

Chapter 11

The Six Opossums of Félix de Azara: Identification, Taxonomic History, Neotype Designations, and Nomenclatural Recommendations

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ABSTRACT

Six species of Paraguayan didelphid marsupials (opossums) were described by the Spanish naturalist Félix de Azara (1742–1821), whose nontechnical accounts were the basis for Latin binomials in current use for several species. Unfortunately, some of Azara's descriptions are problematic and have long been a source of taxonomic confusion. In particular, the names currently used for two species of *Thylamys* are difficult to reconcile with Azara's text. Herein we review the nomenclatural status of Azara's opossums and discuss relevant issues that affect binomial usage. Among other results, we report the rediscovery of the holotype of *Caluromys lanatus* (Olfers, 1818), and we designate neotypes to preserve current usage of the names *Thylamys macrurus* (Olfers, 1818) and *T. pusillus* (Desmarest, 1804).

INTRODUCTION

El mundo era tan reciente, que muchas cosas carecían de nombre, y para mencionarlas habría que señalarlas con el dedo. (The world was so new that many things lacked names, and in order to talk about them it was necessary to point.)

—Gabriel García Márquez, *Cien Años de Soledad*

Although pointing is the oldest and least fallible method for determining the application of names, biological nomenclature was originally based on descriptions. Unfortunately, many early naturalists were unaware of the characters that distinguish closely related taxa, so their descriptions were often found to apply to two or more superficially similar species. The late recognition that descriptions

alone are inadequate to determine stable taxonomic usage was responsible for the development of the type concept and its codification by international biological consensus in the mid-20th century (Mayr et al., 1953). Designating type specimens (the formal equivalent of pointing; Ghiselin, 1995) has the crucial advantage that diagnostic characters omitted in the original description can be determined by subsequent examination, and this practice is now required for all new species. For older names based on diagnostically inadequate descriptions, the International Code of Zoological Nomenclature (ICZN, 1999: Article 75) permits the designation of neotypes as necessary to resolve problems of conflicting or ambiguous application.

The literature of Neotropical mammalogy is, unfortunately, replete with problematic

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names based on old descriptions.⁶ Much of the larger South American fauna, for example, was first made known to the world at large through the publications of intrepid explorer-naturalists such as Georg Markgraf (1610–1644; Whitehead, 1979) or amateur collectors like Albert Seba (1665–1736; Engel, 1937), whose nontechnical accounts were cited as bibliographic sources by Linnaeus (1758) and other early taxonomists. Among those explorers whose faunal descriptions are still the primary authority for determining the application of mammalian technical names, however, none is more important than Félix de Azara (1742–1821).

Félix Francisco José Pedro de Azara y Perera, a Spanish military engineer with no formal biological education, was sent to Buenos Aires in 1781 to help map the boundary between Spanish and Portuguese possessions in South America. Due to lack of Portuguese interest, the border survey was interminably delayed, so Azara occupied his time for some 20 years by describing the geography, indigenous cultures, mammals, and birds of the region now delimited by Paraguay, Uruguay, and the Argentine provinces of Buenos Aires, Corrientes, Entre Ríos, and Misiones. Among his considerable accomplishments (Beddall, 1975; Mones and Klappenbach, 1997), Azara described some 75 species of native mammals, of which about 80% were previously unknown to science (Hershkovitz, 1987).

Azara's mammalian descriptions first appeared in a French translation (Azara, 1801: hereafter, the "*Essais*"), which was based on a preliminary Spanish draft completed in 1796 and sent to his brother in Paris. A revised draft, longer than the first and differing from it in certain details, was subsequently published in Madrid (Azara, 1802: the "*Apuntamientos*"). Additional comments on mammalian identifications were provided in a later work summarizing his South American travels and observations (Azara, 1809: the "*Voyages*"). Throughout these publications, Azara used only vernacular (Amerindian and/or Spanish) names for

the species he reported, but his descriptions served as the bibliographic basis for Latin binomials authored by Desmarest (1804), Oken (1816), Olfers (1818), and others. Although Azara dispatched specimens to Madrid on more than one occasion (Cabrera, 1934b), few examples are known to have survived to the present day.

Azara's descriptions are detailed enough to permit unambiguous identifications of many species, but some have long been sources of taxonomic confusion. Among the Latin names based on Azara's rats, for example, are several cases of problematic usage that have only recently been resolved by neotype designation (Myers and Carleton, 1981; Musser et al., 1998). Scientific names based on Azara's opossums, the identification and taxonomy of which are the topic of this report, include additional examples of ambiguous application that need to be fixed.

The cited bibliographic reference for most of the scientific binomials associated with Azara's opossums is the *Essais* of 1801, in which six species were described (table 1). However, the same six species were also described in the *Apuntamientos* of 1802, which constitutes another primary source of information about the specimens personally examined by Azara. Neither the *Essais* nor the *Apuntamientos* was illustrated, and the plates accompanying the *Voyages* of 1809 do not depict any marsupials. Therefore, with the exception of a single extant holotype (Cabrera, 1916), all of the relevant information regarding the application of technical names for Azara's opossums is contained in his texts.

As explained below, textual information provided in the *Essais* and the *Apuntamientos* is sufficient to determine the application of some names based on Azara's opossums, but not others. Two cases of consistent usage require no remedial nomenclatural action, but four problematic cases merit attention. Below, we designate neotypes for two names, recommend that another be suppressed, and state our opinion that a fourth should not be used to replace any currently accepted name.

Materials and Methods

Qualitative external and craniodental characters mentioned in this report are those

⁶ For relevant examples, see the accounts for *Monodelphis brevicaudata*, *Dasyprocta leporina*, and *Myoprocta acouchy* in Voss et al. (2001).

TABLE 1
Vernacular and Technical Names of Azara's Opossums

Name in the <i>Essais</i> ^a	Name in the <i>Apuntamientos</i> ^b	Latin name(s) ^c
Micouré premier, ou micouré proprement dit	El Micuré	<i>paraguayensis</i> Oken, 1816 ^d <i>leucotis</i> Wagner, 1847 <i>paraguayensis</i> Allen, 1902
Micouré second, ou micouré laineux	El Lanoso	<i>lanata</i> Olfers, 1818 <i>lanigera</i> Desmarest, 1820
Micouré troisième, ou micouré à queue grosse	El Coligrueso	<i>crassicaudata</i> Desmarest, 1804 <i>crassicaudis</i> Olfers, 1818 <i>macroura</i> Desmoulin, 1824 <i>ferruginea</i> Larrañaga, 1923
Micouré quatrième, ou micouré à queue longue	El Colilargo	<i>marmota</i> Oken, 1816 ^d <i>macrura</i> Olfers, 1818 <i>grisea</i> Desmarest, 1827
Micouré cinquième, ou micouré à queue corte	El Colicorto	<i>brevicaudis</i> Olfers, 1818 <i>wagneri</i> Matschie, 1916
Micouré sixième, ou micouré nain	El Enano	<i>pusilla</i> Desmarest, 1804 <i>nana</i> Oken, 1816 ^d <i>nana</i> Olfers, 1818

^a Azara (1801).

^b Azara (1802).

^c Epithets based on Azara's descriptions. All of these names were originally combined with *Didelphis* Linnaeus (sometimes misspelled *Didelphys*), feminine in gender (ICZN, 2006), the genus commonly used for most American marsupials throughout the early 19th century. The cited bibliographic reference for all but one of these names is the *Essais* (Azara, 1801), the unique exception being *Didelphis ferruginea* Larrañaga, 1923, which was based on the description of the Coligrueso in the *Apuntamientos* (Azara, 1802).

^d Unavailable due to inconsistent use of binomial nomenclature in Oken's work (ICZN, 1956).

defined and illustrated by Voss and Jansa (2003, 2009). Following Clemens (1966: 3), we identify the small upper molar cusp posterolabial to the paracone but anterolabial to the metacone as styler cusp C (styC). In those species of *Thylamys* that possess such a structure, styC contributes to the "serrated" appearance of the styler shelf (Solari, 2003; Carmignotto and Monfort, 2006), which is only shallowly indented by the ectoflexus; species of *Thylamys* that lack styC have styler shelves that are much more deeply notched by the ectoflexus (Solari, 2003; Carmignotto and Monfort, 2006).

External dimensions of examined specimens (in millimeters, mm) and weights (in grams, g) are those recorded by collectors. Except as noted otherwise, collectors of specimens that we examined are known or assumed to have followed the standard American measurement protocol (Hall, 1981): total length (TL) from nose to fleshy tail tip, tail length (LT) from dorsal flexure to fleshy tip, hind foot (HF) from heel to tip of longest claw, ear (Ear) from

notch to distal margin of pinna. We computed head-and-body length (HBL) by subtracting LT from TL.

Craniodental measurements are those defined and illustrated by Voss et al. (2001: fig. 7) and Voss et al. (2004: fig. 2). Briefly, these include condylobasal length (CBL: measured from the occipital condyles to the anteriormost point of the premaxillae), nasal breadth (NB: measured across the triple-point sutures of the nasal, frontal, and maxillary bones on each side), least interorbital breadth (LIB: measured at the narrowest point across the frontals between the orbits), zygomatic breadth (ZB: measured at the widest point across both zygomatic arches), palatal length (PL: measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine, if present), palatal breadth (PB: measured across the labial margins of the M4 crowns, at or near the styler A position), maxillary toothrow length (MTR: measured from the anterior margin of C1 to the posterior margin of M4), length of

molars (LM: measured from the anteriormost labial margin of M1 to the posteriormost point on M4), and length of M1–M3 (M1–M3: measured from the anteriormost labial margin of M1 to the posteriormost point on M3). All craniodental measurements were taken with digital calipers while specimens were viewed at 6–25 diameters magnification under a binocular microscope. Craniodental measurements (which we recorded to the nearest 0.01 mm) are rounded to the nearest 0.1 mm in the tables accompanying this report.

Except as noted below, all analyzed character data (qualitative and morphometric) were obtained from adult specimens as determined by dental criteria. Following Voss et al. (2001), a specimen was judged to be *juvenile* if dP3 is still in place; *subadult* if dP3 has been shed but P3 and/or M4 are still incompletely erupted; and *adult* if the permanent dentition is complete.

Institutional abbreviations associated with examined specimens are: AMNH (American Museum of Natural History, New York), BMNH (Natural History Museum, London), FMNH (Field Museum of Natural History, Chicago), MNCN (Museo Nacional de Historia Natural, Madrid), MNHNP (Museo Nacional de Historia Natural del Paraguay, Asunción), MSB (Museum of Southwestern Biology, Albuquerque), MVZ (Museum of Vertebrate Zoology, Berkeley), MZUSP (Museu de Zoologia, Universidade de São Paulo), OMNH (Oklahoma Museum of Natural History, Norman), TTU (Museum of Texas Tech University, Lubbock), UMMZ (University of Michigan Museum of Zoology, Ann Arbor), USNM (National Museum of Natural History, Washington). The prefix TK identifies field numbers associated with specimens collected by Robert Owen's Paraguayan mammal inventory project (these will eventually be deposited at MNHNP or TTU; R. Owen, personal commun.), and the prefix TWN identifies field numbers associated with specimens collected by Thomas W. Nelson (to be deposited in the Biological Collections of the University of Connecticut).

AZARA'S SIX OPOSSUMS

Azara referred to opossums generically as "micourés" (in the *Essais*) or as "fecundos"

(in the *Apuntamientos*). Because the sequence in which the species were described is the same in both the French and Spanish texts (table 1), it is convenient to follow his enumeration in the following accounts. English translations of relevant passages in the *Apuntamientos* are provided in appendix 1.

The First Opossum

Azara's first opossum clearly corresponds to the species currently known as *Didelphis albiventris* Lund, 1840, an identification supported by many features described in both the *Essais* and the *Apuntamientos*. These include its large size (e.g., maximum total length >800 mm); bold facial markings (black mask and midfrontal streak); white-tipped ears; white underfur; very long guard hairs; a large pouch that opens anteriorly and contains 11 to 13 teats; and a prehensile, basally furred tail, the naked epithelium of which is blackish proximally and whitish distally.

The oldest Latin binomial that is unambiguously based on Azara's first opossum is *Didelphis paraguayensis* Oken (1816), but Oken's work is not available for nomenclatural purposes (Hershkovitz, 1949; ICZN, 1956). *Didelphis paraguayensis* is, however, available from Allen (1902), who used it as a valid name citing Azara's account as its bibliographic basis. *Didelphis leucotis* Wagner (1847) is also based on Azara's description of his first opossum, so *paraguayensis* Allen and *leucotis* Wagner are objective synonyms, and both are subjective junior synonyms of *albiventris* Lund.

Thomas (1888) and Cabrera (1958) thought that *Didelphis azarae* Temminck (1824) was based on Azara's first opossum, and they used it as the oldest available name for the white-eared Paraguayan species. Although Temminck cited Azara's first opossum as a synonym of *D. azarae*, his description was actually based on several specimens of black-eared opossums that he examined in various European museums (Wagner, 1847; Hershkovitz, 1969; Cerqueira and Tribe, 2008). Whether *azarae* is a junior synonym of the black-eared Amazonian species *D. marsupialis* Linnaeus, 1758, or a senior synonym of the southeastern Brazilian species currently known as *D. aurita* Wied,

1826, remains to be determined by examination of Temminck's original material (said by him to be in Paris, Leiden, Vienna, and Frankfurt). In the event that Temminck's syntypes should all prove to be from southeastern Brazil, we recommend that *azarae* be suppressed in order to maintain current usage (Gardner, 1993, 2005; Cerqueira and Tribe, 2008).

The Second Opossum

The next marsupial described by Azara is likewise unambiguously recognizable, corresponding to the species currently known as *Caluromys lanatus* (Olfers, 1818). This identification is supported by many details of Azara's description (including external measurements, presence of a dark midrostral stripe, violet ears, woolly pelage, a tail that is furred more extensively dorsally than ventrally, etc.) and also by a fluid-preserved specimen that he sent to Madrid. Because Olfers explicitly based *lanatus* on Azara's (1801) description of the "Micouré second," and because Azara stated that he had seen but a single example, the Madrid specimen is the holotype by monotypy. Prior to the rediscovery of Olfers' rare and obscure work (Hershkovitz, 1959), this species was widely known as *C. lanigera* (Desmarest, 1820), an objective junior synonym.

The holotype of *Caluromys lanatus* was not found in the Museo Nacional de Historia Natural by Delibes and García-Valdecasas (1987), who stated that no types of nonchiropteran mammals were present in the collection. However, a recent search by one of us (J.B.) happily resulted in the rediscovery of Azara's specimen (figs. 1, 2). Originally preserved in alcohol with registration number 528 (Cabrera, 1916), the type was subsequently prepared as a skin and skull and recataloged as MNCN-M2630. Although both skin and skull are in good condition, the pelage is discolored from long immersion in alcohol. The specimen is a juvenile (with unreplaced dP3/dp3), so Azara's published measurements (in appendix 1) do not represent mature anatomical dimensions. The type locality—stated in the *Essais* but not in the *Apuntamientos*—is Caazapá

(26°09'S, 56°24'W; Paynter, 1989) in Departamento Caazapá, Paraguay.

The Third Opossum

Azara's (1801) description of the "Micouré à queue grosse" was the basis for *Lutreolina crassicaudata* (Desmarest, 1804), the identification of which does not appear to have ever been questioned in the literature.⁷ Diagnostic traits mentioned by Azara include external measurements; a thick, nonprehensile (or weakly prehensile), basally furred, white-tipped tail; the absence of any circumocular mask or other facial markings; small ears; a weakly defined pouch; and a conspicuously carnivorous captive diet. The epithets *crassicaudis* Olfers (1818), *macroura* Desmoulin (1824), and *ferruginea* Larrañaga (1923) are objective junior synonyms.

In the *Essais*, Azara said that he saw a live animal of this species at the "village de Saint-Stanislaw" (= San Estanislao at 24°39'S, 56°26'W in the Paraguayan department of San Pedro; DMA, 1992), and that he had examined a female specimen from Asunción. Neither locality is mentioned in the *Apuntamientos*, however, where the species is simply said to occur in Paraguay and Buenos Aires. Several nominal subspecies of *Lutreolina crassicaudata* have been recognized by authors within the Spanish territory traversed by Azara, including (in addition to the nominotypical form), *L. c. bonaria* Thomas, 1923 (with type locality near Buenos Aires); *L. c. lutrilla* Thomas, 1923 (with type locality in Rio Grande do Sul, but ranging into Uruguay); and *L. c. paranalis* Thomas, 1923 (with type locality in the Argentine province of Santa Fé). All of these are currently treated (e.g., by Gardner, 2005; Stein and Patton, 2008) as synonyms of *L. c. crassicaudata*, but in the event that any are subsequently recognized as valid taxa, it might be desirable to fix the application of *crassicaudata* by neotype selection. Given the widespread assumption that the nominotypical form is the one that occurs in Paraguay (Thomas, 1923; Cabrera, 1958; Ximénez,

⁷ Cabrera (1934a) identified Azara's "coligrueso" as *Marmosa grisea* (= *Thylamys macrurus*, see below), but this was an obvious lapsus that he subsequently corrected (Cabrera, 1958).



Fig. 1. Dorsal and ventral views of the skin of the holotype of *Caluomys lanatus* (Olfers, 1818) in the Museo Nacional de Ciencias Naturales in Madrid (MNCN-M2630). Cabrera (1916) summarized the documentary evidence that this is Azara's original and unique specimen of his second opossum.

1967), it would be appropriate to designate a neotype from that country. However, no taxonomic purpose would be served by doing so at this time.

The Fourth Opossum

Azara's long-tailed opossum (the "Miccouré à queue longue" of the *Essais* and the



Fig. 2. Dorsal and ventral views of the skull and mandibles of the holotype of *Caluomys lanatus* (Olfers, 1818) in the Museo Nacional de Ciencias Naturales in Madrid (MNCN-M2630). The presence of upper and lower milk premolars (dP3/dp3) indicate that this is a juvenile individual.

“Colilargo” of the *Apuntamientos*) was the basis for three Latin binomials: *Didelphys marmota* Oken, 1816; *Didelphys macrura* Olfers, 1818; and *Didelphis grisea* Desmarest, 1827. As noted above, Oken’s names are technically unavailable, so Olfers’ is the senior of these objective synonyms. The obscurity of Olfers’ work (Hershkovitz, 1959) explains why only Desmarest’s name was widely used in the 19th-century literature.

In both the *Essais* and the *Apuntamientos*, Azara said that his description was based on a single male specimen, possibly immature, that was sent to him by his friend Don Josef Casal. In the *Apuntamientos* this specimen is said to have come from Don Josef’s country house, but the *Essais* gives the place of origin as “Tapoua.” According to Tate (1933: 218), this locality is “Tapua . . . some few miles northeast of Asuncion,” which would put it in the Paraguayan department of Central. Gardner (2005: 17), however, stated that “Tapuá” (with an acute accent on the terminal vowel) is in Departamento Presidente Hayes. The geographic discrepancy is significant because the departments of Central and Presidente Hayes lie on opposite banks of the Río Paraguay, which divides the country into two ecologically and zoogeographically distinct parts (Myers, 1982): the Eastern Region and the Chaco (fig. 3). Fortunately, Azara’s posthumously published treatise on the geography of Paraguay (Azara, 1904; edited by R.R. Schuller) makes it clear that Don Josef’s house (in the vice-parroquia of Tapúa, not Tapuá) was in the Eastern Region not far from the left bank of the Río Paraguay.

As described by Azara, his fourth opossum measured 237 mm in total length and the tail was 135 mm; by subtraction, the combined length of head and body was 102 mm. A conspicuous black mask surrounded each eye, and around each black marking was a border of paler fur; between the left and right masks with their pale borders was a dark median line that terminated anteriorly at the level of the inner canthus of the eye. The color of the fur between the ears, over the whole back, and on the tail was said to be like that of the house mouse, but the flanks were paler, as were the sides of the forelegs. The

lower jaw, the throat, and the anterior parts of the forelegs were almost white, and the rest of the ventrum was dirty whitish. All of the fur was short and soft.

Although Azara’s measurements and description of his fourth opossum correspond plausibly with the external characters of the species currently known as *Thylamys macrurus* (see Carmignotto and Monfort, 2006), no unambiguously diagnostic traits are mentioned in either the *Essais* or the *Apuntamientos*. In fact, Azara’s description has been stretched to fit several other small didelphids. Thomas (1888), for example, identified Azara’s Micouré à queue longue with the species currently known as *Marmosops incanus*, for which he used the name *Didelphys (Micoureus) grisea* Desmarest. Later (Thomas, 1894), he changed his mind and used the name *Micoureus griseus* for a specimen of *Thylamys* collected in Corrientes, Argentina. After discovering the priority of Oken’s name, Thomas (1896) used *Marmosa marmota* for what he believed to be the same species in Paraguay and Corrientes, but he subsequently (Thomas, 1912) designated one of his Corrientes specimens as the type of *Marmosa citella*, a new species. Currently, *citella* is regarded (e.g., by Gardner, 2005; Creighton and Gardner, 2008) as a junior synonym of *Thylamys pusillus* (Desmarest, 1804), a name based on Azara’s sixth opossum (see below).

Tate (1933) used the name *Marmosa marmota marmota* (Oken) for the large *Thylamys* that occurs in eastern Paraguay, but he also recognized a smaller form in the Chaco that he identified as *M. marmota verax* Thomas (1921). Cabrera (1958) used *Marmosa (Thylamys) grisea* (Desmarest) for the taxon that Tate (1933) called *M. marmota marmota* and referred *verax* to the synonymy of *M. (T.) pusilla*. As if the situation were not sufficiently confusing by this time, Hershkovitz (1959) argued—not without reason (see below)—that Azara’s fourth and sixth opossums were conspecific and used the name *M. pusilla* (Desmarest, 1804) for both. However, Kirsch and Calaby (1977) recognized *M. (T.) grisea* and *M. (T.) pusilla* as valid species based on Azara’s fourth and sixth opossums, respectively. Current usage of the binomen *Thylamys macrurus* dates from Gardner and Creighton (1989).

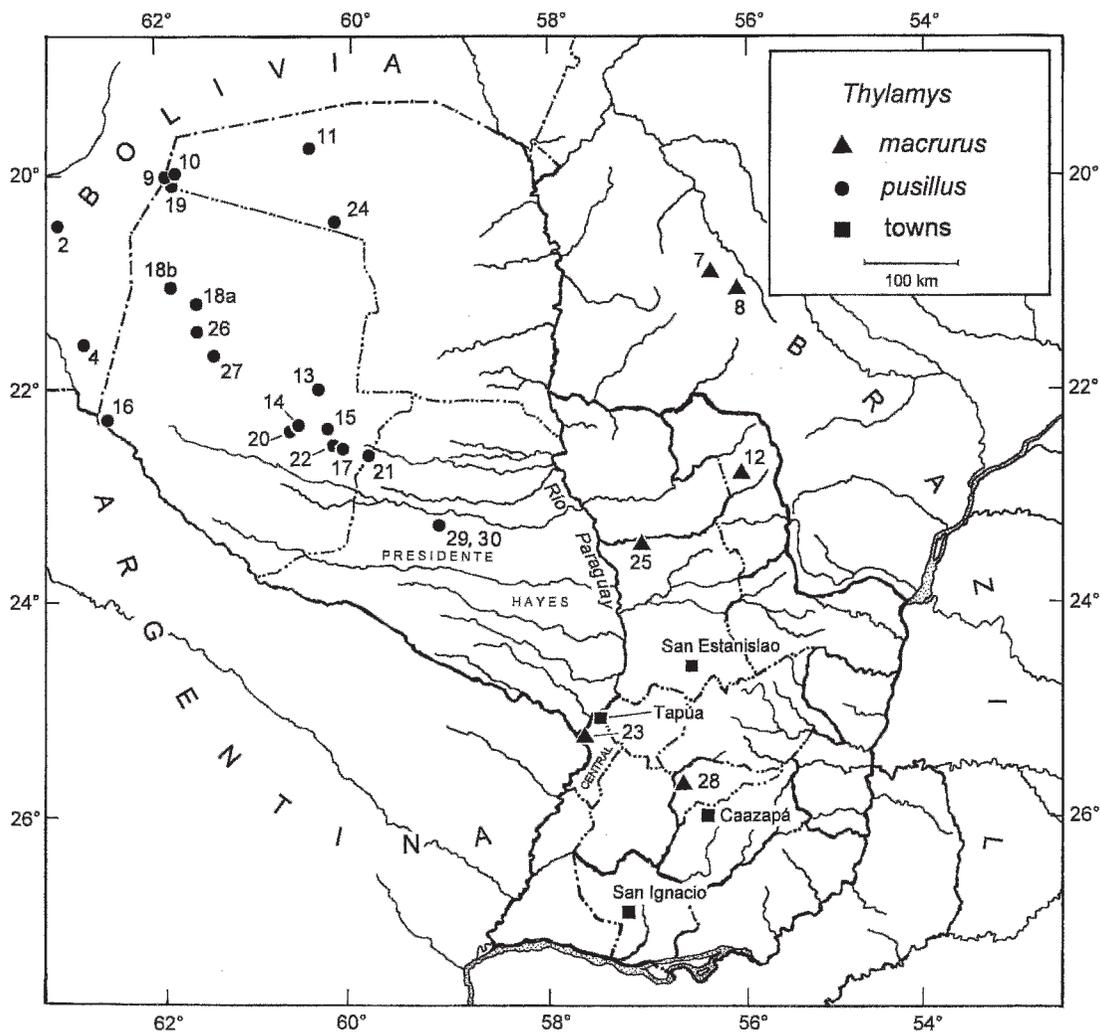


Fig. 3. Map of collecting localities for examined Paraguayan specimens of *Thylamys* (numbers correspond to gazetteer entries in the appendix). Some adjacent Brazilian and Bolivian collecting localities are also mapped, but not all of those listed in the gazetteer are shown. The locations of Paraguayan towns mentioned in Azara's opossum accounts are also indicated; coordinates of most of these can be found in standard gazetteers (e.g., Paynter, 1989; DMA, 1992), but the location of Tapúa is based on a map in Frakes (1989). That part of Paraguay to the east of the Río Paraguay is commonly known as the Eastern Region, and the part to the west is commonly known as the Chaco (Myers, 1982).

Names based on Azara's fourth opossum have therefore been applied to several zoological species, and key issues of identification remain unresolved. In particular, the taxonomic distinctness of Azara's fourth and sixth opossums has never been effectively established (see below), so current use of *Thylamys macrurus* is problematic in the absence of type material. We therefore select

as neotype of *Thylamys macrurus* (Olfers, 1818) an adult female specimen in the University of Michigan Museum of Zoology (UMMZ 125243), consisting of a skin and skull collected by Thomas W. Nelson (original number TWN 103) at 28 km SW Pedro Juan Caballero (22°34'S, 55°37'W) in Departamento Amambay, Paraguay, on 9 February 1977. Based on this specimen and

other examined material, we provide an emended diagnosis of the species and summarize other pertinent information in the taxonomic accounts below.

The Fifth Opossum

Azara's micouré à queue courte was the basis for *Didelphys brevicaudis* Olfers (1818), a name that was entirely forgotten in the subsequent systematic literature until rediscovered by Hershkovitz (1959). *Didelphis* (*Monodelphis*) *wagneri* Matschie (1916) is an objective junior synonym.⁸ The zoological taxon in question is clearly a species of *Monodelphis*, as indicated by Azara's measurements (indicating a very small species with a tail much shorter than the combined length of the head and body), and his description of its small ears, squat body, short fur, and distinctive coloration (grizzled grayish brown dorsally with reddish flanks).

Azara's account of this species in the *Essais* was based on a specimen obtained by his friend Pablo Blas Nosedá. According to Glick and Quinlan (1975), Nosedá was a parish priest at the Jesuit mission settlement of San Ignacio Güazú (= San Ignacio at 26°52'S, 57°03'W; Paynter, 1989) in Departamento Misiones, Paraguay. In the *Apuntamientos*, however, Azara stated that he had seen specimens from between 27° and 34° South latitude; within the geographic limits of his known itineraries (Mones and Klappenbach, 1997: apéndice V), this additional material might have come from southern Paraguay, northern Argentina, or Uruguay.

Although *brevicaudis* Olfers, 1818, has been infrequently mentioned in the literature, it is not a *nomen oblitum* in the technical sense of the International Code of Zoological Nomenclature (ICZN, 1999; contra Gardner, 2005). Therefore, it can be used to replace subjective junior synonyms in current use, if any exist. Whether it should be used for that purpose is debatable, however, nor is it clear

what currently accepted name(s) might be affected.

The red-flanked Paraguayan species of *Monodelphis* is currently known as *M. sorex* (Hensel, 1872). According to Pine and Handley (2008), *brevicaudis* might be a senior synonym of *sorex*, but those authors caution that another reddish-flanked species, *M. dimidiata* (Wagner, 1847), is known from localities not far from Paraguay and might occur there too. Such uncertainties could obviously be resolved by neotype selection, but we have not made a close study of these taxa, and it seems irresponsible to take such action without having seen all of the relevant type material. Furthermore, the names *sorex* and *dimidiata* are now widely used, and no biological purpose would be served by replacing either with *brevicaudis*. Therefore, another defensible option would be to petition the International Commission on Zoological Nomenclature to use its plenary powers to suppress *brevicaudis*, which has only been used as a valid name by a few authors (e.g., Hershkovitz, 1959; Wetzel and Lovett, 1974; Brown, 2004). Although the latter course of action would effectively conserve current binomial usage (Gardner, 2005; Pine and Handley, 2008), it is possible that Paraguayan populations of red-flanked *Monodelphis* are taxonomically distinct from other named forms and would then need a new name. Only careful revisionary work based on first-hand examination of types and other relevant specimens can establish the appropriate action to take in this matter.

The Sixth Opossum

Azara's micouré nain of the *Essais* was the basis for *pusilla* Desmarest, 1804, another name that has historically been associated with several different didelphid species. The names *nana* Oken, 1816, and *nana* Olfers, 1818, are objective junior synonyms that have never been used as valid names.

Azara (1801, 1802) introduced his sixth opossum as a new species, one not previously mentioned by Buffon, Brisson, Linnaeus, or other authors discussed in previous accounts. His description was based on two males, said to be adults, that were captured by Indians from San Ignacio Güazú (= San Ignacio at

⁸ Matschie's name was proposed as a replacement for "*Didelphis brachyura*" (= *D. brachyuros* Schreber, 1778) as mistakenly applied by Wagner (1855) to Azara's fifth opossum. Wagner's usage was a misidentification because *brachyuros* Schreber is an objective junior synonym of *brevicaudata*, Erxleben, 1777, a distinct species from the Guiana Region of Amazonia (Voss et al., 2001).

26°52'S, 57°03'W; Paynter, 1989) in the Paraguayan department of Misiones. Among other characters, this species was said to be small (his measurements work out to a head-and-body length of about 90 mm with a somewhat longer tail), and to be colored essentially like the fourth opossum (with a blackish circumocular mask, whitish eyebrows, grayish dorsum, and whitish venter).

Notwithstanding Azara's reference to grayish dorsal pelage, Thomas (1888) applied *pusilla* Desmarest to material in the British Museum representing two different species with distinctly reddish fur: *Cryptonanus guahybae* (Tate, 1931) and *Gracilinanus microtarsus* (Wagner, 1842). Later, Thomas (1900) recognized *Marmosa microtarsus* (Wagner) and *M. pusilla* (Desmarest) as distinct species, but he applied the latter binomen to the taxon currently known as *Gracilinanus agilis* (Burmeister, 1854). Tate (1933) used *M. pusilla* for the species of *Thylamys* previously known as *M. citella* Thomas (1912), and Desmarest's name has been used consistently thereafter for one or more species of *Thylamys*.

Based on specimens that we examined, there are only two unambiguously distinguishable species of *Thylamys* in Paraguay: a large species in the Eastern Region, and a small species in the Chaco (fig. 3). Both species are also known from neighboring countries, but they have never been found in sympatry, and their Paraguayan distributions are separated by the Río Paraguay (as are those of many other mammals; Myers, 1982). As explained above, the large species of *Thylamys* in the Eastern Region is currently known as *T. macrurus*, whereas the small Chacoan species is currently known as *T. pusillus*. The latter usage is now well established and is, in fact, universally accepted by modern authors (e.g., Gardner, 1993, 2005; Flores et al., 2000, 2007; Solari, 2003; Braun et al., 2005; Carmignotto and Monfort, 2006; Creighton and Gardner, 2008).

The essential problem, hitherto unaddressed in the literature, consists in the fact that the type locality of *Thylamys pusillus* (San Ignacio) is in the Eastern Region, whereas all known Paraguayan specimens currently identified as belonging to this species are from the Chaco. Two explana-

tions for this discrepancy suggest themselves. Either (1) Azara's sixth opossum was not the same as the species currently known as *T. pusillus*, or (2) the species currently known as *T. pusillus* really does occur in the Eastern Region but has yet to be found there by modern collectors.

The first explanation is plausible because nothing in Azara's description is unambiguously diagnostic and there is at least one notable discrepancy. Although Azara's measurements and color descriptors fit the species currently known as *Thylamys pusillus* reasonably well, they are equally applicable to immature specimens of *T. macrurus*. Because Azara did not examine skulls to determine dental eruption sequences, there is no way to be sure that his specimens were really mature (as he believed them to be). Furthermore, *T. pusillus* has a conspicuously incrassate tail (swollen with stored fat), whereas the sixth opossum was said to have a tail that was more slender than that of the fourth opossum (*T. macrurus*).

The second explanation—that *Thylamys pusillus* really occurs in the Eastern Region but has yet to be collected there—is surely possible, because the mammalian fauna of Paraguay is still incompletely known. However, existing collection records for these species (mapped in fig. 3) together with zoogeographic expectations from well-documented patterns of regional endemism (Myers, 1982) tend to suggest that, if any *Thylamys* is eventually collected in the department of Misiones, it is more likely to be *T. macrurus* than *T. pusillus*. Altogether, it seems impossible to convincingly justify current usage of these names based on Azara's texts.

If Azara's fourth and sixth opossums were really the same species, then the appropriate name for the eastern Paraguayan *Thylamys* currently known as *T. macrurus* is *T. pusillus*, and the small Chacoan species should be known by one of the names currently treated as subjective junior synonyms of the latter (e.g., *verax* Thomas, 1921). Needless to say, such changes would destabilize current nomenclature, and they would serve no useful biological purpose. We therefore select as neotype of *Thylamys pusillus* (Desmarest, 1804) an adult male specimen in the Museum

of Vertebrate Zoology (MVZ 144311), consisting of a skin and skull collected by Philip Myers (original number 800) near the Trans-Chaco highway 460 km NW of Villa Hayes in Departamento Boquerón, Paraguay, on 7 April 1973. Based on this specimen and other examined material, we provide an emended diagnosis of the species and summarize other pertinent information in the taxonomic accounts below.

SPECIES ACCOUNTS

Based on the neotypes designated above and other examined material, we here summarize relevant taxonomic information about *Thylamys macrurus* and *T. pusillus*, including type localities, known distributions, emended diagnoses, brief comparisons with other congeneric forms, and remarks about problems that we encountered in attempting to identify museum specimens, allocate putative synonyms, etc.

Thylamys macrurus (Olfers, 1818)

NEOTYPE: Skin and skull of an adult female in the University of Michigan Museum of Zoology (UMMZ 125243) collected by Thomas W. Nelson (original number TWN 103) on 9 February 1997.

TYPE LOCALITY: Twenty-eight kilometers SW Pedro Juan Caballero, Departamento Amambay, Paraguay. Although this locality (copied from the field label tied to the skin of UMMZ 125243) appears to be on private land according to modern satellite imagery, the collector of the neotype (and two juvenile specimens with the same locality data) recently told us that all of his trapping near Pedro Juan Caballero was done within the boundaries of Parque Nacional Cerro Cora, which lies about 12 km to the NW. According to this source (T.W. Nelson, personal commun.), local habitats consisted of forest that “had a mostly closed, at least medium-tall canopy with some large trees, along with some open agricultural areas that were starting to return to forest.” The area was “definitely not savanna-like, but certainly not undisturbed primary forest either.” This recollection is supported by taxonomic identifications of small mammals collected at the

same locality, which include both moist-forest and open-country species: *Monodelphis domestica*, *Dasypus novemcinctus*, *Artibeus lituratus*, *Glossophaga soricina*, *Myotis nigricans*, *Cebus libidinosus*, *Mazama americana*, *Thrichomys pachyurus*, *Akodon montensis*, *Nectomys squamipes*, *Oligoryzomys nigripes*, *Hylaeamys megacephalus*, and *Cerradomys maracajuensis*. Other species collected within the park's boundaries include *Didelphis albiventris*, *Marmosa (Micoureus) constantiae*, *Carollia perspicillata*, *Sturnira lilium*, *Platyrrhinus lineatus*, *Eptesicus furinalis*, and *Sooretamys angouya*.

DISTRIBUTION: Based on specimens that we examined and other captures reported by Cáceres et al. (2007), *Thylamys macrurus* appears to be restricted to Mato Grosso do Sul (Brazil) and the Eastern Region of Paraguay. A single Bolivian locality reported by Anderson (1997) and an Argentinian locality mapped by Brown (2004) are both based on misidentifications. The Bolivian specimen in question (AMNH 263549) is an example of *Marmosops ocellatus* (see Voss et al., 2004: 31), and the Argentinian specimen (BMNH 98.8.19.9) is the holotype of *Marmosa citella* (possibly a subjective synonym of *T. pusillus*; see below).

There exist substantive discrepancies between Paraguayan and Brazilian habitats where *Thylamys macrurus* has been collected. At both the type locality (described above) and at 7 km NE Concepción (where Eduardo Palma collected a fourth Paraguayan specimen; appendix 2: locality 25), the dominant natural habitat consisted of tall subtropical moist (semi-evergreen) forest. Due to human intervention, this habitat is currently interspersed, throughout eastern Paraguay, with agricultural fields, regenerating secondary growth, and pastures. Similar conditions almost certainly occurred in the 19th century near Asunción (where N.L. Holden collected a fifth Paraguayan specimen; appendix 2: locality 23), and near Sapucay (where W. Foster collected a sixth example; appendix 2: locality 28).

By contrast, Brazilian captures of *Thylamys macrurus* are all from the Cerrado (Eiten, 1972, 1978), a vast mosaic of xeromorphic vegetation types ranging from treeless savanna (campo limpo) to open

TABLE 2
Measurements (mm) and Weights (g) of Subadult and Adult Specimens of *Thylamys macrurus*

	BMNH	BMNH	MSB	MZUSP	MZUSP	MZUSP	UMMZ	MZUSP
	99.11.17.1	3.4.7.21	70700	32094	32095	32096	125243 ^a	3782
Age	subadult	adult	adult	adult	adult	adult	adult	adult
Sex	male	female	female	female	female	female	female	male
HBL	—	147 ^b	130	126	108	106	135	110
LT	—	161 ^b	154	153	143	138	140	132
HF	—	15 ^b	18	19	16	17	17	—
Ear	—	25 ^b	23	27	23	24	25	—
CBL	29.2	33.3	33.4	32.5	29.9	29.6	34.2	31.9
NB	2.8	2.9	3.4	3.5	2.8	2.5	2.9	2.6
LIB	4.6	5.4	5.2	5.3	4.9	4.3	5.4	4.7
ZB	16.9	18.9	18.3	19.2	17.0	16.0	19.2	17.8
PL	16.2	18.2	17.9	17.1	16.4	15.8	18.6	17.7
PB	—	11.0	10.4	10.4	9.5	9.4	10.9	10.1
MTR	12.1	12.8	12.6	12.1	11.9	12.1	12.9	12.4
LM	6.6	6.4	6.3	6.4	6.1	6.5	6.5	6.4
MI-3	5.8	5.4	5.4	5.5	5.3	5.6	5.4	5.5
Weight	—	—	57	55	30	31	54	—

^a Neotype.

^b Measurement method unknown, but probably not following the standard American protocol.

woodlands (campo cerrado) and deciduous forests (cerradão). Within this landscape, *Thylamys macrurus* appears to be most consistently associated with open woodlands and deciduous forests (Carmignotto and Monfort, 2006; Cáceres et al., 2007), habitats that do not resemble any intact vegetation formations that we have seen in eastern Paraguay. We showed photographs of Cerrado habitats in which Brazilian specimens of *T. macrurus* were trapped to T.W. Nelson (collector of the neotype, see above), who emphatically stated that it was unlike the secondary moist forest in which he trapped *T. macrurus* near Pedro Juan Caballero.

EMENDED DIAGNOSIS: *Thylamys macrurus* is distinctively larger in most measured dimensions (table 2) than other congeneric species, from which it also differs in qualitative external and craniodental traits. The tail is distinctly longer (by about 22%) than the combined length of the head and body. Although the presence of caudal subcutaneous fat is less externally evident than in other congeneric species, the tail of *T. macrurus* (fig. 4) is still visibly incrassate (contra Palma, 1995, 1997; Creighton and Gardner, 2008). The tail is bicolored proximally (dark above, whitish below), but the terminal one-

fifth to one-third is entirely white. The ventral surface of the tail is modified for prehension distally, with a naked median groove and a fleshy apical pad bearing dermatoglyphs. The body pelage is distinctly tricolored (sensu Tate, 1933: 209), with a dark grayish or grayish-brown middorsal region, paler flanks, and sharply defined ventral countershading. The dorsal fur is short (usually 8–9 mm long middorsally), and the ventral fur is mostly self-white or -cream from chin to anus; however, a narrow lateral zone of gray-based hairs is usually present. The manual claws are short (not, or only slightly extending beyond the fleshy apical pad of each digit), and the ventral surface of the manus has six separate dermatoglyph-bearing plantar pads encircling a concave, densely tubercular central palmar region. The supraorbital margins are indistinctly beaded in large specimens, some of which (e.g., MZUSP 32094) have indistinct postorbital processes. The zygomatic arches are wide relative to cranial length (the average ratio of zygomatic breadth to condylobasal length expressed as a percentage [$ZB/CBL \times 100$] is about 56%). Distinct maxillary palatal vacuities are invariably present, although these openings are some-



Fig. 4. *Thylamys macrurus* in life (MZUSP 32094), photographed at Fazenda Califórnia, Mato Grosso do Sul, Brazil, by A.P. Carmignotto.

times small. The posterolateral palatal foramina usually extend anteriorly to a point that is lingual to the M4 protocones, but they are not as long as in most other congeneric species (Carmignotto and Monfort, 2006: fig. 6). The auditory bullae are relatively small, the distance between the left and right bullae greatly exceeding the width of either bulla. Styler cusp C is consistently present on M1–M3.

COMPARISONS: The known geographic range of *Thylamys macrurus* is adjacent to the distributions of three congeneric species, with which it merits brief comparisons. The smaller Brazilian species *T. karimii* and *T. velutinus* differ from *T. macrurus* (among other characters) by having longer claws that extend well beyond the fleshy apical pads of the manual digits; manual plantar pads are fused together and do not surround a central palmar concavity; a tail that is substantially shorter than the combined length of head and body; no prehensile modifications on the underside of the tail tip; indistinctly tricolored body pelage; and much longer posterolateral palatal foramina (see illustrations in

Carmignotto and Monfort, 2006). Both species occur in Cerrado (*T. velutinus*) or Cerrado and Caatinga (*T. karimii*) landscapes that are drier and more seasonal than those inhabited by *T. macrurus* in eastern Paraguay and Mato Grosso do Sul.

Thylamys pusillus, the only other species of *Thylamys* known to occur in Paraguay, differs from *T. macrurus* by being substantially smaller (with nonoverlapping molar dimensions; tables 2, 3), by lacking a pale tail tip, by its entirely self-white ventral fur (lacking lateral zones of gray-based hairs), by having much longer posterolateral palatal foramina, and by usually lacking styC on M3. Based on specimens that we examined (fig. 3), the ranges of *T. pusillus* and *T. macrurus* are separated by the Río Paraguay and by the seasonally inundated pantanales (palm savannas) of the eastern Chaco.

SPECIMENS EXAMINED: **Brazil**—Mato Grosso do Sul, Campo Grande (MZUSP 3782), Fazenda Califórnia (MZUSP 32094–32096), Fazenda Santa Terezinha (MZUSP 32097). **Paraguay**—Amambay, 28 km SW

TABLE 3
Measurements (mm) and Weights (g) of Adult Specimens of *Thylamys pusillus*

	Neotype ^b	Sample statistics ^a	
		Females ^c	Males ^d
HBL	101	99 ± 11 (85–117) 14	101 ± 10 (81–114) 16
LT	104	114 ± 12 (92–131) 14	117 ± 9 (104–134) 16
HF	13	14 ± 2 (11–19) 15	14 ± 1 (12–16) 16
Ear	20	21 ± 2 (18–24) 15	21 ± 2 (18–25) 16
CBL	26.1	26.5 ± 1.2 (24.4–28.9) 15	26.6 ± 1.0 (25.4–28.5) 18
NB	2.2	2.4 ± 0.3 (2.0–3.1) 15	2.3 ± 0.3 (1.6–2.7) 18
LIB	3.8	4.1 ± 0.2 (3.6–4.5) 15	4.0 ± 0.2 (3.7–4.2) 18
ZB	14.8	15.2 ± 0.9 (14.1–16.7) 14	15.0 ± 0.6 (13.9–16.1) 18
PL	14.0	14.2 ± 0.6 (13.4–15.4) 15	14.3 ± 0.5 (13.6–15.3) 18
PB	8.0	8.6 ± 0.3 (7.9–9.1) 15	8.5 ± 0.3 (8.0–9.1) 18
MTR	10.2	10.2 ± 0.4 (9.6–10.9) 15	10.3 ± 0.3 (10.0–11.2) 18
LM	5.2	5.4 ± 0.2 (5.0–5.6) 15	5.4 ± 0.2 (5.2–5.8) 18
M1–3	4.5	4.6 ± 0.2 (4.3–4.9) 15	4.6 ± 0.2 (4.4–5.1) 18
Weight	20	21 ± 6 (14–31) 15	22 ± 5 (11–31) 16

^a Tabulated statistics include the sample mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size.

^b MVZ 144311, male.

^c AMNH 260025, 275442; FMNH 164086, 164097; MSB 67016, 87105; TK 63360, 65215, 65458, 65463, 65592, 65601, 66463, 66468; UMMZ 176357.

^d AMNH 246444, 246446, 275440, 275445, 275446; FMNH 164088, 164096; MVZ 144311, 144312; TK 60217, 60227, 63367, 65612, 66469, 66476; TWN 240, 275; UMMZ 124676.

Pedro Juan Caballero (UMMZ 125243, 125259, 125260); *Central*, Asunción (BMNH 99.11.17.1); *Concepción*, 7 km NE Concepción (MSB 70700); *Paraguarí*, Sapucay (BMNH 3.4.7.21).

Thylamys pusillus (Desmarest, 1804)

NEOTYPE: Skin and skull of an adult male in the Museum of Vertebrate Zoology at the University of California Berkeley (MVZ 144311) collected by Philip Myers (original number PM 800) on 7 April 1973.

TYPE LOCALITY: On the Trans-Chaco highway 460 km NW of Villa Hayes, in Departamento Boquerón, Paraguay. The neotype was trapped on the ground in dense, thorny vegetation that included quebracho (*Schinopsis* sp. and/or *Aspidosperma quebracho-blanco*), palo santo (*Bulnesia sarmientoi*), palo borracho (*Chorisia insignis*), and several species of cacti; however, a small, apparently natural grassy opening was also adjacent to the trap site.

DISTRIBUTION: Specimens that we examined document the presence of *Thylamys pusillus* only in the Chaco Boreal of western

Paraguay and southeastern Bolivia. With exceptions as noted below, specimens previously reported in the literature as *T. pusillus* that we examined from other regions proved to be misidentified. Records of *T. pusillus* from the Bolivian highlands (e.g., most of the material that Anderson [1997] listed from Chuquisaca), for example, are based on *T. venustus*, whereas Brazilian records (e.g., those mapped by Brown [2004] are based on *T. karimii*, and Patagonian records (e.g., those reported by Birney et al., 1996) are based on *T. pallidior*. Although *T. pusillus* might occur in the Chaco Austral of northern Argentina (Flores et al., 2000, 2007), the specimens that we examined from that region differ morphologically from Paraguayan and Bolivian material and might represent yet another species (see below).

Thylamys pusillus is found in xerophytic woodlands that are dominated by low (usually <15 m), thorny, deciduous trees including quebracho, palo santo, palo borracho, and labón (*Tabebuia nodosa*). The understory typically includes algarrobo (*Prosopis* spp.), *Maytenus* spp., *Mimosa* spp.,

Ephedra spp., and several species of cacti. Dense patches of spiny bromeliads (caraguatá: *Bromelia hieronymi*, *B. serra*) provide groundcover that is nearly impenetrable to mammalian or avian predators. Short (1975: 173) referred to these forests as “dry (Algarrobo-Quebracho-Palo Santo) woodlands” and provided a detailed description and photographs of this uniquely Chacoan habitat.

EMENDED DIAGNOSIS: *Thylamys pusillus* exhibits a distinctive range of morphometric variation (table 3) and differs from other congeneric species in many qualitative traits. The tail, consistently longer than the combined length of the head and body (by about 14–16%), is distinctly incrassate, sharply bicolored (dark above, whitish below), and the ventral surface is modified for prehension distally (with a naked median groove and a fleshy apical pad bearing dermatoglyphs). The body pelage is distinctly tricolored (sensu Tate [1933: 209]), with a dark grayish or brownish-gray middorsal region, paler flanks, and sharply defined ventral counter-shading. The dorsal fur is short (usually 7–8 mm long middorsally), and the ventral fur is entirely self-white or -cream (not gray based) from chin to anus. The manual claws are short (not, or only slightly extending beyond the fleshy apical pad of each digit), and the ventral surface of the manus has six separate dermatoglyph-bearing plantar pads encircling a concave, densely tubercular central palmar region. The zygomatic arches are wide relative to cranial length (the average ratio of zygomatic breadth to condylobasal length \times 100 is about 55%–56%); distinct maxillary palatal vacuities are almost always present; the posterolateral palatal foramina are very long (extending well anterior to the protocone of M4 on each side); the auditory bullae are relatively small by comparison with those of other species; and styC is usually present on M1 and M2, but it is usually absent from M3.

COMPARISONS: Diagnostic comparisons of *Thylamys pusillus* with *T. macrurus* have already been discussed. The Brazilian species *T. karimii* (synonymized with *T. pusillus* by Gardner, 1993) is craniodentally similar but differs from *T. pusillus* by having longer claws that extend well beyond the fleshy apical pads

of the manual digits; manual plantar pads that are fused together, lack dermatoglyphs, and do not surround a central palmar concavity; a tail that is substantially shorter than the combined length of head and body; no prehensile modifications on the underside of the tail tip; and indistinctly tricolored body pelage (see illustrations in Carmignotto and Monfort, 2006). Geographically, *T. karimii* is endemic to the Cerrado and Caatinga biomes north and east of the Chacoan region inhabited by *T. pusillus*.

Thylamys pallidior (treated as a subspecies of *T. pusillus* by Cabrera, 1958) differs externally from *T. pusillus* by its much longer fur (usually >10 mm middorsally) and longer manual claws (which always extend beyond the fleshy apical pad of each digit). Cranially, *T. pallidior* differs from *T. pusillus* by its longer and more slender rostrum, narrower zygomatic arches, much larger bullae, and by the consistent absence of maxillary fenestrae (fig. 5). A diagnostic dental difference consists in the absence of styler cusp C from M1–M3 in *T. pallidior*, whereas styC is consistently present on M1 and M2 in *T. pusillus*. Based on material that we examined, *Thylamys pallidior* (which may represent a complex of two or more morphologically similar species; Braun et al., 2005) occurs from south-central Peru (on the west side of the Andes; Solari, 2003) across the Bolivian highlands into northwestern and Patagonian Argentina; apparently, it occupies a wide range of arid habitats including Puna grasslands, Monte desert, and Patagonian steppe (Flores et al., 2000, 2007).

REMARKS: The only subjective junior synonym of *Thylamys pusillus* that we can confidently recognize as such is *Marmosa verax* Thomas (1921), the holotype of which (BMNH 20.12.18.34) is a very old adult female with stained (yellowish) ventral fur from “Mision, west of Concepcion,” a locality said to be in the Paraguayan Chaco (Thomas, 1921: 521), but one that we have been unable to associate with definite geographic coordinates.⁹ Apart from its advanced age (and correspondingly large mea-

⁹ A plausible candidate, however, is Misión Central (23°27'S, 58°20'W; DMA, 1992), about 90 km due west of Concepción in Presidente Hayes department.

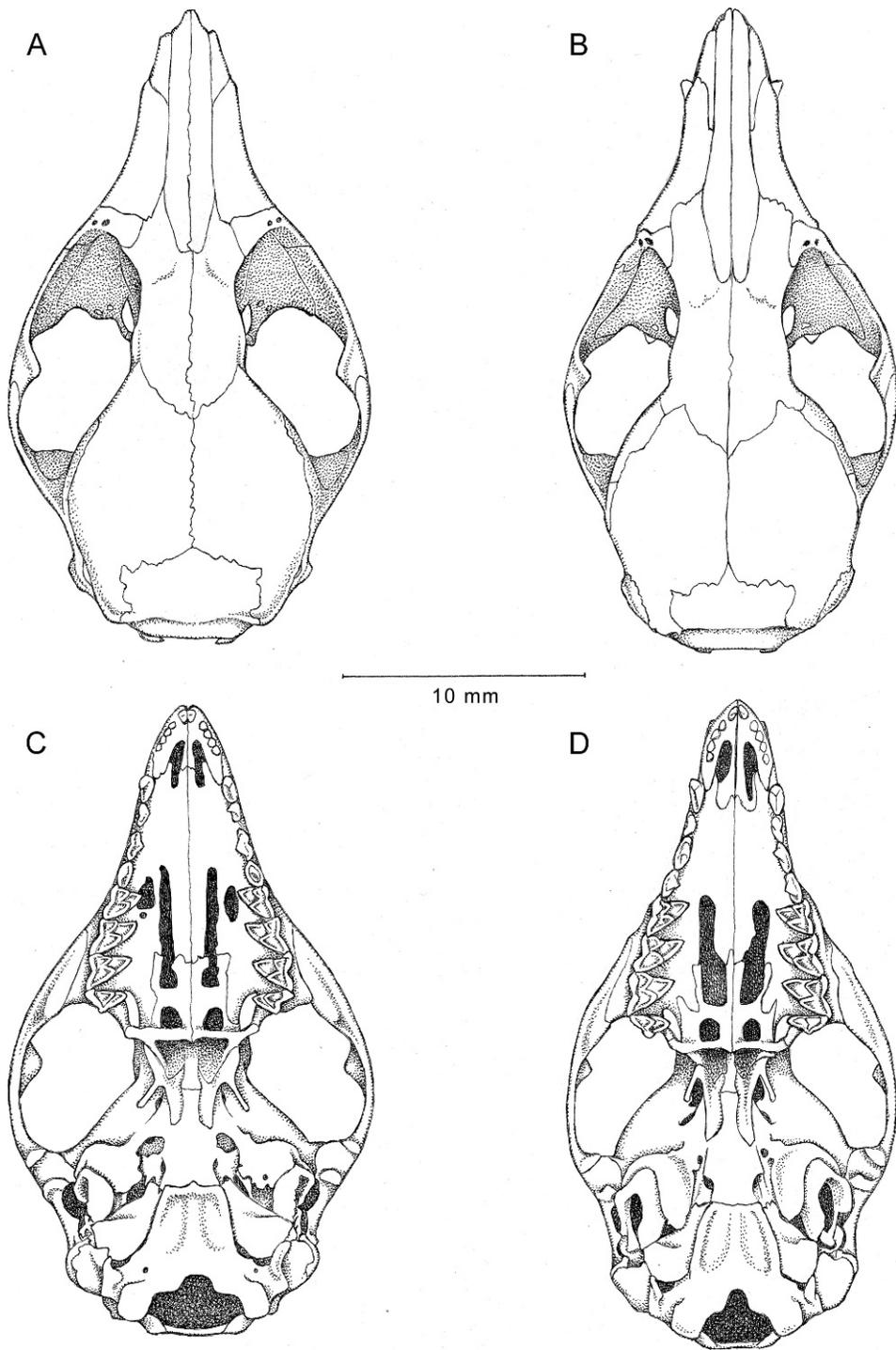


Fig. 5. Dorsal and ventral cranial views of *Thylamys pusillus* (A, C; AMNH 275445) and *T. pallidior* (B, D; AMNH 262408) illustrating diagnostic qualitative cranial characters mentioned in the text.

surements; e.g., CBL = 29.8 mm), this specimen does not differ in any respect from other material that we refer to *T. pusillus*.

Marmosa citella Thomas (1912) has been considered a junior synonym of *Thylamys pusillus* by most authors (e.g., Tate, 1933; Cabrera, 1958; Creighton and Gardner, 2008), and this opinion may be correct. However, our cursory examination of the holotype (BMNH 98.8.19.9) during a brief visit to London that was primarily devoted to another project did not allow us to come to a definite conclusion, nor do our notes contain information about several key characters (such as the presence or absence of styC on the upper molars). The chief difficulty in admitting this synonymy is that the type locality of *citella* (Goya, at 29°08'S, 59°16'W; Paynter, 1995) in the Argentine province of Corrientes is so distant from any others from which we have seen similar material.

Although specimens resembling *Thylamys pusillus* have been taken across much of northern Argentina (in the provinces of Chaco, Entre Ríos, Formosa, Santiago del Estero, Salta, and Tucumán; Flores et al., 2000, 2007), most of the *pusillus*-like Argentinian material that we examined is substantially smaller (e.g., with LM < 5 mm) than the western Paraguayan and southeastern Bolivian specimens that we consider to represent typical *pusillus*. In addition, styC is more consistently distinct on M3 in *pusillus*-like Argentinian specimens than it is in Paraguayan and Bolivian material. Among the small, *pusillus*-like Argentinian specimens we examined is BMNH 21.4.21.8, the subadult male holotype of *Marmosa bruchi*, which Thomas (1921) described from Alto Pencoso (33°26'S, 66°56'W; Paynter, 1995) in western San Luis province. Although *bruchi* is currently considered a synonym of *T. pallidior* (e.g., by Gardner, 2005; Creighton and Gardner, 2008), its short fur, distinct maxillary vacuities, and well-developed styC on M1 and M2 better match the diagnostic traits of *T. pusillus* as recognized here. The name *pulchellus* Cabrera (1934a) may be a junior synonym of *bruchi* (as suggested by Cabrera, 1958), but we have not seen the holotype.

Interestingly, Braun et al. (2005) found that cytochrome-*b* sequences from Argenti-

nian specimens of "*pusillus*" were about 3% divergent from a single Paraguayan sequence in their phylogenetic analysis of the genus *Thylamys*. We examined their voucher material and found that the Paraguayan specimen (with field number TK 66469) is a typical example of *pusillus*, whereas their *pusillus*-like Argentinian material (e.g., AK14628 [= OMNH 23483] and OMNH 23479) more closely resembles *bruchi* in size and dental morphology. Although we are encouraged to think that *bruchi* may be a valid species of *Thylamys*, closely related to but phenotypically and genetically distinct from *T. pusillus*, it remains for future researchers to determine whether there is a gradual or abrupt morphological transition from the small Argentinian phenotype to the larger Paraguayan-Bolivian phenotype, and to discover whether specimens sorted by size form reciprocally monophyletic haplotype groups.

SPECIMENS EXAMINED: **Bolivia**—*Chuquisaca*, 3.8 km by road E Carandayti (AMNH 261268); *Santa Cruz*, 53 km E of Boyuibe (AMNH 275441; MSB 87105), Tita (AMNH 260025); *Tarija*, Estancia Bolívar (AMNH 275440, 275442, 275445, 275446; MSB 67016), 8 km S [and] 10 km E Villa Montes (AMNH 246442–246444, 246446–246449, 246452). **Paraguay**—*Alto Paraguay*, Destacamento Militar Gabino Mendoza (TTU-TK 65601, 65632, 65635), Fortín Pikyrenda (TTU-TK 65592, 65612), Palmar de las Islas (TTU-TK 65458, 65463); *Boquerón*, Estancia "El 43" (TTU-TK 60217, 60227), Estancia Toledo (FMNH 164097), Experimental Farm (FMNH 164095, 164096), Guachalla (FMNH 54369), Orloff (FMNH 63862), Parque Cué (TTU-TK 63360, 63367), Parque Nacional Teniente Agripino Enciso (TTU-TK 65031, 65104, 65215, 66463, 66468, 66469, 66476), Schmidt Ranch (FMNH 164086), 410 km NW Villa Hayes (MVZ 144312, 144313), 460 km NW Villa Hayes (MVZ 144311); *Chaco*, 50 km WNW Fortín Madrejon (UMMZ 124676); *Nueva Asunción*, 1 km SW km 620 [of] Trans-Chaco Road (UMMZ 176357); 19 km by road WSW km 588 [of] Trans-Chaco Road (UMMZ 176358, TWN 240, 275, 390). *Presidente Hayes*, 295 km NW Villa Hayes (MVZ 144310).

DISCUSSION

There are many reasons why the systematics of South American mammals are still so poorly understood. Among others, the continental fauna remains incompletely inventoried; the geographic, morphological, and genetic limits of numerous species are still undocumented; and the taxonomic application of many old names is a persistent source of confusion. In the absence of surviving original material (holotypes, syntypes, etc.), the last problem has often been addressed by restricting the type locality (as by Thomas, 1911; Cabrera, 1958) and examining "topotypes," but neither of these conventions, however useful they might be in practice, have any binding nomenclatural significance under the International Code of Zoological Nomenclature (ICZN, 1999). A better option, when it is necessary to fix the application of names, and when the consequences of failing to do so are dire, is the designation of neotypes. Like sharp-edged tools, however, neotypes are potent instruments that should be used with care.

This report on Azara's opossums was prompted by ongoing revisionary research with South American didelphids, the nomenclature of which is not uniquely problematic. Indeed, other groups of mammals described by Azara also merit critical review and remedial action as necessary to stabilize taxonomic usage. Although some problems associated with Azara's rats have now been resolved (Tate, 1932; Myers and Carleton, 1981; Musser et al., 1998), others persist. For example, the ambiguous application of *Oxymycterus rufus* Fischer, 1814, is unlikely ever to be resolved without a neotype (Hershkovitz, 1994; Oliveira, 1998; Musser and Carleton, 2005; Gonçalves and Oliveira, 2004). Other groups have received little critical attention.

The only general introduction to Azara's mammals (Hershkovitz, 1987) was written more than 20 years ago and contains noteworthy errors that should be corrected in any future taxonomic assessment of this author. Inter alia, the basis for *Coendou insidiosus* (Olfers, 1818) was not Azara's (1801) description of "Le Couiy" but an examined specimen in the Berlin Zoological Museum (Voss and Angermann, 1997). Also,

the basis for some of the Paraguayan bats described by Geoffroy (1810), including *Platyrrhinus lineatus* and *Sturnira lilium*, is controversial: whereas Hershkovitz (1987) claimed that these binomens were based on Azara's (1801) text, other authors (e.g., Rode, 1941; Carter and Dolan, 1978; Sánchez-Hernández and Romero-Almaraz, 2003; Velasco, 2005) have alleged that type material (not collected by Azara according to Cabrera, 1958) is present in the Muséum National d'Histoire Naturelle (Paris). In effect, more bibliographic and specimen-based research is needed before Azara's mammalogical legacy can be accurately evaluated.

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APPENDIX 1

TRANSLATED DESCRIPTIONS FROM
THE *APUNTAMIENTOS*

These are free English renderings of Azara's (1802, vol. 1: 209–263) opossum accounts. In preparing these translations, we often inserted verbs and other parts of speech omitted in his semitelegraphic Spanish descriptions, as otherwise the style would appear too eccentric for easy comprehension. Such minor insertions are not indicated as such below, but substantive editorial comments are enclosed in square brackets. Where the exact translation of certain words seemed uncertain, the original Spanish is quoted parenthetically. Because biological nomenclature should not require Talmudic parsing of ancient texts, we did not try to eliminate or explain all of the ambiguities inherent in these agreeably nontechnical accounts, which are chiefly of historical rather than scientific interest.

We omitted some anecdotal material (indicated by ellipses) that has no obvious relevance for the identification of the species in question. Likewise, we do not include Azara's lengthy discussions of American marsupials previously described by Buffon, Daubenton, and other contemporaneous naturalists. However, we retained all details, no matter how trivial, that concern the morphology, species-specific behavior, or geographical origin of Azara's own material. In combination with the main facts of each account, these minor details are sometimes telling.

Azara used morphometric data to supplement his qualitative descriptions, but he only explained how a few of his standard measurements were taken. Total length ("longitud") was measured with a cord passed along the dorsal midline from the tip of the snout to the tip of the tail; anterior height ("altura delante") was measured from the withers to the tip of the longest claw of the manus; posterior height ("altura detras") was measured from the highest point on the hip to the tip of the longest claw of the pes; anterior circumference ("circunferencia delante") was measured around the chest where it joins the forelimbs; and posterior circumference ("circunferencia detras") was measured around the flanks. Unhelpfully, Azara said that he measured the tail in the same way that he measured total length, leaving the interpretation of this important dimension somewhat ambiguous for lack of a definite anterior endpoint.

Because Azara's qualitative descriptions are limited to behavioral and external-morphological traits, his measurements of the upper jaw ("mandibula superior") are puzzling anomalies. On the assumption that this dimension was not obtained from osteological preparations, we tried to replicate his reported values using externally visible features of museum specimens in various ways. The best matches we obtained suggest that he measured the upper jaw across the bases of the left and right canine teeth. On the same assumption, his measurements of the canine were probably made from the gumline (not the bony alveolar margin) to the apex of the tooth.

Azara's basic measurement units were "pulgadas del pie de rey de Paris," or inches (twelfths) of the old French foot (*pie du roi*). In addition, he measured small structures in "lineas," which correspond to the *lignes* of French watchmakers. According to Darton and Clark (1994) the metric equivalents of these obsolete units are 1 *pulgada* = 27.073 mm and 1 *linea* = 2.256 mm; therefore, we used these conversion factors to compute the values provided in square brackets throughout the following accounts.

Of the Micuré

The Guaranis give it this name, whose last syllable means "stinking," and the Spaniards call it *comadreja*. It is not uncommon in Paraguay, nor in Buenos Aires, and it hides itself in tall grass and in holes in the ground made by itself or by other animals; but it also inhabits the forests and the edges of woods and climbs trees to eat fruit. One captive adult individual permitted its owner, but no other person, to handle it for eight days without showing gratitude; and although it did not want to eat meat, because it was given oranges and beef blood: I have seen that other individuals eat only meat. Invariably this animal urinates and defecates when it is annoyed, dispersing a very bad smell that can be irritating, although it dissipates in a few hours with ventilation and is not sufficient to prevent the animal from being killed and eaten by my wild cats.

Along the abdomen of the female there is a slit or opening like that which results when a fat man unfastens some buttons of his waistcoat ("chupa"). Inside, along the borders or folds, there is a cavity that increases in size to the rear; such that at the front it is nothing, and in the rear where the cavities of the sides are united, it is already a capacious pouch, which extends internally to the pubis. In the interior of the cavity, which opens and shuts at will by parting or uniting the lips of the slit, one finds 13 teats, one in the middle and the rest on the periphery of an ellipse. One adult female had only 11 teats, and another, which was not quite adult with the pouch and its lips not very perceptible, also had 11 teats; from which I infer that the number of them varies from 11 to 13, and that the females do not have a perceptible pouch until they need it, as one notices from the cubs. . . .

Although some adults do not exceed 26¼ inches [711 mm], I will describe the largest I have seen. Total length 30 inches [812 mm]; tail 13½ inches [356 mm], of which 4¼ inches [115 mm] are furred, the rest to the tip with only extremely sparse hairs that scarcely emerge from the scales. The tail is round [in cross section], except the prehensile part, where there is some flattening on the underside. Its circumference at the base is 2⅝ inches [77 mm]; the circumference of the body where the forelimbs join the trunk is 9½ inches [257 mm], and the circumference around the flanks is 9¾ inches [264 mm]. The height in front is 8⅞ inches [221 mm], and the height behind is 8½ inches [230 mm]. The greatest width of the head is 2¼ inches [61 mm], the length of the head is 4½ inches [122 mm], and from the front of the ear to the tip of

the snout is $3\frac{1}{2}$ inches [95 mm]. The upper jaw exceeds 7 lines [16 mm]; and the biggest whiskers, laid back toward the ear, almost touch it, and others go upward. Behind the angle of the mouth there are seven long hairs or whiskers [the genal vibrissae], the lower ones white and the rest black. The ear is two inches [54 mm] in height, $1\frac{3}{4}$ inches [47 mm] in breadth, elliptical, very thin, dark at the base, the rest white, and more drooping ("mas caida") than in the other species. The canine teeth are 6 lines [14 mm], and the nostrils are separated from each other by a white groove. The middle and longest finger of the hand is 9 lines [20 mm]. The scrotum is dark, with short straw-colored fuzz. The testicles are 11 lines [25 mm] long, 7 lines [16 mm] in thickness in front, less behind, have a stem, and are separated in life 7 lines [16 mm] from the body by the skin that encloses the ligaments and begins in the orifice [cloaca]. The dead and pulled-out penis [i.e., drawn from the cloaca of a dead animal] extends 20 lines [45 mm] from the anus, half of which is cylindrical and the rest divided to the tip into two little members each of which is $2\frac{1}{2}$ lines [6 mm] in diameter, being cylindrical for two-thirds of their length and then tapering to a point. The female has the two passages [urogenital and rectal ducts] in one orifice.

A dark marking begins behind the eye and narrowly surrounding it continues to the whiskers. Another somewhat blacker marking begins on the center of the snout in front of the tear duct [anterior canthus of the eye] and extends upward to between the ears, where it greatly expands and continues to the nape. The arms and legs are black, and the fur below the radius and on the metatarsus and face is very short. All the rest of the coat has two kinds of hairs: the shorter kind is abundant, dense, and soft yellowish white, with the points black on all of the dorsum and flanks, and between the arms, although one notices the black more along the face, flanks, and tail. The other type of hair is two inches [54 mm] long, whitish, thick, sparse, erect, and emerges notably above the other, more on the back and toward the tail and flanks. Both kinds of hairs are intermingled, soft, lax, not stiff, and whatever pressure or breeze has a paintbrush-like effect on them ("los apincela"); that is, they are so accumulated that joining together many black tips, form something like patches, leaving whitish holes [i.e., the cumulative effect is that bunching together the blackish tips of the overfur exposes the whitish underfur]. The [proximal] three inches of naked tail are blackish, and the rest to the tip yellowish white. An albino or entirely white individual was caught in Misiones.

Of the Lanoso

I have not seen any but the present male, which was given me in Paraguay by Don García Francia, assuring me, as others have, that the female has a pouch similar to that of the Micuré, where it puts the young. It was given to me dead, and to this I attribute the fact that it did not smell bad. I described it when I did not have the knowledge that I do today; and

putting it in alcohol, I sent it to the Royal Cabinet of Madrid.

Total length $22\frac{1}{2}$ inches [600 mm]; tail $13\frac{1}{2}$ inches [365 mm], of which the terminal part is hairless for $4\frac{1}{2}$ inches [122 mm] dorsally and 9 inches [244 mm] ventrally. Its circumference at the base is 19 lines [43 mm]; and it is not conical or round [in cross-section], but prismatically triangular with the angles very beveled, and a sort of canal follows the ventral midline. The circumference of the body is 5 inches [135 mm]. Head length $2\frac{1}{4}$ inches [61 mm], width $1\frac{1}{2}$ inches [41 mm] between the ears, and decreasing to the point of the snout, which has a groove that separates the nostrils. The whiskers are black and very long. There are also some [the genal vibrissae] behind and below the eye, whose iris is the color of vicugna wool. Equally there are some blond hairs behind the eye, and white ones in the canal of the lower jaw [the interramal vibrissae]. The ear is 12 lines [27 mm] high, 6 lines [14 mm] in width, elliptical, somewhat drooping ("caida"), hairless inside and half hairless on the outside, very thin, purple, and near the anterior base there is a point that projects from the border. The upper jaw exceeds 4 lines [9 mm]; it has 10 incisors: the middle ones, which are somewhat longer and stouter, form a spandrel at the point [i.e., they converge at their tips, creating an open triangular space between them]. Below there are eight incisors, which leave a gap in the middle that is filled by the two long upper ones; where furthermore one sees two canine teeth separated by a gap on each side, the exterior and largest of which is 4 lines [9 mm]. The lower canines and molars in total are 16 [i.e., there are 16 lower teeth counting those on both sides, in addition to the eight lower incisors]. The scrotum, which lacks fur and is pale blue, hangs down 10 lines [23 mm]. The testicles are 6 lines [14 mm] in diameter with a nipple ("pezon" [presumably the epididymis]) on the underside, and they are excessively compressed ("demasiado oprimidos" [?]).

Arising from the snout is a dark streak one line [2 mm] wide, that continues until it ends on the nape. The outline of the eye [i.e., the circumocular mask] is bright reddish brown; and between it and the aforementioned streak there is light grayish brown. The occiput, the fronts and sides of the arms, the front of the legs, and the tarsus, are reddish-tobacco colored. The midback ("espinazo") is the same, although more opaque; and the rest of the body is pale grayish brown, much paler ventrally, and between the fore- and hind limbs. The fur of the face is very short: that of the back, tail, and the posterior part of the legs is one inch [27 mm] long, and over the rest of the body not so long; but all very dense, woolly, soft, and excellent for lining clothes. The naked part of the tail is white. My friend Don Pedro Blas Noséda caught another male in the country at about 27° [S latitude], and fed it for some days with watermelon, because it did not want to eat meat.

Of the Coligrueso

Although all of the opossums have very thick tails, that of this one is so thick at the base, that it almost

appears a continuation of the body; and the animal supports itself less with the tail than do the aforementioned species. The ears are smaller, less rounded, and somewhat more upright; and the face is not so flat, nor the snout as long and pointed, nor is there a groove between the nostrils, and the neck is as thick as the head. In a rural house I saw one tied to a bench; and I noted that it had dug a shallow hole in the dirt floor, and that a tame parrot having approached, it killed the bird instantly. It allowed itself to be handled, despite being an adult, and having been captured only a few days before. It was fed with raw meat: I gave it a dead mouse, and it ate the head. It seemed to me as stupid, quiet, and torpid as the Micuré, and I did not notice a bad odor, perhaps because I did not see it irritated. Neither did I note any smell from two other identical males, nor from two females that I had. It lives in Paraguay and Buenos Ayres in the fields, entering houses at times for the same purpose as the Micuré.

Total length 23 inches [623 mm]: tail 11 inches [298 mm], round [in cross section], and its circumference at the base $2\frac{1}{2}$ inches [68 mm]. The anterior circumference of the body $6\frac{2}{3}$ inches [180 mm], and behind $6\frac{1}{4}$ inches [183 mm]. Beneath the eye is a clear cinnamon color, which turning the corner at the angle of the mouth, and occupying all of the underside of the head, continues for all of the underside of the animal. The hands, feet, and face from the eyes forward, are darker; and the rest without exception hardly differs in coloration from the little house mouse, its fur not much longer than that of the rat. Somewhat more than a third of the tail has fur like that of the body; and the rest is hairless with sparse short black hairs that arise from between the scales, also black, except for the terminal $1\frac{1}{2}$ inches [41 mm] that are white. The scrotum is hairy and pendent as in all the opossums.

They sold me a female, saying that it had been seen to kill a viper. Its total length was 20 inches [541 mm]: tail $8\frac{3}{4}$ inches [237 mm] long, two inches [54 mm] around at the base. It only differs from the male in that the clear cinnamon color in that one was in this one white or yellowish white. In place of the pouch of the previously described females, it [the female coligruesa] has between its hind legs two obvious folds, open in an ellipse, that enclosed a very small sinus. Inside the folds were the teats in the periphery of another long concentric ellipse; with the odd feature that there were four teats on the right side, two on the left, and none in the middle. Another young female was the same, except that the folds were hardly perceptible, and I did not count the teats. Those of the first [female] were so noticeable, that it seemed to me they had only recently been suckled; and also I had neglected to observe with greater care, if those that were lacking on the left side and in the center, were simply not suckled [and therefore undeveloped].

In addition to the aforementioned specimens I caught two identical males, a young one of 15 inches [406 mm], and the other of 21 inches [569 mm]. The tail of this one was 10 inches [271 mm]: the circumference around the body where the arms join was $5\frac{1}{2}$ inches [153 mm], and behind a little less. The whiskers

were almost 3 inches [81 mm]: and the difference in the pelage consisted, in that the bright cinnamon-colored area of the first male was in this one bright tobacco red; and the rest of the coat of the same tobacco based on grey-brown. The scrotum hung 9 lines [20 mm], and the canine tooth had 5 lines [11 mm].

Of the Colilargo

I have not seen any [specimen] but the present one, which Don Josef Casal caught in his country house and sent to me, writing that it is called *anguyá-guayquí* in Paraguay; but as no one can make sense of such a name, whose first part means "mouse," and whose second part no one understands, I have judged it more convenient to call it colilargo, because it is [long-tailed].

Total length $8\frac{3}{4}$ inches [237 mm]: tail 5 inches [135 mm], all naked, very soft and shiny ("lustrosa"). The scrotum lacks fur, and does not hang as in the other species, and this circumstance, and the fact that the testicles are very tiny and inactive ["holgados"], leaves me in no doubt that this individual is not an adult. One line's width [ca. 2 mm] around the eye is black and notable [i.e., there is a prominent circumocular mask]. Outside this ring there is another whitish one, and between it and the other eye there is a dark line that terminates at the level of the tear duct ("lagrimal"). Between the ears, all of the dorsum, and the tail, are colored like the house mouse; but the sides of the body are paler, especially the sides of the arms. The lower jaw, the underside of the head, and the anterior of the arms, are almost white, and the rest of the venter is dirty white. All of the pelage is as soft and short as that of the aforementioned house mouse, and perhaps more so.

Of the Colicorto

Thus I call it for the brevity of its tail by comparison with other opossums, and deprecate the name *anguyá* (mouse) which the Guaraní give it. I have only had two males, caught in the countryside below the 27th and 34th parallels [of S latitude]. Another was brought to my friend Noséda, which he put in a cage; and having escaped, it entered the burrows of some common rats; which ganged up to throw it out and persecuted it, compelling it to flee and cry repeatedly *ché ché*. Noséda responded to these cries, and having caught it, he returned it to the cage, where it died in a month. It ate little, and afterward it rubbed its snout very rapidly with its hands. My friend fed it raw meat, and amused himself by showing it to the animal from a distance, because this much annoyed it, leaping and squeaking in order to grab it. One day he gave it a little mouse, and killing it in a moment, it ate the entrails leaving the rest. It drank hastily with its tongue, and after a few days was very tame; but when irritated, it discharged a bad odor, although not strong.

Length $6\frac{3}{4}$ inches [183 mm]: tail $2\frac{1}{4}$ inches [61 mm], very thick and hairless, less than 3 lines

[7 mm, presumably in diameter] at the base. Circumference in front, $3\frac{1}{2}$ inches [95 mm], around the belly 4 inches [108 mm]. The ear 4 lines [9 mm] high, 6 lines [14 mm] wide, hairless, and more erect and smaller than those of other opossums. The body is more flattened, thicker, and stubbier than all the rest of the opossums, and the scrotum hangs much, being dark-skinned with short whitish fuzz. The male that Noséda described was $8\frac{1}{2}$ inches [230 mm] long, and the other measurements in proportion.

All of the pelage is short and soft like that of the mouse. Under the eye and a very little bit above it, all of the side of the head and of the body to the tail is bright cinnamon; and the underside is somewhat lighter. Over the snout it is grizzled brown ("pardo"), and all the rest of the animal is frosted grayish brown ("pardo aplomado"), or rather a mixture, because some hairs have whitish points, which one sees among the others.

Besides the observations cited above that I made of captive animals, Noséda wrote me as follows. "On the 13th of December I was brought a female with 14 cubs, dead or moribund, of hurts given them upon capture and afterward. Nevertheless, placing them near the teats, the two hardest pups took the teats; but the mother starting to run about, they could not continue [suckling] from their weakness, dying on the third day. There were something like eight that had been born, according to those who chased the mother [another female?] at that time without being able to catch her; and they said, that the young dragged on the ground as the mother ran without loosening their hold on the teats. When I saw them they were naked, blind, and $1\frac{1}{2}$ inches long, without the tail of 4 lines [9 mm]. They were found with the mother in a swampy patch of tall grass ("pajonal del campo"); and having hidden in a hole in the ground, it was flooded with water, making her leave and run with the young dragging along, as they were when they went in the hole, because she never left them behind. She did not have a pouch; but one could see between the hind legs a swollen udder, that encroached a little toward the belly; and in this were 14 teats, so small that one could hardly count them. The milk dried up several days after the death of the young, at which time it was necessary to use a magnifying glass to see the teats. I did not notice a bad smell as I did in the male. Her length was $6\frac{4}{5}$ inches [184 mm]: the tail 2 inches [54 mm]. The bright cinnamon color of the male was only seen on the sides of the head and of the neck, because the sides of the body were made grizzled brown ("pardeaba") by being blended with the grayish color of the back. The underparts were a lighter cinnamon ("bayas acaneladas") or whitish cinnamon ("acaneladas blanquizcas")."

Of the Enano

I don't know another name that suits it better, nor have I had but two identical males, which were sold to me on different days in October by Indians of San Ignacio Güazú, saying that they had caught them in their huts.

Length 7 inches [190 mm]; tail 3 b inches [99 mm], all naked, and somewhat more slender in proportion to that of the Colilargo. The ear is quite upright and rounded, 6 lines [14 mm] high and 4 lines [9 mm] wide. The whiskers are much finer than those of the common little mouse, and the testicles pendant and a little loose in the scrotum. Together they are 5 lines [11 mm] in diameter; which makes me believe that the individuals are adults. I did not notice a bad odor.

The fur is short and soft like that of the aforementioned mouse. The narrow outline of the eye is of a blackness that extends to the tear duct ("lagrimal"), and the eyebrow above this color is faintly whitish, there being between it and the other a dark triangle that is scarcely noticeable. Between the ears, over the whole dorsal surface of the animal, the flanks, and on the outside of the four legs, are somewhat darker gray than the aforementioned little mouse, which is present [which was compared with it at the same time?]. Under the eye on the upper jaw there is a patch of yellowish white; and under the head, all the ventrum, and the insides of the legs, is a whitish more clear than that of the aforementioned mouse. The tail is somewhat lighter [in color] than the body; and the scrotum is dark with short white fuzz.

APPENDIX 2

Gazetteer

Below are listed all of the localities from which we examined specimens of *Thylamys macrurus* and *T. pusillus* in the course of this study. Italicized place names are those of the largest political divisions (state/department/province) within countries; boldface identifies collection localities as they appear in the text of this report. Unless recorded by the collector, geographic coordinates and elevation above sea level (in meters, m) are provided in square brackets with a cited secondary source for these data. Numbered localities are plotted on the accompanying map (fig. 3).

BOLIVIA

1. **Chuquisaca, 3.8 km by road E Carandayti** (20°46'S, 63°03'W, 480 m): *Thylamys pusillus* (coll. B.R. Riddle, 10 July 1985).
2. **Santa Cruz, 53 km E of Boyuibe** (20°27'S, 62°50'W, 600 m): *Thylamys pusillus* (coll. S. Anderson and M.L. Campbell, 6–8 July 1991).
3. **Santa Cruz, Tita** (18°25'S, 62°10'W, 300 m): *Thylamys pusillus* (coll. J.A. Cook, 19 October 1984).
4. **Tarija, Estancia Bolívar** (21°38'S, 62°34'W, 400 m): *Thylamys pusillus* (coll. S. Anderson, F. Guerra, and R. de Urioste, 18–20 August 1991).
5. **Tarija, 8 km S [and] 10 km E Villa Montes** ([21°19'S, 63°25'W; Anderson, 1997], 467 m), E bank R. Pilcomayo: *Thylamys pusillus* (coll. G. Schmitt, 30 April–7 May 1979).

BRAZIL

6. *Mato Grosso do Sul, Campo Grande* [20°27'S, 54°37'W, 543 m; Carmignotto and Monfort, 2006]: *Thylamys macrurus* (coll. J.L. Lima, 13 June 1930).
7. *Mato Grosso do Sul, Fazenda Califórnia* [20°41'S, 56°52'W, 650 m; Carmignotto and Monfort, 2006]: *Thylamys macrurus* (coll. A.P. Carmignotto, 14–15 April 2002).
8. *Mato Grosso do Sul, Fazenda Santa Terezinha* [20°50'S, 56°37'W, 615 m at Bonito; Carmignotto and Monfort, 2006]: *Thylamys macrurus* (coll. N.C. Cáceres, 26 June 2002).

PARAGUAY

9. *Alto Paraguay, Destacamento Militar Gabino Mendoza* (20°03'S, 61°51'W, 420 m): *Thylamys pusillus* (coll. F. Pintos, 21 May 1997).
10. *Alto Paraguay, Fortín Pikyrenda* (20°05'S, 61°47'W, 420 m): *Thylamys pusillus* (coll. F. Pintos, 21–22 May 1997).
11. *Alto Paraguay, Palmar de las Islas* (19°37'S, 60°31'W, 150 m): *Thylamys pusillus* (coll. S.J. Presley, 9 May 1997).
12. *Amambay, 28 km SW Pedro Juan Caballero* [22°38'S, 55°57'W, no elevation; DMA1992]: *Thylamys macrurus* (coll. T.W. Nelson, 1–11 December 1976, 9 February 1977).
13. *Boquerón, Estancia "El 43"* (21°56'S, 60°15'W, 80 m): *Thylamys pusillus* (coll. F. Pintos, 18 August 1995).
14. *Boquerón, Estancia Toledo*, 35 km W Filadelfia [ca. 22°21'S, 60°23'W; estimated from map]: *Thylamys pusillus* (coll. C.J. Yahnke, 14 March 1997).
15. *Boquerón, Experimental Farm*, 11 km W Filadelfia [ca. 22°21'S, 60°09'W; estimated from map]: *Thylamys pusillus* (coll. C.J. Yahnke, 17 June 1997).
16. *Boquerón, Guachalla* [= Fortín Guachalla at 22°27'S, 62°20'W, ca. 250 m; Paynter, 1989]: *Thylamys pusillus* (coll. P. Willim, 14 August 1945).
17. *Boquerón, Orloff* [= Colonia Mennonita at 22°30'S, 60°00'W, ca. 175 m; Paynter, 1989]: *Thylamys pusillus* (coll. J. Unger, 17 January 1946).
- 18a. *Boquerón, Parque Nacional Teniente Agripino Enciso* (21°09'S, 61°32'W, 250 m): *Thylamys pusillus* (coll. S.J. Presley, 23 March 1997).
- 18b. *Boquerón, Parque Nacional Teniente Agripino Enciso*, near Puesto Siracua (from 21°03'S, 61°45'W to 21°02'S, 61°46'W, 255 m): *T. pusillus* (coll. C.W. Dick, G. González, and I. Mora, 25–27 September 1998).
19. "Boquerón," *Parque Cué* (20°08'S, 61°48'W, 390 m): *Thylamys pusillus* (coll. S.J. Presley, 8 September 1996). This locality is actually in the department of Alto Paraguay.
20. *Boquerón, Schmidt Ranch*, 10 km E Corrales [ca. 22°25'S, 60°27'W; estimated from map]: *Thylamys pusillus* (coll. C.J. Yahnke, 10 May 1997).
21. *Boquerón, 410 km NW Villa Hayes* [ca. 22°34'S, 59°48'W]: *Thylamys pusillus* (coll. P. Myers, 24 September 1973).
22. *Boquerón, 460 km NW Villa Hayes* [ca. 22°22'S, 60°12'W]: *Thylamys pusillus* (coll. P. Myers, 7 April 1973).
23. *Central, Asunción* [25°16'S, 57°40'W, 77 m; Paynter, 1989]: *Thylamys macrurus* (N.L. Holden, probably ca. 1899).
24. "Chaco," *50 km WNW Fortín Madrejon* [20°26'S, 60°19'W]: *Thylamys pusillus* (coll. P. Myers, 7 August 1976). This locality is now in the department of Alto Paraguay.
25. *Concepción, 7 km NE Concepción*, Escuela Agropecuaria (23°21'S, 57°23'W, no elevation): *Thylamys macrurus* (coll. E. Palma, 25 November 1992).
26. "Nueva Asunción," *1 km SW Km 620 Trans-Chaco Road* [21°22'S, 61°31'W; estimated from map]: *Thylamys pusillus* (coll. T.W. Nelson, 17 February 1978). This locality is now in the department of Boquerón.
27. "Nueva Asunción," *19 km by road WSW Km 588 Trans-Chaco Road* [21°36'S, 61°26'W; estimated from map]: *Thylamys pusillus* (coll. T.W. Nelson, 27 May–8 June 1978). This locality is now in the department of Boquerón.
28. *Paraguari, Sapucay* [= Sapucaí at 25°41'S, 56°57'W, ca. 220 m; Paynter, 1989]: *Thylamys macrurus* (coll. W. Foster, ca. 1903).
29. *Presidente Hayes, Estación Experimental Chaco Central*, 2 km W Cruce Pioneros [23°14'S, 59°11'W; estimated from map]: *Thylamys pusillus* (coll. C.J. Yahnke, 23 August 1997).
30. *Presidente Hayes, 295 km NW Villa Hayes* [ca. 23°14'S, 59°11'W; estimated from map]: *Thylamys pusillus* (coll. P. Myers, 24 June 1972).