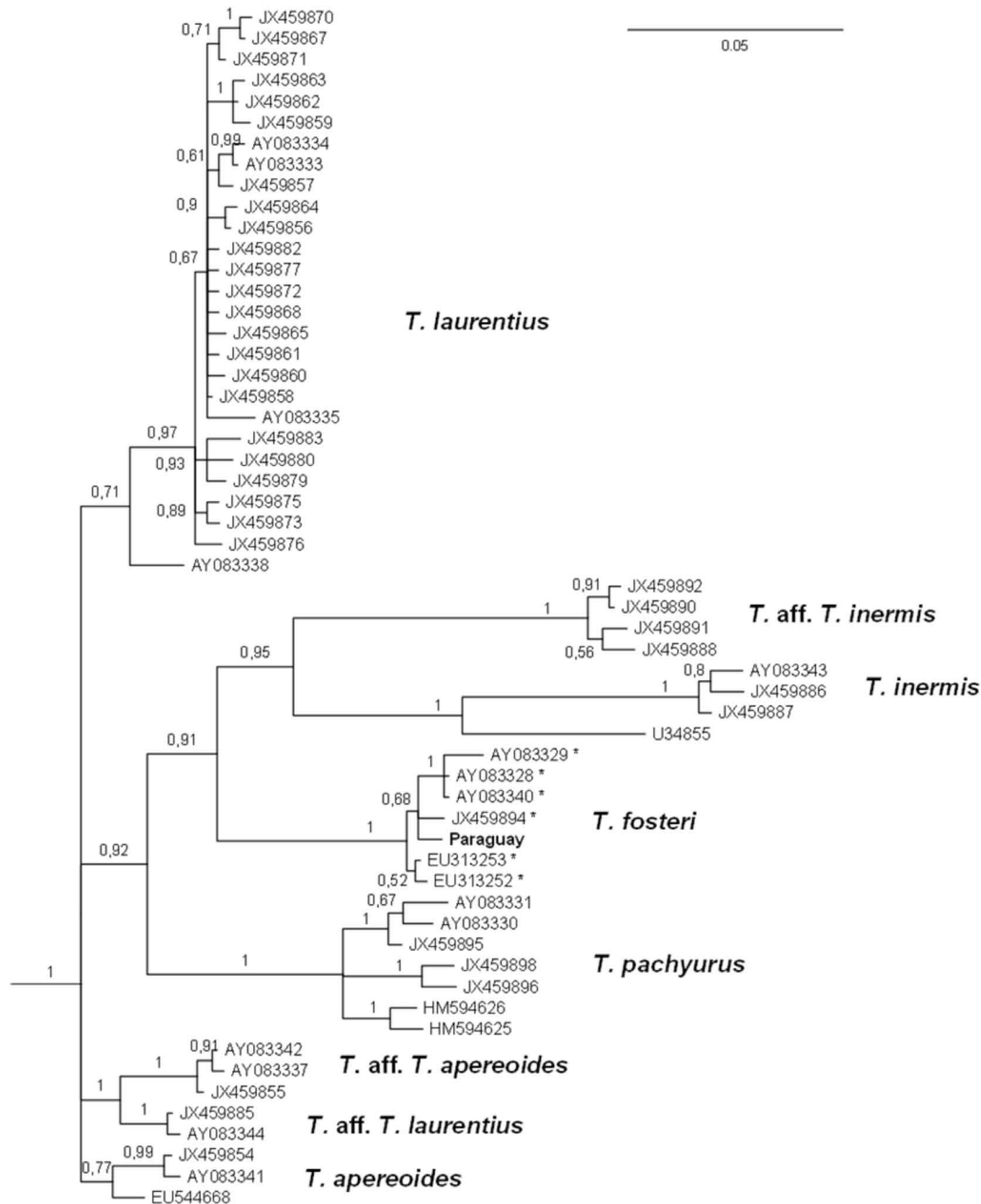
*Thrichomys* compose the echimyid subfamily Eumysopinae (see current delimitation of the subfamily in Patton and Emmons in press) were downloaded, when available, from GenBank (no DNA sequence of *Carterodon* was available) to compose the outgroup.



**Figure 1.** Map showing the collecting localities of the specimens of *Thrichomys fosteri* Thomas 1903 analyzed in the present study. Details of the Paraguayan localities (1-5) are provided in Appendix I. Localities from Mato Grosso do Sul, Brazil are: 6) Bela Vista, 7) Fazenda Taboco, and 8) Corumbá (see Nascimento et al. 2013). The star indicates the type locality of *Thrichomys fosteri*.

When possible, eumysopine sequences were gathered from specimens belonging to the type species of each genus: *Clyomys laticeps* (AF422918), *Euryzygomatomys spinosus* (JF297804), *Hoplomys gymnurus* (AF422922), *Lonchothrix emiliae* (AF422921), *Mesomys hispidus* (KF590696), *Proechimys simonsi* (U35414; no sequence of *P. trinitatis* was available), and *Trinomys albispinus* (EU313251). Sequence alignment was done with

Clustal X (Thompson *et al.* 1997) using the default values for all alignment parameters; no adjustment by eye was needed. MEGA 5 (Tamura *et al.* 2011) was used to calculate observed sequence divergence percentages (using the whole matrix; i.e., 86 sequences of *Thrichomys*) and to find the substitution model that best fits the data (HKY + G + I).



**Figure 2.** Majority-rule consensus resulting from the Bayesian analysis based on the first 801 bases of the cyt b gene of *Thrichomys*. Numbers indicate posterior probability values of the nodes at their right. Terminal labels refer to GenBank accession numbers; those haplotypes of specimens from the Brazilian state of Mato Grosso do Sul are indicated by an \*. The Paraguayan haplotype is labelled Paraguay.

The phylogenetic reconstruction was done with Bayesian inference (Huelsenbeck 2001) implemented in MrBayes 3 (Ronquist and Huelsenbeck 2003) using two independent runs with three heated and one cold Markov chain each. With the exception of base composition and HKY parameters, which assumed a Dirichlet process prior, uniform interval priors were assumed for all parameters. Chains were run for 10 million generations and trees were sampled every 1000 generations per chain. Log-likelihood

values were plotted against generation time for each run in order to check for stable log-likelihood value convergence. The first 25% of the trees were discarded as burn-in; the remaining ones were used to compute a 50% majority rule tree.

## Results

Descriptive statistics for the sample of juveniles and for a subset of adult specimens are provided in Table 1. The skull of one of these specimens is shown in Figure 3. The specimens examined closely match Thomas's (1903) description of *Thrichomys fosteri* in size and qualitative characters. They are also a good match for the description of *T. pachyurus* (including *fosteri*) given by Pessôa *et al.* (in press).

**Table 1.** Descriptive statistics for external and cranial measurements for two samples (juvenile: ages 1 and 2; adult: ages 3 and 4) of Paraguayan *Thrichomys* (see text for variable definitions and details of age classes). Sample sizes are given in parentheses. Measurements are in millimeters and mass in grams.

|              | Juveniles   |       |             | Adults      |       |           |
|--------------|-------------|-------|-------------|-------------|-------|-----------|
|              | Mean        | SD    | range       | Mean        | SD    | range     |
| Total length | 350.25 (16) | 64.82 | 237-467     | 438.00 (13) | 24.11 | 404-468   |
| Tail length  | 159.19 (16) | 34.60 | 83-210      | 201.15 (13) | 16.11 | 176-226   |
| Hind foot    | 41.94 (16)  | 4.45  | 34-49       | 47.43 (13)  | 2.56  | 43-53     |
| Ear          | 21.81 (16)  | 2.17  | 19-26       | 24.00 (13)  | 1.18  | 22-27     |
| Mass         | 178.20 (15) | 84.04 | 61-326      | 320.07 (13) | 82.13 | 204-500   |
| GLS          | 46.93 (14)  | 4.53  | 38.5-54.9   | 54.91 (15)  | 2.69  | 50.0-59.6 |
| CIL          | 40.58 (13)  | 3.38  | 34.2-46.9   | 47.29 (15)  | 2.52  | 42.7-51.7 |
| IFL          | 4.88 (16)   | 0.74  | 3.4-6.1     | 6.08 (15)   | 0.49  | 5.3-6.9   |
| BIF          | 3.84 (16)   | 0.55  | 2.7-5       | 4.76 (15)   | 0.41  | 3.8-5.4   |
| MTRL         | 8.36 (16)   | 1.17  | 5.4-9.6     | 9.63 (15)   | 0.33  | 8.8-10.1  |
| AW           | 7.74 (16)   | 0.42  | 6.9-8.5     | 8.91 (15)   | 0.43  | 8.1-9.8   |
| LPB          | 8.11 (16)   | 0.96  | 6.3-9.6     | 9.39 (15)   | 0.78  | 8.4-11.3  |
| DL           | 8.84 (16)   | 0.97  | 7.3-10.5    | 10.69 (15)  | 0.62  | 9.5-11.6  |
| BOL          | 6.92 (15)   | 0.66  | 5.8-8.2     | 8.05 (15)   | 0.62  | 7.3-9.5   |
| ZB           | 24.38 (14)  | 1.08  | 22.5-27     | 27.71 (15)  | 1.21  | 25.4-29.3 |
| IOC          | 11.23 (15)  | 0.96  | 9.7-13.2    | 13.17 (15)  | 0.73  | 11.9-14.9 |
| MB           | 19.03 (14)  | 2.84  | 10-21.6     | 21.51 (15)  | 0.68  | 20.5-22.4 |
| BB           | 20.16 (16)  | 0.86  | 18.7-22     | 21.36 (15)  | 0.75  | 20.2-22.5 |
| OCW          | 9.03 (15)   | 0.52  | 7.7-9.7     | 9.69 (15)   | 0.34  | 9.2-10.3  |
| OL           | 12.88 (15)  | 0.80  | 11.1-13.9   | 14.21 (15)  | 0.77  | 12.9-15.8 |
| NL           | 14.93 (16)  | 2.16  | 11.3-18.9   | 18.53 (14)  | 0.96  | 17.2-20.0 |
| RL           | 16.75 (15)  | 2.13  | 13.6-20.8   | 20.69 (15)  | 1.26  | 18.9-23.0 |
| RW1          | 7.79 (16)   | 0.80  | 6.7-9.5     | 9.19 (15)   | 0.63  | 7.8-10.2  |
| RW2          | 6.69 (16)   | 0.63  | 5.6-8.0     | 8.03 (15)   | 0.71  | 6.9-9.7   |
| CD           | 16.76 (13)  | 0.71  | 15.54-17.94 | 18.34 (15)  | 0.74  | 16.9-19.6 |

All specimens karyotyped have  $2n = 34$ ,  $FN = 64$ . The karyotype includes 12 pairs of metacentric chromosomes, four pairs of small submetacentric, and a large subtelocentric X chromosome; poor quality material precluded determining the morphology of the Y chromosome.

The Paraguayan sample used for the genetic analysis ( $n = 15$ ) shows no variation; all specimens had the same haplotype. Observed genetic variation between the Paraguayan haplotype and haplotypes from other populations ranges from 0.5 % (comparison with

haplotype EU313253 of *T. fosteri*) to 8.5 % (comparison with haplotype JX459886 of *T. inermis*). The phylogenetic analysis of cyt b DNA sequences (Fig. 2) recovered a strongly supported (PP = 1) genus *Thrichomys*. At the base of the *Thrichomys* clade is a polytomy involving four main lineages: 1. *T. laurentius*; 2. (((*T. inermis*, *T. aff. T. inermis*) *T. fosteri*) *T. pachyurus*); 3. (*T. aff. T. apereoides*, *T. aff. T. laurentius*); and 4. *T. apereoides*. The Paraguayan haplotype falls within the clade (PP = 1) formed by haplotypes of specimens from Mato Grosso do Sul, Brazil and referred by Nascimento *et al.* (2013) to *Thrichomys fosteri*. Average p-distance value between haplotype pairs of *Thrichomys fosteri* is 0.4 % (Table 2).

|                                  | intraspecific | <i>T. pachyurus</i> | <i>T. aff. T. inermis</i> | <i>T. inermis</i> | <i>T. aff. T. laurentius</i> | <i>T. laurentius</i> | <i>T. apereoides</i> | <i>T. aff. T. apereoides</i> |
|----------------------------------|---------------|---------------------|---------------------------|-------------------|------------------------------|----------------------|----------------------|------------------------------|
| <i>T. pachyurus</i> (9)          | 0.022         |                     |                           |                   |                              |                      |                      |                              |
| <i>T. aff. T. inermis</i> (6)    | 0.007         | 0.092               |                           |                   |                              |                      |                      |                              |
| <i>T. inermis</i> (4)            | 0.037         | 0.086               | 0.095                     |                   |                              |                      |                      |                              |
| <i>T. aff. T. laurentius</i> (2) | 0.001         | 0.064               | 0.070                     | 0.087             |                              |                      |                      |                              |
| <i>T. laurentius</i> (34)        | 0.006         | 0.067               | 0.081                     | 0.090             | 0.033                        |                      |                      |                              |
| <i>T. apereoides</i> (5)         | 0.006         | 0.064               | 0.075                     | 0.090             | 0.024                        | 0.034                |                      |                              |
| <i>T. aff. T. apereoides</i> (5) | 0.001         | 0.062               | 0.081                     | 0.092             | 0.022                        | 0.042                | 0.029                |                              |
| <i>T. fosteri</i> (21)           | 0.004         | 0.075               | 0.072                     | 0.082             | 0.057                        | 0.065                | 0.057                | 0.062                        |

**Table 2.** Observed variation (*p*-distance) of the cytochrome b gene within and among eight putative species of *Thrichomys*. Numbers in parentheses refer to the number of sequences studied for each species (see Fig. 2 for details of the analyzed sequences).

## Discussion

The Paraguayan mammal fauna is diverse, both in terms of species numbers as well as phylogenetically. With continuing additions to the list of species recorded for Paraguay (e. g., D'Elía *et al.* 2008; de la Sancha *et al.* 2009, 2012; Smith *et al.* 2011), these numbers are expected to grow. In general, the mammal biota of the country is far from being adequately known; for most species of mammals, available knowledge covers little more than distributional data. Further, for those few species that occur in Paraguay and whose general biology has been studied, Paraguayan populations have seldom been included in the investigations.

Among the least studied groups of Paraguayan mammals are those of the family Echimyidae. Six species of Echimyidae (*sensu* Emmons *et al.* in press) are known to occur in Paraguay: *Clyomys laticeps* (Thomas 1909), *Euryzygomatomys spinosus* (G. Fischer 1814), *Kannabateomys amblyonyx* (Wagner 1845), *Myocastor coypus* (G. I. Molina 1782), *Proechimys longicaudatus* (Rengger 1830), and one species of *Thrichomys*.

The taxonomic history of the latter is complex. A few years after its description by Trouessart, (1880), *Thrichomys* was placed under *Cercomys* by Thomas (1912) and as a result Paraguayan populations were regarded for several years as *C. fosteri* (e. g. Tate,



1935, but see Bertoni, 1914, 1935 who continued using *T. fosteri*). Later, Ellerman (1941) referred *C. fosteri* to the synonymy of *Cercomys cunicularis* (F. Cuvier 1829).



**Figure 3.** Dorsal, ventral and lateral view of the skull and lateral view of the right jaw of *Thrichomys fosteri* (UMMZ 125551) from Paraguay (details of collection locality in Appendix 1).

*Thrichomys* was later resurrected from *Cercomys* (see Petter 1973) with *T. apereoides* as its single species (e. g. Woods 1993). In the last decade, as a result of investigations based on karyotypes and phylogenetic analyses (Bonvicino *et al.*, 2002; Braggio and Bonvicino, 2004; Pessôa *et al.* 2004), *T. pachyurus* was removed from the synonymy of

*T. apereoides* and Paraguayan populations were referred to it (e. g. Woods and Kilpatrick 2005). Additional evidence led Nascimento *et al.* (2013) to argue that populations from Mato Grosso do Sul, south-central Brazil and Paraguay should be recognized as a species (*T. fosteri*) distinct from *T. pachyurus*.

Our study is the first to analyze DNA sequence data from Paraguayan *Thrichomys*. The single Paraguayan haplotype found is not only similar to haplotypes found in Mato Grosso do Sul, but it is deeply nested within the clade that includes these haplotypes from Mato Grosso do Sul populations and excludes those of other Brazilian populations (Fig. 2). This agrees with the hypothesis that Mato Grosso de Sul and Paraguayan populations belong to the same species of *Thrichomys*. This clade is sister to a clade formed by haplotypes of *T. inermis* and *T. aff. T. inermis*, from the Brazilian states of Bahia and Tocantins, respectively; the clade from Mato Grosso do Sul and Paraguay differs on average from that of *T. inermis* and *T. aff. T. inermis* by 8.2 and 7.2% (Table 2).

Specimens of *T. inermis* and *T. aff. T. inermis* have  $2n = 26$ ,  $FN = 48$  (Nascimento *et al.* 2013), in contrast to populations from Paraguay and Mato Grosso do Sul, which share  $2n = 34$ ,  $FN = 64$ . Taken together, these data indicate that the species from Mato Grosso do Sul and Paraguay is distinct from all other members of the genus, including *T. pachyurus* ( $2n = 30$ ,  $FN = 56$ ). We have not analyzed sequences from Sapucaí (current spelling of Sapucay), Paraguari, Paraguay, the type locality of *T. fosteri*; Companhia Minas-Cue is about 75 km towards the northwest of Sapucaí, and our closest sample comes from Saltos de Pirareta, ca. 18 km to the north of Sapucaí (Fig. 1). However, our specimens, including those sequenced (Appendix 1), are consistent with the original description of *T. fosteri* (Thomas 1903), including a quantitative comparison (not shown) of the type (an old adult male) of *T. fosteri* and the two males of class 4 available to us. The type of *T. fosteri* has only two measurements that fall outside the range defined by the two old males examined by us; these variables are length of the incisive foramen (type 5.6% larger than the average of our two oldest males) and zygomatic breadth (type 3.2% larger than the average of our two oldest males). Therefore, we agree with Nascimento *et al.* (2013) that the correct name to apply to the species from Mato Grosso do Sul and Paraguay is *T. fosteri*. Future studies are needed to clarify if Bolivian specimens also belong to this form as suggested by Anderson (1997) based on their morphology.

The Paraguayan sample available to us lacks genetic variation in the locus sampled; 15 specimens, collected at a single locality, show the same *cyt b* haplotype. Future studies will clarify how genetic variation is geographically partitioned among Paraguayan populations of *T. fosteri* for this and other loci. However, it is noteworthy that most Paraguayan mammal species so far analyzed also show low levels of genetic variation (e.g., *Akodon paranaensis*, D'Elía *et al.* 2008; *Akodon montensis*, Valdez and D'Elía 2013; *Dasybus novemcinctus*, Frutos and Van Den Bussche 2002; *Marmosa paraguayana*, de la Sancha *et al.* 2012; *Oligoryzomys nigripes*, Francés and D'Elía 2006; *Scapteromys aquaticus*, D'Elía and Pardiñas 2004). Although our sampling of *T. fosteri* is far from adequate to constitute a phylogeographic study, it is of interest that the Paraguayan haplotype discovered is well nested within haplotypes of animals from Mato Grosso do Sul (Fig. 2). This result allows advancing a scenario, which should be further tested, in which variants from Paraguay, and by extension Paraguayan populations, are derived from populations from south-central Brazil. Similar scenarios in which Paraguayan

populations are young (i.e., species would have recently expanded into Paraguay) have been suggested for different mammal species (e. g. D'Elía *et al.* 2008; de la Sancha *et al.* 2012; Valdez and D'Elía 2013). Remarkably, these species show different life histories, *Akodon montensis* is a forest specialist while others (e. g. *Necomys lasiurus*) inhabit open areas; as such, it is difficult to invoke a single scenario accounting for these patterns (but see Valdez and D'Elía 2013).

We expect that the data here provided as well the hypotheses advanced will contribute to a much needed comprehensive revision of the genus *Thrichomys* as well as incrementally improve our knowledge of Paraguayan mammals.

## Acknowledgments

We first express our gratitude to R. D. Owen for inviting us to contribute this work to this special volume of *Therya*. Several people provided valuable assistance during field work in Paraguay including I. Mora, L. Aquino, and R. D. Owen. P. Smith and two anonymous reviewers provided valuable comments on an earlier version of this work. Pablo Jayat made the map of Figure 1. Financial support was provided by FONDECYT 1110737.

## References

- ANDERSON, S. 1997. Mammals of Bolivia, taxonomy and distribution. *Bulletin of the American Museum of Natural History* 231:1–652.
- BANDOUK, A. C., AND S. F. DOS REIS. 1995. Craniometric variation and subspecific differentiation in *Thrichomys apereoides* in northeastern Brazil (Rodentia: Echimyidae). *Zeitschrift für Säugetierkunde* 60:176–185.
- BERTONI, A. DE W. 1914. Fauna paraguaya: Catálogos sistemáticos de los vertebrados del Paraguay. Peces, batracios, reptiles, aves y mamíferos conocidos hasta 1913. Pp. 1 - 86, en Descripción Física y Económica del Paraguay 59. (Bertoni M.S., ed.). Establecimiento Gráfico M. Brossa. Asunción, Paraguay.
- BERTONI, A. DE W. 1939. Catálogos sistemáticos de los vertebrados del Paraguay. Mamíferos, aves, reptiles y batracios comprobados hasta 1937. *Revista de la Sociedad Científica del Paraguay* 4: 3-49.
- BONVICINO, C. R., I. B. OTAZU, AND P. S. D'ANDREA. 2002. Karyologic evidence of diversification of the genus *Thrichomys* (Rodentia, Echimyidae). *Animal Cytogenetics and Genome Research* 97:200–204.
- BORODIN, P. M., S. C. BARREIROS-GOMEZ, A. I. ZHELEZOVA, C. R. BONVICINO, AND P. S. D'ANDREA. 2006. Reproductive isolation due to genetic incompatibilities between *Thrichomys pachyurus* and two subspecies of *Thrichomys apereoides*. *Genome* 49:159–167.
- BRAGGIO, E., AND C. R. BONVICINO. 2004. Molecular divergence in the genus *Thrichomys* (Rodentia: Echimyidae). *Journal of Mammalogy* 85:316–320.
- CABRERA, A. 1961. Catálogo de los mamíferos de America del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales Zoología* 4:309–732.
- CAÑÓN C., G. D'ELÍA, U. F. J. PARDIÑAS, AND E. P. LESSA. 2010. Phylogeography of *Loxodontomys micropus* with comment on the alpha taxonomy of *Loxodontomys* (Cricetidae: Sigmodontinae). *Journal of Mammalogy* 91:1449–1458.

- DE LA SANCHA, N., G. D'ELÍA, F. NETTO, P. PÉREZ, AND J. SALAZAR-BRAVO. 2009. Discovery of *Juliomys* (Rodentia, Sigmodontinae) in Paraguay, a new genus of Sigmodontinae for the country's Atlantic Forest. *Mammalia* 73:162-167.
- DE LA SANCHA, N., G. D'ELÍA, AND P. TETA. 2012. Systematics of the subgenus of mouse opossums *Marmosa (Micoureus)* (Didelphimorphia, Didelphidae) with noteworthy records from Paraguay. *Mammalian Biology* 77:229-236.
- D'ELÍA, G., AND U. F. J. PARDIÑAS. 2004. Systematics of Argentinean, Paraguayan, and Uruguayan swamp rats of the genus *Scapteromys* (Rodentia, Cricetidae, Sigmodontinae). *Journal of Mammalogy* 85:897-910.
- D'ELÍA, G., I. MORA, P. MYERS, AND R. D. OWEN. 2008. New and noteworthy records of Rodentia (Erethizontidae, Sciuridae, and Cricetidae) from Paraguay. *Zootaxa* 1784:39-57.
- DOS REIS, S. F., L. C. DUARTE, L. R. MONTEIRO, AND F. J. VON ZUBEN. 2002. Geographic variation in cranial morphology in *Thrichomys apereoides*: II. Geographic units, morphological discontinuities, and sampling gaps. *Journal of Mammalogy* 83:345-353.
- DOS REIS, S. F., AND L. M. PESSÔA. 2004. *Thrichomys apereoides*. *Mammalian Species* 74:1-5.
- HUELSENBECK, J. P. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294:2310-2314.
- EMMONS, L. H., Y. L. R. LEITE, AND J. L. PATTON. In press. Family Echimyidae Gray, 1825. In *Mammals of South America, Volume 2, Rodents* (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). University of Chicago Press. Chicago, USA.
- FRUTOS, S. D., AND R. A. VAN DEN BUSSCHE. 2002. Genetic diversity and gene flow in nine-banded armadills in Paraguay. *Journal of Mammalogy* 83:815-823.
- LARA, M. C., J. L. PATTON, AND DA M. N. SILVA. 1996. The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution* 5:403-413.
- LEAL-MESQUITA, E. R., V. FAGUNDES, Y. YONENAGA-YASSUDA, AND P. L. B. ROCHA. 1993. Comparative cytogenetic studies of two karyomorphs of *Thrichomys apereoides* (Rodentia, Echimyidae). *Genetics and Molecular Biology* 16:639-651.
- LEITE, Y. L., AND J. L. PATTON. 2002. Evolution of South American spiny rats (Rodentia, Echimyidae): the star-phylogeny hypothesis revisited. *Molecular Phylogenetics and Evolution* 25:455-464.
- MOOJEN, J. 1952. *Os Roedores do Brasil*. Instituto Nacional do Livro, Rio de Janeiro. Rio de Janeiro, Brazil.
- MYERS, P., J. L. PATTON, AND M. F. SMITH. 1990. A review of the *boliviensis* group of *Akodon* (Rodentia: Sigmodontinae), with emphasis on Peru and Bolivia. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 177:1-104.
- NASCIMENTO, F. F., A. LAZAR, A. N. MENEZES, A. D. M. DURANS, J. C. MOREIRA, J. SALAZAR-BRAVO, P. S. D'ANDREA, AND C. R. BONVICINO. 2013. The Role of historical barriers in the diversification processes in open vegetation formations during the Miocene/Pliocene using an ancient rodent lineage as a model. *PLoS ONE* 8(4): e61924. doi:10.1371/journal.pone.0061924

- NEVES, A. C. DA S. A., AND L. M. PESSÔA. 2011. Morphological distinction of species of *Thrichomys* (Rodentia: Echimyidae) through ontogeny of cranial and dental characters. *Zootaxa* 2804:15–24.
- PATTON, J. L. AND L. H. EMMONS. In press. Subfamily Eumysopinae Rusconi, 1935. In *Mammals of South America, Volume 2, Rodents* (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). University of Chicago Press. Chicago, USA.
- PESSÔA, L. M., M. M. DE OLIVEIRA CORRÊA, J. A. DE OLIVEIRA, AND M. O. G. LOPES. 2004. *Karyological and morphometric variation in the genus Thrichomys (Rodentia: Echimyidae)*. *Mammalian Biology* 69:258–269.
- PESSÔA L. M., W. C. TAVARES, A. C. A. NEVES, AND A. L. G. DA SILVA. In press. Genus *Thrichomys* E.-L. Trouessart, 1880. En *Mammals of South America, Volume 2, Rodents* (Patton, J. L., U. F. J. Pardiñas, and G. D'Elía, eds.). University of Chicago Press, Chicago, USA.
- PETTER, F. 1973. Les noms de genre *Cercomys*, *Nelomys*, *Trichomys* et *Proechimys* (Rongeurs, Echimyides). *Mammalia* 37:422–426.
- RONQUIST, F. AND J. P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:572–1574.
- SMITH, P., R. D. OWEN, K. ATKINSON, H. DEL CASTILLO, AND E. NORTHCOTE-SMITH. 2011. First Records of the Southern Naked-Tailed Armadillo *Cabassous unicinctus* (Cingulata: Dasypodidae) in Paraguay. *Edentata* 12:53–57.
- TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI, AND S. KUMAR. 2011. MEGA5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28:2731–2739.
- THOMAS, O. 1903. New species of *Oxymycterus*, *Thrichomys*, and *Ctenomys* from S. America. *Annals and Magazine of Natural History ser.7*, 11:226–229.
- THOMAS, O. 1912. The generic names *Cercomys* and *Proechimys*. *Proceedings of the Biological Society of Washington* 25:115–116.
- THOMPSON, J. D., T. J. GIBSON, F. PLEWNIAK, F. JEANMOUGIN, AND D. G. HIGGINS. 1997. The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 25:4876–4882.
- TROUESSART, E. L. 1880. Catalogue des mammifères vivants et fossils. *Ordre des rongeurs*. *Bulletin de la Société d'Études Scientifiques d'Angers* 10:58–212.
- VALDEZ, L., AND G. D'ELÍA. 2013. Differentiation in the Atlantic Forest: phylogeography of *Akodon montensis* (Rodentia, Sigmodontinae) and the Carnaval-Moritz model of Pleistocene refugia. *Journal of Mammalogy* 94:911–922.
- WOODS, C. A. 1993. Suborder Hystricognathi. Pp. 771–806 en *Mammal species of the world: a taxonomic and geographic reference*, 2nd ed. (Wilson D. E., and D. M. Reeder, eds.). Smithsonian Institution Press. Washington, USA.
- WOODS, C. A., AND C. W. KILPATRICK. 2005. Infraorder Hystricognathi. Pp. 1538–1600 en *Mammal species of the world: a taxonomic and geographic reference*, 3d ed. (Wilson, D. E., and D. M. Reeder, eds.). The Johns Hopkins Press. Baltimore, USA.

---

*Sometido: 19 de diciembre de 2013*  
*Revisado: 15 de marzo de 2013*  
*Aceptado: 25 de marzo de 2013*  
*Editor asociado: Robert Owen*  
*Diseño gráfico editorial: Gerardo Hernández*

---

## **Appendix 1**

Paraguayan specimens of *Thrichomys fosteri* analyzed in this study. Localities are mapped in Figure 1. Voucher specimens are housed at the following collections: University of Michigan Museum of Zoology (UMMZ), Ann Arbor, USA and Colección de Mamíferos, Universidad Austral de Chile (UACH), Valdivia, Chile. Specimens used in the morphometric analysis are indicated by an <sup>m</sup> and those used in the genetic analysis are signalled by an <sup>\*</sup>.

1) Amambay, 4 km by road SW Cerro Cora: UMMZ 125549<sup>m</sup>, UMMZ 125550<sup>m</sup>, UMMZ 125551<sup>m</sup>. 2) Chaco, 50 km WNW Madrejón, Misión Nuevo Tribu: UMMZ 124302<sup>m</sup>, UMMZ 125552<sup>m</sup>. 3) Cordillera, 1.6 km by rd. S Tobati: UMMZ 126044<sup>m</sup>, UMMZ 126045<sup>m</sup>, UMMZ 126046<sup>m</sup>, UMMZ 126047<sup>m</sup>, UMMZ 126048<sup>m</sup>, UMMZ 126049<sup>m</sup>, UMMZ 126050<sup>m</sup>, UMMZ 126092<sup>m</sup>, UMMZ 126093<sup>m</sup>, UMMZ 126094<sup>m</sup>, UMMZ 126095<sup>m</sup>, UMMZ 126096<sup>m</sup>, UMMZ 126097<sup>m</sup>, UMMZ 126098<sup>m</sup>, UMMZ 126099<sup>m</sup>, UMMZ 126100<sup>m</sup>, UMMZ 126101<sup>m</sup>, UMMZ 126102<sup>m</sup>, UMMZ 126103<sup>m</sup>. 4) Cordillera, Compania Minas-Cue, Emboscada, Prop. of Am. Filipinni Mora: UMMZ 174959<sup>m\*</sup>, UMMZ 174960<sup>m\*</sup>, UMMZ 174963<sup>m\*</sup>, UMMZ 174964<sup>m\*</sup>, UMMZ 174966<sup>m\*</sup>, UMMZ 174967<sup>m\*</sup>, UMMZ 175100<sup>\*</sup>, UACH 7264<sup>\*</sup>, UACH 7265<sup>\*</sup>, UACH 7266<sup>\*</sup>, UACH 7267<sup>\*</sup>, UACH 7268<sup>\*</sup>, UACH 7269<sup>\*</sup>, UACH 7270<sup>\*</sup>, UACH 7271<sup>\*</sup>. 5) Paraguari, 17km SE Piribebuy by rd., Saltos de Pirareta: UMMZ 124301<sup>m</sup>.