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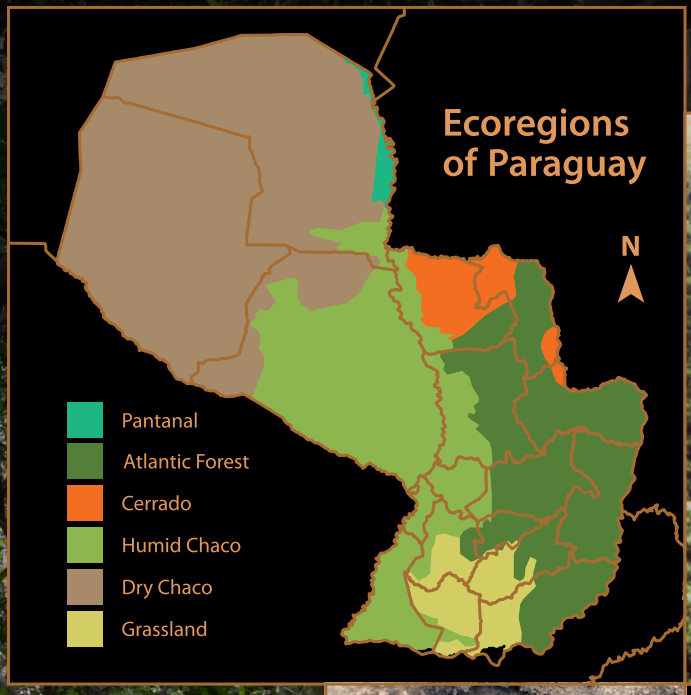
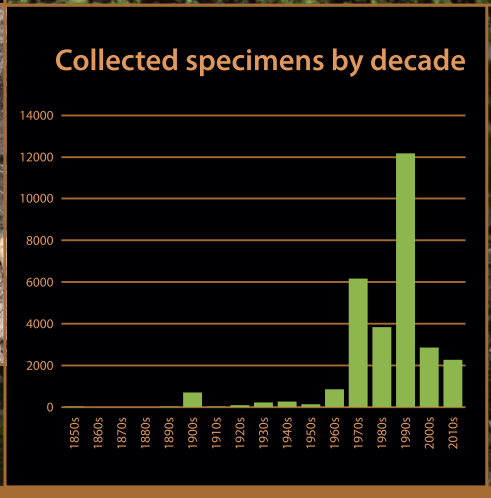
Volume 1

Paraguayan Mammals and Mammalogy

Mamíferos y mastozoología de Paraguay

Robert D. Owen and **Paul Smith**





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Paraguayan Mammals and Mammalogy

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Cover photos

1. **Background**: A view inside the Upper Paraná Atlantic Forest, in the Reserva Natural del Bosque Mbaracayú, Canindeyú Department, northeastern Paraguay. This is a subtropical semideciduous seasonal rainforest, characterized by numerous vines among the trees. This reserve, which includes both Atlantic Forest and Cerrado habitats, is noteworthy for having the confirmed presence of 12 didelphid species (Owen *et al.*, 2018) and 16 mammalian carnivore species (Zuercher *et al.*, 2022). Descriptions of physical and climate characteristics of Paraguay are found in Chapter 1. Photo by Robert D. Owen.
2. **Upper left**: Map of the ecoregions of Paraguay. As discussed in Chapter 3, numerous arrangements of Paraguay's ecoregions have been proposed by various authors. We believe that this one, modified from Clay *et al.* (2008), best depicts the ecoregions of the country.
3. **Upper right:** Aerial view of the Río Confuso ('Confused River'), in central Paraguay. This river and the surrounding vegetation are characteristic of the lower reaches of the rivers and wetlands as they flow slowly eastward toward their confluence with the Paraguay River. Photo by Robert D. Owen.
4. **Lower left:** A juvenile Pilar tuco-tuco, *Ctenomys pilarensis* Contreras 1993. This species is found in sandy soils of Ñeembucú Department, in the Humid Chaco ecoregion of southwestern Paraguay. This is one of three mammal species known to be endemic to Paraguay, all three of which are tuco-tucos. Keys to the orders and families of Paraguayan mammals are found in Chapter 7. Photo by Jorge Ayala, courtesy of Fundación Para La Tierra.
5. **Lower right:** Graph indicating the numbers of Paraguayan mammal specimens collected in each decade since 1859, when the first specimens that we are aware of, were collected. Chapter 5 includes detailed discussions of when, where, by what collectors from which countries, these specimens were collected, as well as what institutions they are housed in.

CONTENTS

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PARAGUAYAN MAMMALS AND MAMMALOGY: AN INTRODUCTION TO A WORK IN PROGRESS

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Abstract

Despite having one of the longest histories of mammalian research on the South American continent, Paraguayan mammalogy remains under-developed due to a lack of trained researchers and opportunities for study, and cultural under-valuation of biological sciences. While this situation is improving with government investment in scientific endeavor, capacitation of educators and greater societal awareness of environmental issues, Paraguay still lags behind its neighbours in the production of zoological literature, and mammalogy is no exception. This review aims to provide a succinct overview of the current state of knowledge about Paraguayan mammals and mammalogy. We hope this will provide a detailed and solid framework for ongoing work and serve as a stimulus for future research. We include seven sections which provide an environmental and historical context to the current knowledge of Paraguayan mammals:

1. **Description of the physical parameters of Paraguay**—its location within the South American continent, as well as the political divisions, geology, geography, and climate of the country.
2. **An introduction to the mammalian paleontology of Paraguay and the Southern Cone**, briefly reviewing South America's "splendid isolation" and the Great American Biotic Interchange following the formation of the Panama Land Bridge between North and South America. We include a taxonomic list of the fossil species reported from Paraguay.
3. **A summary of the current biological scenario** with an introduction to the ecoregions, ecosystems, conservation hotspots and protected areas in Paraguay.
4. **A brief history of mammal research in Paraguay and the region**, including an extensive bibliography for this research history. We also provide a referenced update of the taxonomy of the most recently published list of Paraguayan mammals.
5. **Detailed information on the scientific collections of Paraguayan mammals** of which we are aware, in Europe and North and South America. Several supplemental tables illustrate the history and geographic and taxonomic coverage of over 31,000 mammal specimens collected in Paraguay, housed in at least 46 collections in 13 countries in Europe and the Americas.

6. **A gazetteer of over 500 localities where mammals have been collected in Paraguay.**
7. **An introduction to the extensive mammalian diversity of Paraguay, with keys to the Orders and Families of Paraguayan mammals.** In a few cases (Orders or Families with only one Paraguayan representative) the key continues to the species level. We present two separate keys for each group, one based on external characters observable on an entire and intact individual (either live or freshly dead), and the other based on craniodental characters. We have many times been frustrated by keys which combine these two types of characteristics, and which seldom are both observable from a single specimen. To avert possible misidentification of a domestic animal's skull as a native species, we also included commonly encountered non-native species (livestock, pets, or other introduced species) in the keys to craniodental characters.

The "work in progress" referred to in the title of this paper will eventually include extensive reviews of most of the mammalian orders encountered in Paraguay. We anticipate completion and publication of separate papers on the Order Didelphimorphia, the edentates (Orders Cingulata and Pilosa), the Order Carnivora, and the ungulates (Orders Perissodactyla and Artiodactyla). We are hopeful that other authors will produce similar works on the Order Primates and on the Order Rodentia (and including Lagomorpha therein). For the Order Chiroptera, we call the reader's attention to López-González (2005), an excellent treatment of Paraguayan bats, although several new discoveries and some taxonomic changes have occurred since its publication.

1 PHYSICAL PARAMETERS

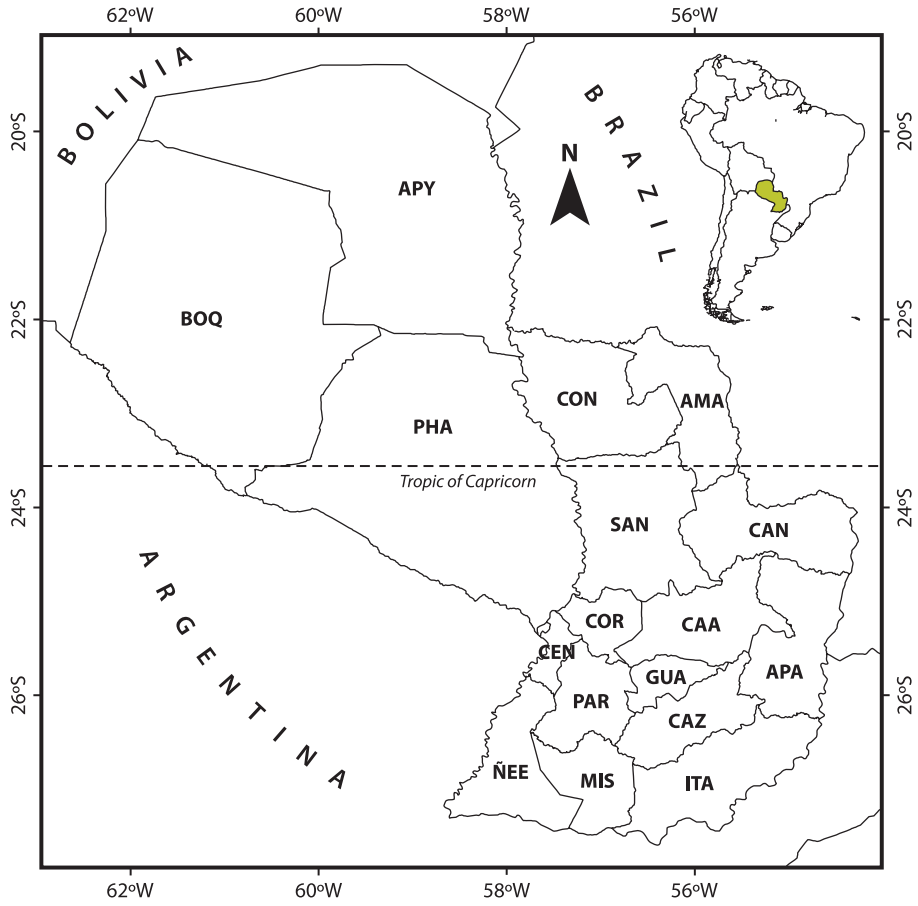

Figure 1. Map showing Tropic of Capricorn and political departments of Paraguay. Departments as follows: Chaco region – Alto Paraguay (**APY**), Boquerón (**BOQ**), Presidente Hayes (**PHA**); Oriental region – Amambay (**AMA**), Alto Paraná (**APA**), Caaguazú (**CAA**), Canindeyú (**CAN**), Caazapá (**CAZ**), Central (**CEN**) (including the Capital District), Concepción (**CON**), Cordillera (**COR**), Guairá (**GUA**), Itapúa (**ITA**), Misiones (**MIS**), Ñeembucú (**ÑEE**), Paraguarí (**PAR**), San Pedro (**SAN**). Inset map shows Paraguay's location in South America.

Location

Paraguay is one of two landlocked countries in South America (along with Bolivia, its neighbor to the north and northwest). It is located in south-central South America, between approximately 19°18' and 27°35' S latitude, and 54°17' and 62°38' W longitude, covering an area of 406,752 km² (**Fig. 1**). Lying in the transition between tropical and subtropical South America, it is traversed by the Tropic of Capricorn, with roughly half of its

area on either side of the Tropic. Paraguay lies between three larger countries. Brazil borders it on the northeast and east, with the Apa and Paraná rivers forming parts of that boundary. Argentina is to the southeast, south, and southwest, with the common border defined by the Paraná, Paraguay, and Pilcomayo rivers. To the northwest and north of Paraguay lies Bolivia, separated from Paraguay mostly by "dry borders," and by the final approximately 35 km of the Negro River before its confluence with the Paraguay River.

The country is roughly divided into western and eastern regions by the Paraguay River as it flows out of the Pantanal toward its confluence with the Paraná River at the southern end of the country. The two regions thus separated exhibit marked differences in geology, geography, climate, biota, and history, both pre- and post-colonial.

Political divisions

Since 1992, Paraguay has been divided into 17 departments plus the Capital District (**Fig. 1**). The Occidental (western) region, west of the Paraguay River, is generally referred to as the Chaco. It includes the departments of Boquerón, Alto Paraguay, and Presidente Hayes. The Oriental (eastern) region includes the Capital District and the remaining 14 departments (roughly from northwest to southeast: Concepción, Amambay, San Pedro, Canindeyú, Central, Cordillera, Caaguazú, Alto Paraná, Paraguarí, Guairá, Ñeembucú, Misiones, Caazapá, and Itapúa). Each department has a capital and its own government and governor. The 17 departments are further subdivided into districts. The number of districts in a department range from one (Boquerón) to 30 (Itapúa), roughly reflecting the population density within the departments.

Geology

M. S. Bertoni (1921) provided an early review of the geology of Paraguay, in which he noted that only the most general aspects of Paraguayan geology were known at that time. Eckel (1959) and Tirado Sulsona (1959) published reviews of the geography and geology (including sections on mineral and water resources) and on the soils of Paraguay, respectively. Harrington (1950, 1956) and Fúlfaro (1996) provided extensive reviews of the geology of eastern Paraguay, and Clebsch Kuhn (1991) of western Paraguay. A detailed review of the geologic structure, tectonic history, and mineral resources of the country was provided by Palmieri and Velázquez (1982). More recently, Orme (2007a) provided a comprehensive review of the tectonic framework of South America.

Paraguay is underlain by three cratons (stable portions of the continental crust): the Río Apa and (marginally) the Amazonia to the north and the Río de la Plata to the south (Fúlfaro, 1996). Two large geological basins are found in eastern and western Paraguay. The Paraná Basin lies from Mato Grosso to Rio Grande do Sul states in Brazil, and extends westward into Paraguay. In its central region (in Brazil) the infill deposits are up to 7,000 meters thick. The Paraná River drains this basin. The Chaco Basin is found west of the Paraguay River, and extends well into Argentina and Bolivia, as far as the Andean thrust front. Although underlain by marine sediments from the Paleozoic through the Late Cretaceous,

the more superficial sediments are both aeolian and stream-carried fine sand and clays of Paleogene, Neogene and Quaternary origin. Volcanic activity from various periods from Precambrian through early Tertiary has resulted in tholeiitic basalts near the Paraná River and other volcanic deposits between Asunción and Villarrica, and in Amambay, Misiones, and Alto Paraguay departments. These have mostly been covered by the sediments of the two basins mentioned above, and outcrop only as low hills in most cases.

The geologic history of cratons interspersed by basins, volcanism, and marine and terrestrial alluvium has resulted in a relatively complex mosaic of geologic formations (**Fig. 2**). A good discussion of the resultant soils, with detailed maps, is provided by González Erico (2007).

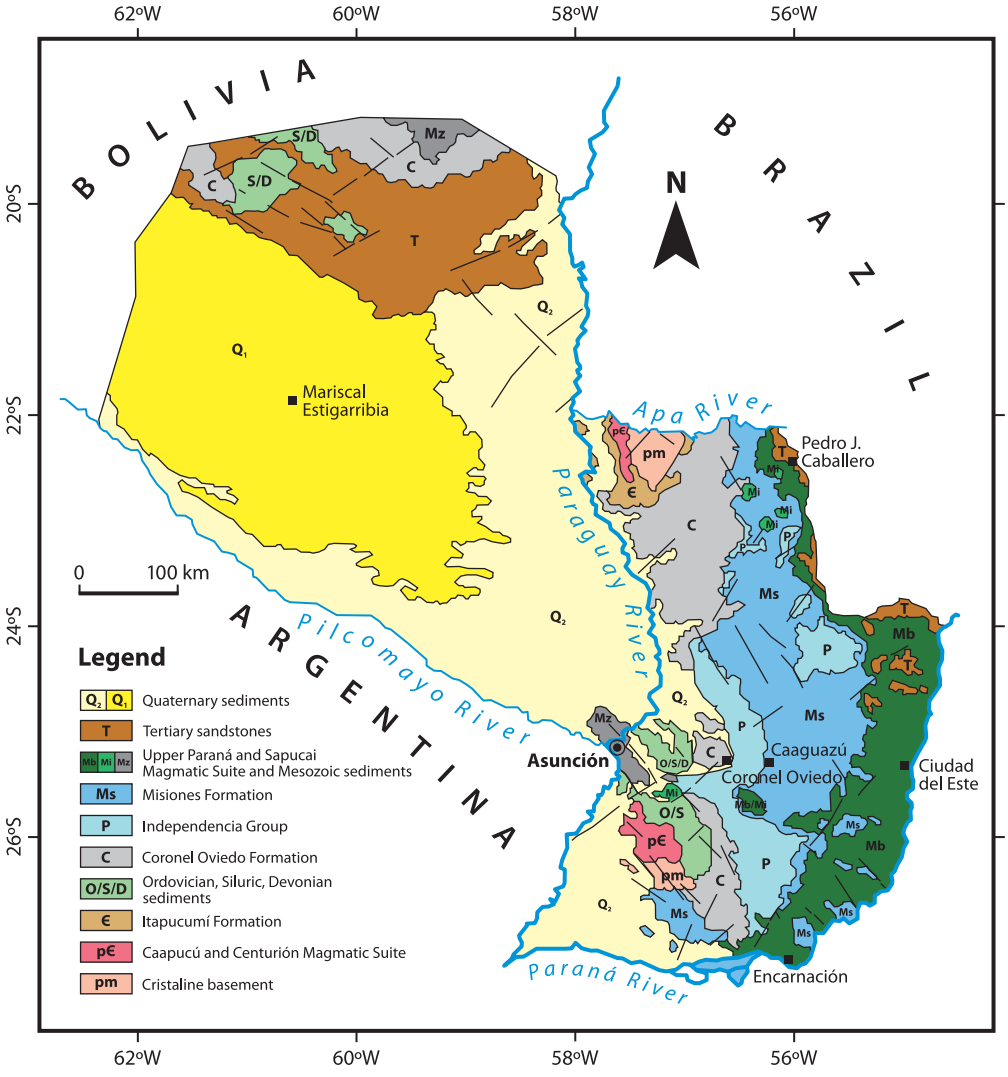

Figure 2. Geologic map of Paraguay (modified from González, 2000).

Geography

Topography

The entire country is one of low relief, with elevations ranging from 50 meters above sea level at the junction of the Paraguay and Paraná rivers to an extreme of 842 m on Cerro Peró (also known as Cerro Tres Kandú) about 30 km southeast of Villarrica in Guairá Department. There is, however, a marked difference in the topography on the two sides of the Paraguay River, which bisects the country along a north-south line. That portion east of the river, called Paraguay Oriental, is gently rolling to hilly, with nearly level valleys. Some of the relatively low hills and mountains occur in rather distinct chains. Made up in large part of soft sedimentary rocks or of deeply weathered basalt, the hills are being degraded by erosion processes and present a low rounded outline in most places. Here and there, however, where there are outcrops of harder sedimentary or igneous rocks, they have more rugged shapes and present bits of spectacular scenery, albeit on a rather small scale.

The Chaco Boreal on the western side of the Paraguay River, the Paraguayan part of the Gran Chaco, is a vast aggrading alluvial plain that rises almost imperceptibly westward from the river toward the foothills of the Andes in Bolivia and Argentina. The monotony of this nearly level, poorly drained plain is broken only in its most northern part, where there are a few good-sized hills that mark places where islands of bedrock protrude above the thick alluvium.

Hydrology

A review of the hydrology of Paraguay, including sections on hydrologic cycles and precipitation, river basins, and aquifers, was presented by Larroza and Fariña (2007). Additional resources on more specific aspects of hydrology are discussed in the following paragraphs.

Aquifers

Much of Paraguay is underlain by groundwater deposits (aquifers), most of which are transboundary (shared with surrounding countries—**Fig. 3**). These include the Yrenda-Toba –Tarijeño (shared with Argentina [A] and Bolivia [Bo]), the Pantanal (Bo, Brazil [Br]), Agua Dulce (Bo), Aquidauana-Aquidabán (Br), Caiuá/Bauru-Acaray (Br), Serra Geral (A, Br, Uruguay [U]), and Guaraní (A, Br, U). The Guaraní Aquifer System is the largest aquifer in Paraguay (and one of the largest in the world) and covers an area of 1,087,879 km². It is formed predominantly by "sandy sedimentary rocks of the Paraná Basin (Brazil and Paraguay), the Chaco-Paranaense Basin (Argentina) and the Northern Basin (Uruguay)" (OAS, 2009; Villar, 2016). Most (90%) of the aquifer is confined and the recharge area is only 124,650 km². The aquifer lies mostly in Brazil which is the main user of its waters, but it also is an important source of municipal, industrial and agricultural water for eastern Paraguay.

Figure 3. Aquifers of Paraguay and surrounding countries (Villar, 2016).

Several smaller aquifers are contained entirely within Paraguay, such as the Patiño, Adrián Jara, Caacupé, Alto Paraná, and Misiones (Godoy and Paredes, n/d), Chaco Central, Palmar de las Islas, and Itacurubí Aquifers (UNESCO – IHP, 2009).

Rivers

All of Paraguay lies within the great basin of the Paraná-Paraguay watershed, which also drains appreciable parts of Bolivia, Brazil, Argentina, and Uruguay and empties into the estuarine River Plate (Río de la Plata), above Buenos Aires. The true Paraná River heads at the southern tip of Paraguay at the confluence of its two main branches, the Paraguay and the Upper Paraná rivers. The Paraguay River is the larger of these two. It heads in

Mato Grosso, Brazil, and trends nearly due south, bisecting Paraguay in its lower reaches. It has a total fall of only 250 meters in its 2,500 km course, and except during seasonal or exceptional flooding it flows quite slowly. In its Paraguayan portion it is several hundred meters wide in most places and is characterized by innumerable meanders and by frequent channel shifts. An extensive channelization project to facilitate year-round navigation is being developed jointly by Argentina, Paraguay, Bolivia and Brazil, which would include extensive riverine and wetland habitat modification from the mouth of the Paraná River to near Cáceres, Brazil (Hamilton, 1999; Baigún and Minotti, 2021).

The Paraguay River and its tributaries drain all but the southeastern portion of the country. The Pilcomayo River, arising 2,000 km westward in the Andes in Bolivia, and forming much of the international boundary with Argentina, is the largest tributary on the western or Chaco side of the river. Except for its length and relative continuity, it is similar to the other streams that drain the Chaco. Normally, they are sluggish, intermittent, and discontinuous streams that wind their way slowly across the nearly level plains between banks that are seldom more than a couple of meters high. During rainy season they overflow their banks and spread over much of the land. Their loads of mud, silt, and fine sand debris, carried down from the Andes, are redistributed over the plains during periods of overflow or by changes of course that take place on most streams, if not from year to year, at least from decade to decade. Most of the eastern part of Paraguay drains into the Paraguay River through seven main tributaries and several smaller ones. Five of them are 180 to 275 km long and all are slow and shallow in most places and subject to frequent shifts in channel.

The Upper Paraná River, about 3,000 km long, arises deep in southeastern Brazil; in its lower reaches it forms the eastern and southeastern boundary of Paraguay for a distance of 850 km. On its way toward Paraguay it meanders slowly across high basalt plains, but where it first touches Paraguay (in northeastern Canindeyú Department) it once plunged abruptly over a series of jagged basalt escarpments to form the waterfalls of Saltos del Guairá (now inundated by Itaipú Lake). From these falls to Encarnación it is incised in basalt and follows a relatively straight, narrow and swift course as compared with its upstream or downstream portions. From Encarnación to its junction with the Paraguay River the stream is broad and shallow, characterized by shifting, braided channels. The southeastern part of the country drains to the Upper Paraná River by means of 11 major tributaries, only two of which are more than 150 km long. These, too, are slow meandering streams and resemble the tributaries of the Paraguay River in all but two important respects. First, though their meanders superficially resemble the aimless wanderings of the rivers farther west, on closer study they are seen to be related to fracture patterns in the basalt flows that underlie most of the area. Second, most of the tributaries make their final descent into the Upper Paraná gorge by a series of low step-like falls or rapids where they cross the edges of the basalt flows.

Natural lakes and wetlands

There are two fairly large, permanent but shallow, lakes in the country, Lago Ypoá and Lago Ypacaraí in Paraguarí and Central departments, respectively. Other smaller permanent lakes include Laguna Blanca in San Pedro Department, and Lago General Díaz in Alto

Paraguay Department. Due to the prevalence of low-lying flat areas, both in some areas of eastern Paraguay and especially in the lower Chaco region, much of the land becomes inundated, either seasonally or during years of exceptional precipitation (*e.g.*, from El Niño events), resulting in countless intermittent ponds, lagoons, and swamps, some of them extensive. These wetlands constitute an important aspect of the hydrology of Paraguay, and are reviewed in detail in Salas-Dueñas *et al.* (2004).

Man-made reservoirs

Paraguay relies extensively on two binational hydroelectric plants, Itaipú and Yacyretá, for electricity. The Itaipú dam, which contains the world's second largest hydroelectric plant, is situated in Alto Paraná Department, eastern Paraguay on the Upper Paraná River, between Brazil and Paraguay. The lake has a surface area of 1,350 km², and extends 170 km upstream from the dam near the town of Hernandarias, to just upstream from the Saltos de Guairá waterfalls, a 114-m high series of cataracts that was completely inundated by the Itaipú Reservoir.

The Yacyretá Dam, co-owned by Paraguay and Argentina, is also on the Upper Paraná River, near Ayolas in Itapúa Department, southern Paraguay. The reservoir extends upstream from the dam for approximately 110 km, to just upstream from the city of Encarnación. In addition to these two large binational dams and lakes, Paraguay has two wholly-owned

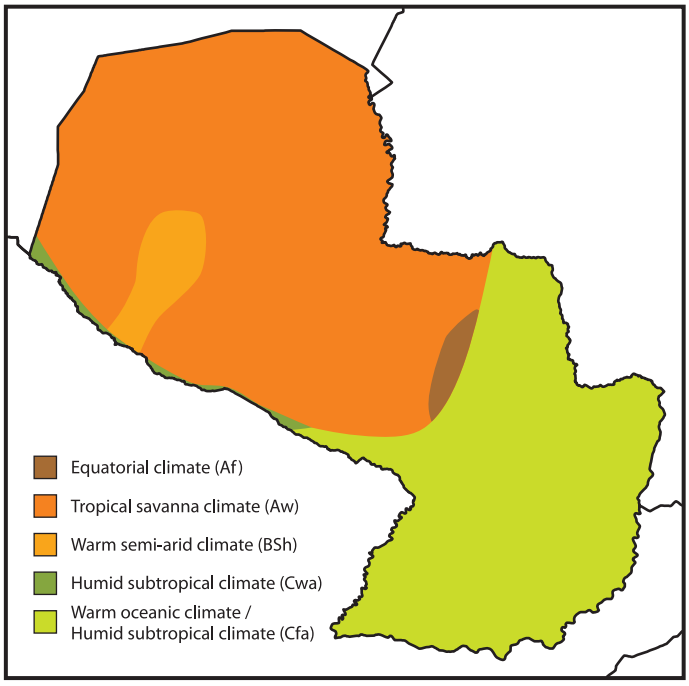

Figure 4. Modified Köppen climate classification map of Paraguay (from Peel *et al.*, 2007).

hydroelectric dams, both in Alto Paraná Department on tributaries of the Upper Paraná River: the Yguazú Dam is on the Yguazú River, a tributary of the Acaray River, and the Acaray Dam is on the Acaray River, near its confluence with the Upper Paraná River.

Climate

Paraguay's climate includes both tropical and subtropical regions. Orme (2007b) provided a discussion of tectonism, climate and landscape change. Separated by long distances from both the Atlantic and Pacific oceans, and by the Andes Mountains from the Pacific, Paraguay is subject only to continental, rather than maritime climatic influences. Fariña Sánchez (1973) divided the country into six climatic regions, based on the climate criteria of Thornthwaite (1933). More recently, the modified Köppen system of Peel *et al.* (2007) divides Paraguay into five climatic regions (**Fig. 4**). In this system, the Chaco is largely occupied by climate type Aw (tropical savannah), and the eastern region primarily by Cfa (warm oceanic / humid subtropical). A finger of BSh (warm semi-arid) climatic type extends northward into the southwestern Chaco from Argentina, and a narrow strip of Cwa (humid subtropical) follows the more northwestern reaches of the Pilcomayo River. Finally, a narrow north-south strip of Af (equatorial) climate type occurs east of the Paraguay River, in Concepción and San Pedro departments.

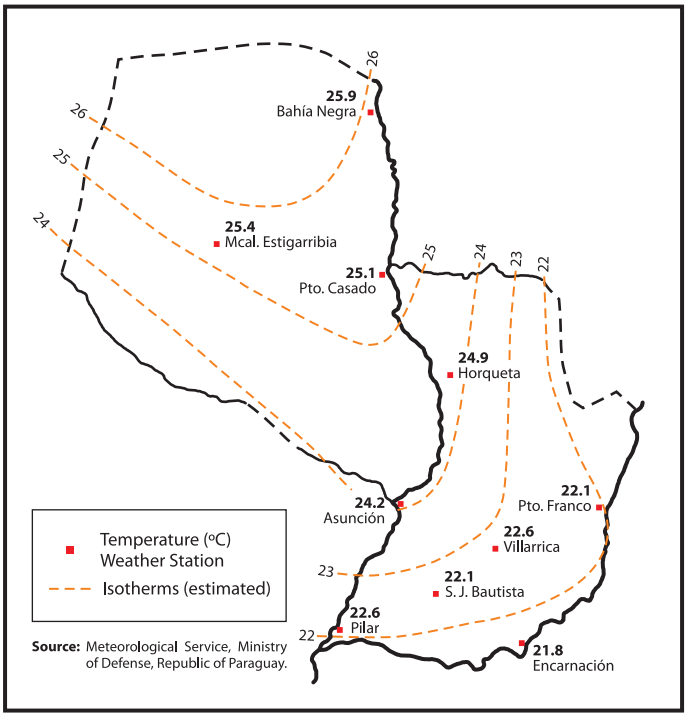

Figure 5. Mean temperature (degrees Centigrade) across Paraguay, expressed as isotherms (Fariña Sánchez, 1973, Fig. 3.2).

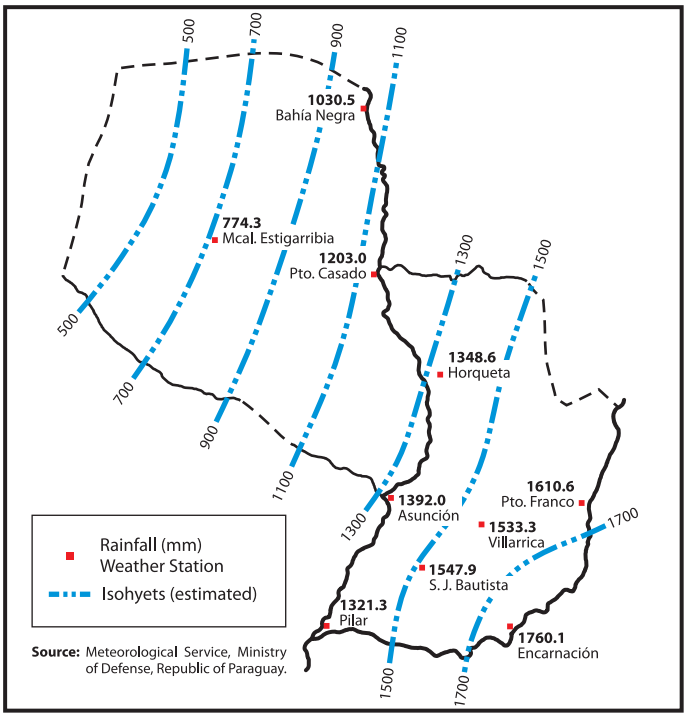

Figure 6. Mean annual precipitation (mm) across Paraguay, expressed as isohyets (Fariña Sánchez, 1973, Fig. 3.3).

The prevailing winds during much of the year are from the north and northeast, through Brazil. These winds are warm to hot, and generally of intermediate humidity. In the winter, cold fronts arrive from the south and southwest, through Argentina. During periods of high heat and humidity, or the intrusion of a cold front into a warm humid air mass, strong thunderstorms may occur, with strong winds, heavy rainfall, and frequent lightning. These storms often result in injury and mortality to both livestock and humans, due to wind damage, flooding and lightning.

Temperature

Mean annual temperature in Paraguay varies from 21 °C along the Upper Paraná River in southern Paraguay to 26 °C in the northern Chaco (**Fig. 5**). December, January, and February are the warmest months, with temperatures as high as 42 °C in Encarnación and Asunción, and 44 °C in the Chaco. June, July and August are the cold months, with temperatures occasionally as low as -6 °C in Encarnación and -7 °C in the Chaco.

Precipitation

Mean annual precipitation varies considerably across Paraguay, along a roughly southeast to northwest gradient (**Fig. 6**). Southeastern Paraguay receives over 1,700 mm annually

on average, and the northwestern Chaco less than 500 mm per year. Virtually all precipitation is in the form of rain, with small amounts occasionally contributed by hail, and very minimal amounts by frost or the exceedingly rare light snowfall. Rains are generally heaviest from October through February or March, then diminishing variably until August, usually the driest month (Gorham, 1973a).

Seasonality and interannual variability

As indicated above, the usual annual weather pattern is one of warm to hot rainy months in spring and summer (October–February), and cooler drier months from April–August. Precipitation levels in tropical and subtropical regions of the Americas, including northern Paraguay, correlate at least generally with ENSO patterns (Rasmusson, 1985; Marengo, 2004). For example, a strong El Niño event occurred from early 2015 into early 2016, resulting in considerably higher rainfall than normal in northeastern Paraguay (Vazquez and Vazquez, 2017).

Both seasonal and interannual variation in precipitation levels may have important effects on mammalian populations. Combining figures for all small mammal species on three mark-recapture grids in the Atlantic Forest ecoregion of Canindeyú Department, 261, 210, and 200 individuals were encountered in July 2015, November 2015, and February 2016 (during the El Niño event), respectively. The following year, after the El Niño event was past, the same sampling periods produced 118, 76, and 198 individuals, respectively (Owen *et al.*, unpubl. data). Thus, populations were much higher during an unusually wet July–November period, than they were during that same period in a more typical (non-El Niño) year.

2 MAMMALIAN PALEONTOLOGY IN SOUTH AMERICA AND PARAGUAY

As reviewed by Simpson (1980), three major groups of terrestrial mammals appear to have arrived (either by evolution *in situ* or by migration) in South America, not including the recent arrival of humans, along with their commensal and domestic mammals. The first of these included the three basal lineages which had evolved in Gondwanaland, the southern supercontinent which during the Cretaceous included the current continents of South America, Africa, Antarctica, Australia, and the sub-continent of India. These three lineages were the Didelphimorphia (marsupials), Xenarthra (sloths, anteaters, armadillos, and similar forms) and Notoungulata (a large variety of forms distantly related to Perissodactyla, all extinct). Both the Didelphimorphia and the Xenarthra experienced broad and successful radiations, and continue to be important components of the South American fauna to this day.

The southern continents, including South America, were completely separated from each other by the end of the Cretaceous (ca. 65 million years ago—mya). In the Eocene, around 40–35 mya, two new groups of mammals arrived, which were the primates and the caviomorph rodents. As South America was well separated from other land masses at this time, these two groups apparently arrived by "waif dispersal", rafting and/or island-hopping either from North America or Africa. Debate continues on the geographic origin of both of these migrations, as well as whether the original immigrants of each group consisted of one, a few, or many species (Webb, 1991; Barbière *et al.*, 2019; Morgan *et al.*, 2023; Ronez *et al.*, 2023). Regardless, both the caviomorph rodents and the primates experienced radiations into many of the diverse habitats found in South America.

Much more recently, another important incursion occurred with the uplifting of what is now Central America to form a land bridge between North and South America. This connection resulted in the Great American Biotic Interchange, beginning roughly 4–3 mya in the late Pliocene and continuing to the present day (Simpson, 1980; Flynn and Weiss, 1998). Immigrants from North America into South America include the Insectivora (shrews), Lagomorpha (rabbits), sciuromorph and myomorph Rodentia (squirrels and mice), Carnivora (dogs, bears, otters, raccoons, skunks, cats), Perissodactyla (tapirs), and Artiodactyla (peccaries, camelids, deer). As the term "Interchange" indicates, several South American forms also immigrated into North America, although the northward migrations included fewer species, and was limited primarily to tropical and subtropical North America (Webb, 1991).

Of these recent arrivals via the Panama land bridge, the Insectivores, Lagomorphs, and Perissodactyls are represented by only a few extant species in South America. The Carnivores and Artiodactyls are both represented by a moderate number of species presently, but the group which has radiated dramatically is the rodent family Cricetidae, and within that

family the subfamily Sigmodontinae, which includes approximately 86 genera and 400 species (D'Elía and Pardiñas, 2015).

Chiroptera (bats), also highly diversified and successful in South America, are capable of long flight, including over water. Thus, they probably arrived in South America at various times throughout the Cenozoic and are not associated with any particular incursion of terrestrial mammals (Morgan *et al*., 2023). However, their fossil record is scant everywhere, including in South America (Czaplewski, 1996; Gunnell and Simmons, 2005; Teeling *et al*., 2005; Eiting and Gunnell, 2009).

Relatively few mammalian fossils or fossil localities are known from Paraguay, in comparison with other countries of the Southern Cone and all are from the Quaternary (Pleistocene–Holocene). Although Cuvier (1796) described *Megatherium americanum* from "Paraguay", the locality (Luján) is in what is now the Argentine Pampas region, well outside of the current national boundaries of Paraguay (Hoffstetter, 1978).

A. de W. Bertoni (1924a) reported on specimens of *Glyptodon*, *Megatherium* and "*Mastodon*" collected by C. Rocholl and Bergmann in clay soils of the Pilcomayo in that same year. Bertoni (1925a) documents a near complete skull of *Toxodon platensis* collected at the same locality and which was deposited at the Jardín Botánico de La Trinidad. A. de W. Bertoni (1928) later added *Macrauchenia* (using the *nomen dubium M. boliviensis*) to the inventory of this locality.

Vellard (1934) provided a brief report of *Glyptodon*, *Megatherium*, *Mastodon*, *Toxodon* and *Macranchenia* (sic: *Macrauchenia*) from the lower Chaco at three sites along the Pilcomayo River, including General Bruguez. Harrington (1956) reported that Pleistocene deposits near Asunción "…have yielded a few gliptodontid and gravigrad [presumably proboscidean] remains which have not been studied in detail," but provided no further information.

Hoffstetter (1978) made perhaps the most significant work on fossil mammals from Paraguay to that date, being the first trained paleontologist to review a large collection from the country. He reported on 14 genera of fossil mammals, of nine families: Glyptodontidae, Dasypodidae, Megatheriidae, Mylodontidae, Toxodontidae, Macraucheniidae, Gomphotheriidae, Camelidae, and Cervidae. The fossils were from two localities in the southern Paraguayan Chaco, "Riacho Negro, immediately north of Asunción" and "General Bruguer [apparently Fortín Gral. Bruguez], 180 km WNW of Asunción, on the Rio Pilcomayo." This brief report indicated that both localities were apparently of Pleistocene age and that, with the exception of *Blastocerus*, all fossils examined pertained to extinct genera.

Carlini *et al*. (1998) reported two specimens of *Sclerocalyptus* (Family Glyptodontidae) = *Neosclerocalyptus* found in the process of excavating two ponds in the vicinity of Filadelfia, thus adding another region (central Chaco) to the known fossil localities of Paraguay. One of these specimens is housed at the Museo Jacob Unger in Filadelfia.

Carlini and Tonni (2000) provided a comprehensive account of the fossil mammals known from Paraguay, listing 27 genera, included 14 genera of xenarthrans and ungulates considered "native" (having originated in South America before the Panama land bridge was established, ca. 3 mya), and 13 (both herbivores and carnivores) considered "immigrants" (arriving via the Great American Biotic Interchange across the Panama land bridge).

The authors also included a few extant genera (*Mazama*, *Ozotoceros*, *Blastocerus*—Family Cervidae; *Catagonus*—Family Tayassuidae; and *Panthera*—Family Felidae), mostly extrapolating the Argentinian fossil record. Stratigraphic distributions of these fossil taxa generally ranged from Late Pliocene to Middle Pleistocene or later. All of these taxa were of large to medium-sized mammals, with the smallest being *Catagonus*, the Chacoan peccary.

Báez Presser *et al*. (2004) reviewed paleontological materials known from Paraguay, including mammals. Their summary included information gleaned from earlier publications (mentioned above), as well as several reports found in Paraguayan ministry documents and abstracts of professional meetings. Carlini *et al*. (2004) noted that preliminary studies demonstrate a paleofaunal similarity of north-central Argentina with Pampean – Patagonian elements, and extending to Paraguay and southeastern Bolivia.

Ríos Díaz *et al*. (2014) reported a locality on the left (east) bank of the Paraguay River, in San Pedro Department, from which they recovered fossils of *Megatherium* (Family Megatheriidae), *Toxodon* (Family Toxodontidae), *Notiomastodon* (Family Gomphotheriidae), and *Hemiauchenia* (Family Camelidae). Based both on the geology and the mammalian taxa, they described this as a Late Pleistocene – Early Holocene fauna.

Torres *et al*. (2015) provided the first report of small mammal fossils from Paraguay, from a cave deposit near the confluence of the Apa and Paraguay rivers, in Concepción Department. This area currently exhibits a mixture of Cerrado, Interior Atlantic Forest, Chaco and Pantanal biomes. The authors concluded that the remains were probably deposited by avian predators, mostly likely owls, and were from Late Pleistocene to Early Holocene in age. The fossils, all of the Family Cricetidae, Subfamily Sigmodontinae, represented five genera: *Holochilus*, *Oligoryzomys*, *Graomys*, *Calomys*, and *Akodon* (*A*. cf. *toba*). Because *Graomys* and *A. toba* are currently restricted to the western (Chaco) region of Paraguay, and because no forest-dwelling species were found in the cave deposits, they concluded that the region probably had been slightly more arid, with floral composition more characteristic of Cerrado than of Interior Atlantic Forest.

As mammalian fossil materials and literature have accumulated, both from Paraguay and elsewhere in South America, investigators have begun to conduct more analytic evaluations of paleofaunal affiliations. Marques de Oliveira *et al*. (2017) combined data from numerous published sources to evaluate Quaternary regional similarities. Based on previous work (*e.g.*, Carlini *et al*. [2004]), they combined north-central Argentina, southern Bolivia, and Paraguay into one "fauna", to be compared via cluster analysis with six other South American regions. They concluded that the Brazilian intertropical region, Mato Grosso do Sul, and São Paulo regions formed one cluster (were most similar to one another), and that the region including Paraguay shares most of its taxa with the Pampean and Mesopotamian regions, as well as Rio Grande do Sul.

Mothé *et al*. (2017), inferring from paleodistributional data, evaluated the biogeography and ecological affinities of the two species of Gomphotheriidae in South America, *Notiomastodon platensis* (ocurring in Paraguay) and *Cuvieronius hyodon*. They concluded that the two species were both ecological generalists, resulting from separate incursions from Central America into South America. As the two species have not been recorded from the same locality, the authors suggest that their apparent allo- or parapatry was due

to competitive exclusion. *N. platensis* coexisted with humans for some time, and became extinct in the Early Holocene. In contrast, *C. hyodon* became extinct somewhat before humans are generally believed to have been present in South America, and before the widespread South American megafaunal extinctions of the Pleistocene–Holocene boundary.

Taxonomic list of the fossil mammalian fauna of Paraguay

(Sources: Hofstetter, 1978; Carlini and Tonni, 2000; Prieto *et al*., 2010; Ríos Díaz *et al*., 2014; Torres *et al*., 2015)

Order Cingulata
Family Chlamyphoridae
Subfamily Glyptodontinae

Doedicurus cf. *clavicaudatus* Owen, 1847
Glyptodon cf. *clavipes* Owen, 1839
Panochthus tuberculatus Owen, 1845
Neosclerocalyptus cf. *ornatus* Owen, 1845

Family Pampatheriidae

Holmesina paulacoutoi Cartelle & Bohórquez, 1985
Pampatherium humboldti Lund, 1839 or
P. typum Gervais & Ameghino, 1880

Order Pilosa
Family Megatheriidae

Megatherium americanum Cuvier, 1796

Family Scelidotheriidae

Scelidotherium sp. *sensu lato*

Family Mylodontidae

Glossotherium cf. *robustum* Owen, 1840
Lestodon cf. *armatus* Gervais, 1855
Mylodon darwini? Owen, 1840

Order Notungulata
Family Toxodontidae

Toxodon cf. *platensis* Owen, 1837

Order Litopterna
Family Macraucheniidae

Macrauchenia cf. *patachonica* Owen, 1838

Order Proboscidea
Family Gomphotheriidae

Notiomastodon platensis Ameghino, 1888
Stegomastodon sp.

Order Artiodactyla
Family Camelidae

Hemiauchenia sp.
Palaeolama sp. *sensu lato*

Family Cervidae

Morenelaphus brachyceros Gervais & Ameghino, 1880
Blastocerus dichotomus Illiger, 1815

Order Perissodactyla
Family Equidae

Equus (*Amerhippus*) sp.
Hippidion sp.

Order Carnivora
Family Felidae

Smilodon populator Lund, 1842

Order Rodentia
Family Cricetidae

Holochilus chacarius Thomas, 1906
Oligoryzomys sp.
Graomys cf. *chacoensis* Allen, 1901
Calomys sp.
Akodon cf. *toba* Thomas, 1921

3 ECOREGIONS, ECOSYSTEMS, HOT SPOTS, PROTECTED AREAS

Paraguay lies at the interface of several of the major South American ecoregions—Atlantic Forest, Cerrado, Pantanal and Chaco. Additionally, it is traversed by the Tropic of Capricorn, so that its territory includes both tropical and subtropical regions. It exhibits a strong gradient in annual precipitation levels, with humid forests in the south and east, and semi-arid thorn scrub in the western regions. Many species of both animals and plants reach the terminus of their distributions in Paraguay. Accordingly, and not surprisingly, various authors have defined and delineated the ecoregions of Paraguay in a wide variety of ways.

The terms "ecoregion" and "ecosystem" are often poorly defined and used somewhat interchangeably, depending on the author(s) and their focus. In common usage at least, an ecoregion covers a relatively large area of land and/or water, and contains characteristic, geographically distinct assemblages of ecosystems, faunal and floral communities, and species. As indicated above, Paraguay occurs at the nexus of four major South American ecoregions, and each of these ecoregions may be divided into a number of more or less distinct ecosystems.

An ecosystem is a community of living organisms in conjunction with the abiotic components (temperature, precipitation, soils, winds, insolation, etc.) of their environment, interacting as a system. Most attempts to categorize the Paraguayan landscape into distinct and recognizable biological regions have been based on evaluations of similarities and differences of particular floral or faunal communities. Tortorelli (1967) described five "forest formations" in eastern Paraguay (east of the Paraguay River): Selva del Alto Paraná (east), Selva Central (central), Bosque del Norte (northwest), Parque del Río Paraguay (west-central), and Sabana Arbolada Oriental (southwest). West of the Paraguay River, he delineated four forest formations: Bosque Chaqueño (northeast), Parque Chaqueño (north-central), Sabana Arbolada Chaqueña (southeast), and Monte Occidental (northwest).

Hayes (1995) evaluated avian communities in the context of four phytogeographic regions in eastern Paraguay and three in the west. Although he recognized one fewer region in both eastern and western Paraguay, the delineations were similar to those of Tortorelli (1967). Spichiger *et al*. (1995) took a different approach to defining ecoregions based on dendroflora (tree communities), looking not for arbitrary lines dividing the regions, but for zones where substantially different communities of tree species overlapped, thus forming zones of particularly high diversity ("hot spots"). Their dendrofloral regions also were not found to occur solely in eastern or western Paraguay; rather, three of the five were found to occur on both sides of the Paraguay River. These five floral zones were: Paranean (eastern Paraguay), Residual Pleistocenic Dry Seasonal, Cerrado, Wet Chaco (both eastern and western), and Dry Chaco (western). Based on these five dendrofloral regions, they

identified six regions of overlap, which they defined as hot spots of specific tree diversity, deserving of top priority of protection and study.

López-González (2004) censused bat communities at 26 sites throughout Paraguay, and evaluated these communities in the context of vegetational data for the localities. She found a strong relationship between vegetational communities and the bat assemblages inhabiting them. She concluded that the bat communities reflected the floral communities, and together these indicated three broad ecoregions in Paraguay: Dry Chaco, Floodable Lands, and Eastern Paraguay. The six sites in Floodable Lands were in Alto Paraguay near the Paraguay River, the Wet Chaco, and Ñeembucú. In this scenario, the Paraguay River is not simply the division between eastern and western ecoregions; rather, the seasonally inundated lands on either side of the river constitute a separate ecoregion.

Oren *et al*. (2005) reported results of a workshop involving a detailed assessment of birds, amphibians, reptiles, mammals, and plant communities of the Gran Chaco of Argentina, Bolivia and Paraguay. Their report designated a total of 15 terrestrial ecosystems in the Paraguayan Chaco, four of which were partially or completely east of the Paraguay River. The workshop report evaluated terrestrial and aquatic ecosystems separately, and reported 20 aquatic ecosystems in the Paraguayan Chaco, seven of which are completely or partially east of the Paraguay River.

Rodas *et al*. (2006) recognized five ecoregions in Paraguay (Cerrado, Pantanal, Dry Chaco, Humid Chaco, Upper Paraná Atlantic Forest). In their GAP analysis to evaluate ecosystem protection status within Paraguay, they considered an ecosystem to be a "unique physical environment using data on land cover, elevation, landforms, geology, and bioclimate." Combining these criteria, they recognized 101 ecosystems in Paraguay, with the most (41) in the Dry Chaco and the fewest (5) in the Pantanal, with these numbers roughly reflecting the percentage of land area occupied by the five ecoregions within the country.

Dinerstein *et al*. (1995) included five ecoregions within Paraguay, with portions of the Humid Chaco lying on both sides of the Paraguay River, rather than only west of the river. Clay *et al*. (2008) recognized these same regions, and also distinguished the Mesopotamian Grasslands in southern Paraguay as distinct from the Humid Chaco. That arrangement reflects recognition of the Humid Chaco's extent on the eastern side of the river, as well as the distinctive Grassland region in the south.

Rumbo (2010) also recognized the five ecoregions used by Rodas *et al*. (2006). Based on known presence or absence of each mammalian species within each ecoregion, she found the highest similarity level between the Upper Paraná Atlantic Forest and the Humid Chaco, with the Pantanal being the least similar to any other ecoregion.

Mereles *et al*. (2013), based primarily on the ecosystems defined by Oren *et al*. (2005), concluded that western Paraguay includes five distinct ecoregiones: Médanos (dunes), Cerrado, Pantanal, Chaco Seco (Dry Chaco), and Chaco Húmedo (Humid Chaco). This system was followed in Resolución No. 614/13 (SEAM, 2013), which also recognized six ecoregions in eastern Paraguay: Aquidabán, Amambay, Alto Paraná, Selva Central, Litoral Central, and Ñeembucú (**Fig.** 7). Although perhaps less generally accepted than the five or six ecoregions recognized by several earlier authors (Rodas *et al*., 2006; Clay *et al*., 2008; Rumbo, 2010), this "official" division of Paraguay into 11 ecoregions represents a growing

recognition of the diversity of environments encountered in Paraguay, as a consequence of lying at the nexus of several major South American ecoregions.

More recently, Caccialli *et al*. (2016) proposed seven ecoregions in Paraguay, generally similar to those of Clay *et al*. (2008) but also recognizing a narrow "Central Forest" region consisting of a narrow strip of temperate deciduous forest forming a transition between the Wet Chaco and the Atlantic Forest. Avila Torres *et al*. (2018) recognized a similar region, which they called "Cordillera de los Altos", although it should be noted that this region and the Mesopotamian Grasslands are transposed in the legend for their Fig. 8.

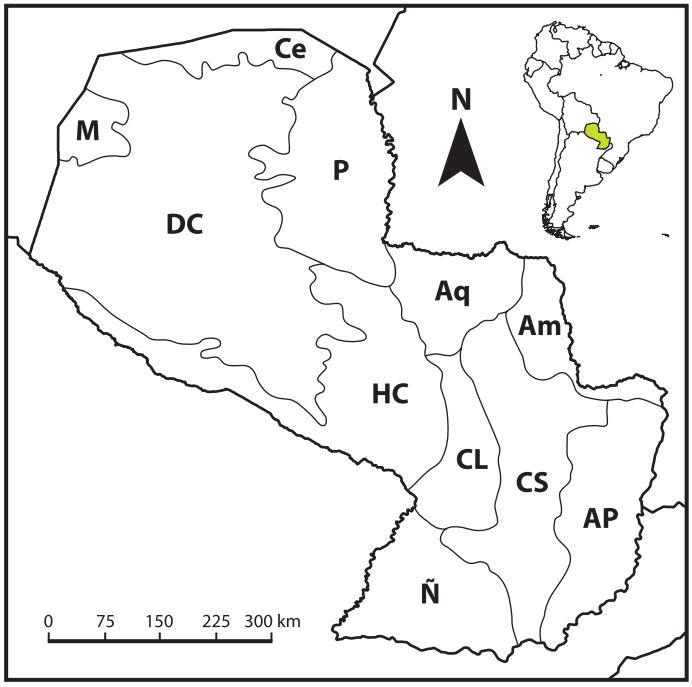

Figure 7. Map showing the ecoregions of Paraguay as recognized by the Ministry of the Environment and Sustainable Development (MADES), as published in Resolución No. 614/13 (SEAM, 2013). Acronyms are: **Am**, Amambay; **Aq**, Aquidabán; **Ce**, Cerrado; **CL**, Litoral Central (Central Litoral); **CS**, Selva Central (Central Selva); **DC**, Chaco Seco (Dry Chaco); **HC**, Chaco Húmedo (Humid Chaco); **M**, Médanos; **Ñ**, Ñeembucú; **P**, Pantanal. Inset map shows Paraguay's location in South America.

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4 HISTORY OF MAMMALOGY IN PARAGUAY

"Mammalogy" signifies the study of mammals. Without doubt, people have been studying mammals in what is now Paraguay for thousands of years, developing an intimate and detailed knowledge base. Although waning in its completeness, this knowledge base still exists to some extent among indigenous and other rural communities (Hill and Hawkes, 1983; Arenas, 1987; Hill and Padwe, 2000; Hill *et al*., 2003; Centrón *et al*., 2013). This body of orally communicated knowledge accumulated through multiple generations of people intimately familiar with local flora, fauna, and natural history in general, is currently referred to as "Traditional Ecological Knowledge" (TEK) (Hawkes *et al*., 1982; Hill and Hawkes, 1983; Arenas, 1987; Johannes, 1989; Williams and Baines, 1993; Berkes *et al*., 2000; Hill and Padwe, 2000; Hill *et al*., 2003; Naidoo and Hill, 2006; Centrón *et al*., 2013). Indeed, in everyday speech many Paraguayan mammals are more commonly referred to by their Indigenous (generally Guaraní) names than by their Spanish names (Cartes, 2014).

Subsequent to the colonization of the Americas by southern Europeans, natural history observations began to be recorded in written form, including the narratives of explorers and naturalists from several European countries. The travels and writings of these early explorers and colonists were reviewed comprehensively by Warren (1949). Although most of these did not specifically mention mammals, many of them do provide vivid and informative impressions of the region during the 16th and 17th centuries. Another detailed account of these early naturalists was provided by Ferreiro (1965), in which the author included useful historical and social context as background for the gradual development of natural history knowledge during that period. Where the information was available to him, Ferreiro also indicated which reports were based on personal observations, which were based on written communications from the actual explorers, and which were based on anecdotes, or on "common knowledge" of the inhabitants of an area.

Gorham (1973b) also reviewed the history of natural history in Paraguay, providing additional information, and emphasizing the importance of Indigenous knowledge in understanding this history. Importantly, he presents a useful and detailed explanation of what was recorded by the early European explorers regarding the relationship of the Indigenous people to the landscape, which he postulates may have been interactive, in the sense of the human occupants modifying vegetative cover in important ways (primarily by fire), resulting in "disclimax" savannahs in areas that otherwise would have been primarily forested. Gorham (1973b) also reviewed the progression of natural history accounts provided by various visitors to Paraguay. In mammalogical terms, key among these early visitors were Jesuit priests (Techo, 1897) including José Sánchez Labrador (Saenz Ollero *et al*., 1989), Martín Dobrizhoffer (Dobrizhoffer, 1822) and Pedro Blas Noseda.

A recent account of Jesuit naturalists is provided by Aguilar (2017) as they passed through the "Manzana de las Luces" in Buenos Aires, in their travels between Europe and Paraguay, which at that time comprised much of the Southern Cone of South America. In addition to a brief chronology of their work in Paraguay, he provides brief biographies of 15 Jesuit scientists who were associated in one way or another with the Manzana de las Luces.

Figure 8. Photograph of a painting of Félix de Azara, by Francisco Goya. The painting and the photograph are in the public domain.

During the late 1700s, Félix de Azara (1742–1821) (**Fig. 8**), who lived in Paraguay from 1781–1800, was certainly the most influential naturalist working in Paraguay. His volumes (1801, 1802) on the quadrupeds of Paraguay and the Río de la Plata, produced using some data contributed by Pedro Blas Noseda (Jesuit parish priest at San Ignacio Guazú), stand as the first comprehensive works on the mammals of the country. The French edition (Azara, 1801) was published first (without the author's approval), and is the basis of all of the scientific names derived from his work which were coined later by authors such

as Anselme Gaëtan Desmarest, Johann Fischer von Waldheim, Étienne Geoffroy Saint-Hilaire, Karl Wilhelm Illiger and Ignaz Franz Werner von Olfers, among others. The Spanish edition (Azara, 1802) was stated by the author to be the definitive work, but contains significant differences from the French version. The life and work of Azara is chronicled by Contreras (2010, 2011a, b, 2012). The meticulous observations contained within these texts were not matched until the work of Johann Rudolph Rengger, a Swiss naturalist who travelled widely in eastern Paraguay (Ramella and Perret, 2011), and who produced a detailed tome on the mammals he encountered. Rengger (1830) described several new taxa, and provided careful morphological and behavioural observations which extensively referenced the earlier work of Azara.

In the several decades following independence from Spain in 1811, Paraguay experienced first an isolationist government, then a progressive administration, and finally a catastrophic war. In the first decades of the 19th century several naturalists were active in Paraguay, including Aimé Bonpland (Humboldt and Bonpland 1821–1822; Cerruti, 2023) (**Fig. 9**), Eberhard Munck af Rosenschöld (Munck af Rosenschöld, 1955), Domingo Parodi (Toursarkissian, 1971), Alfred Demersay (Demersay, 1860–1865), and Alfred Du Graty (Du Graty, 1862), though these were concerned mainly with botanical subjects. Following this period, the second half of the 19th century saw little activity or progress in Paraguayan

Figure 9. Photograph of Aimé Bonpland. This photograph is in the public domain.

natural history, with the country ravaged by the destruction of the Triple Alliance War (1864–1870). A rare exception to this are the works and expeditions of John Graham Kerr (1869–1957) (**Fig. 10**) who visited the Chaco and Pilcomayo regions of Paraguay between 1889–1891 and 1896–1897 (Kerr, 1891, 1892, 1901, 1968).

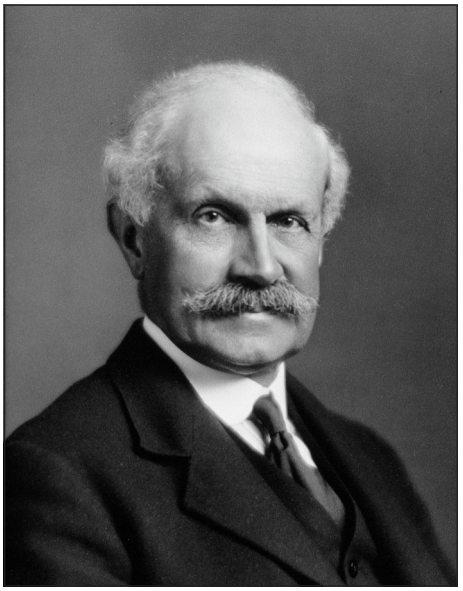

Figure 10. Photograph of John Graham Kerr. Photo credit: T. & R. Annan & Sons Ltd.

The first half of the 20th century was a period of increasing interest in the natural history of this largely unknown region. Much of this interest was still based in Europe (*e.g.*, Thomas, 1901a, 1901b, 1903, 1913, 1915, 1924; and Krumbiegel's numerous publications during 1940–42). However, naturalists from North America (Agar, 1911; Miller, 1913; Wetmore, 1926; Rehn, 1934; and Kaempfer's work in Naumburg, 1928, 1935, 1937, 1939; and Camargo, 1962) were also increasingly active. Much of the material which provided the basis for some of these works was supplied by locally-based collectors such as Guillermo Foster (1873–1915), Jakob Unger Sr. (1894–1959), Juan Francisco Humberto Schade (1902–1976), Adolfo Neunteufel (1909–1984?), and Peter Willim (1912–1999). The life of Unger Sr. is chronicled by Shergalin (2013), and Neunteufel wrote an autobiography about his collecting exploits (Neunteufel, 1941). Foster produced one publication on mammals, a listing of the bats of Paraguay (Foster, 1905), which drew very heavily from an earlier publication by Thomas (1901a).

Emilio Budin (1877–1935) was a Swiss-born naturalist who moved at an early age with his parents to Argentina. His 1906–1907 expedition in the Argentine and Paraguayan Chaco is described at length by Barquez (1997). Although most of the trip was in the Argentine Chaco, he recorded two species of mammals at two localities near the Pilcomayo River in the southern Paraguayan Chaco.

Perhaps the most distinguished Paraguayan-based scientific chronicler of this period however was Moisés S. Bertoni (1857–1929) (**Fig. 11**), who immigrated from Switzerland to Paraguay in 1887, where he lived until his death. He produced several publications considered seminal in the development of modern natural history in Paraguay (*e.g.*, M. S. Bertoni, 1900, 1914, 1918, 1921), as well as founding several journals, including *Anales Científicos Paraguayos*, which had a print run from 1901 until approximately 1922. He assigned his son, Arnaldo de Winkelried Bertoni (1878–1973) (**Fig. 12**) to the study of the biological sciences, and Winkelried made a number of important mammalogical contributions (Bertoni, A. de W., 1904a, b, 1910, 1914a, b, 1915, 1923, 1924a, b, 1925a, b, c, d, 1928, 1930, 1931, 1932, 1939). The life and work of Winkelried is chronicled in Contreras (2019), and his mammalogical contributions are reviewed by P. Smith (2024). The life and work of Moisés is detailed by Baratti and Candolfi (1994, 2019).

Figure 11. Photograph of Moisés S. Bertoni. This photograph is in the public domain.

Figure 12. Photograph of Arnaldo de Winkelried Bertoni. This photograph is in the public domain.

A group of Paraguayan naturalists, including Guillermo Foster and the Bertonis, founded the Museum of Natural History of the Scientific Society of Paraguay in 1912, located at the Botanical Garden of Asunción. The museum served as repository for part of Foster's collections that were not sent abroad, as well as for private collections (Scala, 1987). In 1921 the *Revista de la Sociedad Científica del Paraguay* (Journal of the Scientific Society of Paraguay) began publication. Although not always published regularly, this journal continues to be active, and besides those of Winkelried Bertoni a few other works on mammals have appeared in the journal (Schouten, 1936; Podtiaguin, 1944; ENPAB – GEF, 2004; Cartes *et al.*, 2010, 2011; Owen and P. Smith, 2019; Hiebert *et al.*, 2020; and perhaps a few others in volumes 1–11, which we were unable to review).

Notorious among the foreign collection expeditions of the early 20th century was the Krieg Expedition. Hans Krieg (1888–1970) was the director of the Zoologisches Forschungsmuseum Alexander Köenig (ZFMK) in Bonn, Germany, and leader of the Deutsche

Gran Chaco Expedition, which visited Paraguay from May 1931 to March 1932. Krieg considered himself an ambassador for the Third Reich stating prior to departure that "it is necessary that the people who go abroad are uncompromising and honest supporters of the Third Reich without appearing from the outset as propagandists." The expedition later fell foul of Brazilian law (which had been broken) and significant parts of the collection were confiscated (Sá and da Silva, 2016). Nonetheless some was smuggled back to Germany and the mammalogical results of this expedition were published in a series of works by Ingo Krumbiegel (1903–1990) (Krumbiegel, 1940a-g, 1941a-f, 1942a-d).

Figure 13. Photograph of Boris Podtiaguin. From the archive of Lucia Giovine.

Boris Georgievich Podtiaguin (1892–1959) (**Fig. 13**) was a Russian zoologist and collector, born in Shalsky, who arrived in Paraguay on 22 February 1936. He began work at the Sociedad Científica del Paraguay in 1940, later becoming head of the museum. Through principally concerned with ornithology and entomology, his contribution on Paraguayan Chiroptera was one of the most significant locally-published mammalogical treatises of this period (Podtiaguin, 1944). He eventually committed suicide, hanging himself in the building of the Sociedad Científica on 12 May 1959. His life is chronicled by Shergalin (2014).

Between 1953 and 1985 Julio Rafael Contreras (1933–2017) (**Fig. 14**) made a series of field trips to Paraguay sampling the mammal and avian faunae of the country, finally relocating permanently in the country in the city of Pilar in 2002 (Ríos and Capdevilla, 2019). He published numerous contributions on Paraguayan mammals, including the description of two endemic species of tuco-tuco (*Ctenomys*) (Contreras, 1992, 1993, 1994, 2000, 2001, 2010, 2011a, b, 2012; Contreras and Contreras, 1992, 1995; Contreras and Roig,

1992; Contreras and Silvera Abalos, 1995; Giménez *et al.*, 1997; Contreras *et al.*, 2001, 2003; Contreras and Teta, 2003). In the 1990s, he founded the Institute of Bioecology and Subtropical Research (IBIS), associated with the National University of Pilar, Ñeembucú Department. The small mammal collection held by IBIS is now curated by Fundación Para La Tierra which resides in the former residence of Prof. Contreras. His life and work were chronicled by Gasparri *et al.* (2019).

Figure 14. Photograph of Julio Contreras Roqué. Photograph by staff of Para La Tierra.

An increase in knowledge and interest in local faunas led to the establishment, in the mid and late 1970s, of a cooperative effort between the Forest Service of the Paraguayan Ministry of Agriculture and Livestock, the United States Fish and Wildlife Service (USFWS) and the U.S. Peace Corps, with the objective of conducting a complete evaluation of the fauna and of initiating studies on the natural history and conservation status of many vertebrate species of Paraguay. This effort resulted in the establishment of the National Museum of Natural History. Signficant researchers forming part of this project were Daniel M. Brooks, who was sent to the Paraguayan Chaco from August 1989 to August 1990 as a Research Associate for the Zoological Society of San Diego to manage Proyecto Taguá at Fortín Toledo (now Centro Chaqueño para la Conservación e Investigación – CCCI). He also worked on his Master's thesis (Brooks, 1993a) and published a number of short papers on the mammal fauna of the region, especially dealing with carnivores (Brooks, 1990a-d, 1991a-c, 1992a-d, 1993a, b, 1995, 1996a, b); and the primatologist Jody Stallings (Stallings, 1984a, 1985, 1986; Stallings and Mittermeier, 1983; Stallings *et al.*, 1989), who also produced a Master's thesis (Stallings, 1984b) that represented the first significant study of the ecology of Paraguayan primates.

In 1972, Philip Myers and Ralph Wetzel began independent projects that led to a joint effort to review the country's mammal fauna. Thousands of specimens were collected, which

were deposited in collections in Paraguay, the Museum of Vertebrate Zoology (University of California, Berkeley), the Museum of Zoology (University of Michigan) and the University of Connecticut Museum (UCONN, listed as UCS in Chapter 5). Research based on these collections has produced reviews of several groups of mammals (Myers, 1989; Myers and Carleton, 1981; Wetzel, 1980, 1985). They also generated first records of several species for Paraguay (Wetzel and Lovett, 1974; Myers and Wetzel, 1979, 1983; Myers *et al.*, 1983), the description of two rodent species (Myers, 1977a; Myers and Carleton, 1981) and an armadillo (Wetzel, 1980), and publications on natural history and other aspects of the biology of various species (Berrie, 1978; Myers, 1977b, 1981; Nachman, 1992a, b; Nachman and Myers, 1989; Wetzel, 1982). Perhaps the most impressive result of these efforts was the rediscovery of a peccary species which was believed to have been extinct since the Pleistocene (Wetzel *et al.*, 1975; Wetzel, 1981). This species has served as the focus of a series of studies on systematics and ecology (Mayer and Brandt, 1982; Benirshcke *et al.*, 1985; Byrd *et al.*, 1987; Taber, 1990, 1991; Brooks, 1992a; Taber *et al.*, 1993; Wetzel, 1977a, b, 1981). Paraguay was also visited several times at the end of the 1970s and the beginning of the 1980s by researchers from the Geneva Museum. The collections made by these researchers served as the basis for the publications by Baud (1981, 1989) and Roguin (1986).

An extensive volume on nematodes of Paraguayan vertebrates including mammals was published by Rafael Masi Pallarés (1924–2009), who was a medical doctor, parasitologist and long-time faculty member in the Facultad de Ciencias Agrarias y Veterinaria at the National University (Masi Pallarés, 1990). A volume on the vertebrates of Paraguay (including seven chapters pertaining to mammals) was published by Masi Pallarés (2006). He also published a number of articles on parasites and pathology of mammals and other vertebrates (*e.g.*, Masi Pallarés and Valese, 1970; Masi Pallarés and Benítez Usher, 1982). Other parasitological publications pertaining to Paraguayan mammals have also been published in the past several decades, including Goff and Whitaker (1984a, b), Whitaker and Abrell (1997), Lareschi *et al.* (2004), Durden *et al.* (2006), Guglielmone *et al.* (2011), Notarnicola and de la Sancha (2015), Kane and R. Smith (2020), and others listed below resulting from the Texas Tech University research project.

Between 1995 and 2005, Robert D. Owen, Michael R. Willig, Donald Gettinger and students from Texas Tech University, in collaboration with the Museo Nacional de Historia Natural del Paraguay (MNHNP) and the Dirección General de Parques Nacionales y Vida Silvestre (part of the Secretaría de Medio Ambiente del Paraguay, SEAM, since 2000), continuously collected and studied Paraguayan mammals and their ectoparasites. This cooperation resulted in numerous publications (*e.g.*, López-González *et al.*, 1998, 2001; Willig *et al.*, 2000; López-González and Presley, 2001; Chu *et al.*, 2003, 2011; Andelman and Willig, 2002; Gorresen and Willig, 2004; López-González, 2004; Stevens and Willig, 2004; Stevens *et al.*, 2007, 2010; Presley, 2004, 2005, 2007, 2011; Dick, 2005, 2007; Dick and Gettinger, 2005; Gorresen *et al.*, 2005; Graciolli *et al.*, 2006; Dick, 2007; de la Sancha *et al.*, 2007; Presley and Willig, 2008; Presley *et al.*, 2009; Owen *et al.*, 2010; Gettinger *et al.*, 2011; Stevens and Amarilla-Stevens, 2012). An important part of the material collected during this period is deposited in Paraguayan collections and is currently being studied by Paraguayan and foreign researchers. A short collecting expedition in the Dry

Chaco by the Museum für Tierkunde Dresden from January to early February 2001 was accompanied by Jakob Unger Jr., recording 41 mammal species, some of which were collected and resulting in a few mammal publications (Ziegler *et al.*, 2002a, b).

During this period, Richard Stevens and Noé de la Sancha began working with small mammals in Paraguay as Texas Tech University graduate students, writing their doctoral dissertations on different aspects of small-mammal ecology (Stevens, 2002; de la Sancha, 2010). They have since continued working independently in Paraguay, and have authored a number of publications on Paraguayan mammals (*e.g.*, de la Sancha *et al.*, 2011, 2012, 2014, 2017, 2020; de la Sancha, 2014; de la Sancha and D'Elía, 2015; Stuhler *et al.*, 2019; Stevens and Amarilla-Stevens, 2021; Stevens and Grimshaw, 2020; Stevens and Guest, 2022; Vrla *et al.*, 2023).

Currently, Robert D. Owen continues to work on different aspects of Paraguayan mammals, in collaboration with the British naturalist Paul Smith, the American virologist Colleen Jonsson and others (*e.g.*, P. Smith *et al.*, 2013, 2023c; Owen, 2013, 2020, 2021; Owen *et al.*, 2014, 2018a, b, 2019, 2020, 2022, 2023a, b, c; Torres *et al.*, 2015, 2022; P. Smith and Owen, 2016, 2017; Gettinger and Owen, 2016; Eastwood *et al.*, 2018; Barreto Cáceres and Owen, 2019; Owen and Smith, 2019; Sánchez-Martínez and Owen, 2021; Camp *et al.*, 2021; Owen and Camp, 2021; Weiler Gustafson and Owen, 2021; Spruill-Harrell *et al.*, 2021; Owen and Cubilla, 2022, Owen *et al.*, 2022, 2023, 2024; Zuercher *et al.*, 2022).

Fundación Para La Tierra (PLT), a non-profit foundation, was established in 2010 as a research-oriented conservation organization, with one objective being to build a biological research collection. Initially based at Reserva Privada Laguna Blanca (San Pedro Department), they were forced to leave there in 2017, following a legal dispute among the owners of the property. Currently located in the Centro IDEAL in Pilar, PLT runs the only permanent, locally-based primatology projects currently running in Paraguay (P. Smith *et al.*, 2021b; R. Smith *et al.*, 2023) and is continuing to develop a noteworthy collection of both invertebrates and vertebrates, including mammals. A large number of mammalogy publications have resulted from their ongoing research (P. Smith *et al.*, 2011, 2012a, b, 2013, 2021b, 2023, 2024; P. Smith, 2012, 2015, 2019, 2020, 2022a, b, 2023, 2024; Owen *et al.*, 2014, 2018a, 2023, 2024; R. Smith, 2016, 2017; R. Smith and Briggs, 2016; P. Smith and Owen, 2016, 2017; R. Smith *et al.*, 2017, 2020, 2021, 2022; R. Smith and Payne, 2017; Pheasey *et al.*, 2018; P. Smith and Ríos, 2018, 2024; Owen and P. Smith, 2019; Ríos *et al.*, 2019; P. Smith and R. Smith, 2019, 2023; Kane and R. Smith, 2020; Van Lunteren *et al.*, 2021; Wellian and R. Smith, 2021; Alesci *et al.*, 2022; P. Smith and Teta, 2022; Jordan *et al.*, 2023; P. Smith and Hicks, 2023). The catalogue of Para La Tierra publications, including those on mammals and primatology, is available online for download at https://www.paralatierra.org/scientific-papers.

In 2012, the Conservation Program for Bats in Paraguay (PCMPy) was established, and has since affiliated with a network of bat conservation organizations in other Latin American countries. This collaboration has resulted in the designation of nine Important Bat Areas in Paraguay (Barquez *et al.*, 2022). In August 2013, the organizational meeting of the Asociación Paraguaya de Mastozoología (APM https://asopyamasto.wixsite.com/asopyamasto) was held in Asunción, with more than 70 participants, and seven mammalogical congresses have since been held (to 2024). Recently, the APM has joined the Latin

American Mammalogy Network (RELAM). The two UNA graduate programs mentioned below and these two associations represent important milestones for the development of mammalogy as a recognized research field and as appropriate graduate training for academic or other professional careers in Paraguay.

A transboundary collaborative project studying the ecology of the jaguar and aimed at coordinating international conservation efforts has resulted in several publications (McBride and McBride, 2007; Thompson and Martínez, 2015; Thompson and Velilla, 2017; McBride and Thompson, 2018, 2019; Romero-Muñoz *et al*., 2019; Thompson *et al*., 2020, 2021a, 2022).

Numerous publications that have expanded the knowledge of Paraguayan mammals have been produced in recent decades, increasingly as collaborations between Paraguayan and foreign authors. These have included works on mammalian systematics and taxonomy, and parasites and pathogens, as well as studies of community and autecology, behavior and feeding. Studies of distribution, biogeography and effects of anthropogenic landscape and habitat alterations have been appearing with increasing frequency in the literature. These publications are both easily accessed electronically, and too numerous to list here. A *Google Scholar* search of publications from 2014 to May 2023, using the keywords "Paraguay" and "mammal", returns 15,900 results. However, there are few locally-based journals for researchers to publish mammalogical work, with only the *Boletín del Museo Nacional de Historia Natural del Paraguay*, *Reportes Científicos de la FACEN* and *Revista de la Sociedad Científica del Paraguay* still extant. *Paraquaria Natural*, published by the NGO Guyra Paraguay, featured eight volumes from 2013, but ceased publication in 2022 and contains a small number of mammalogical papers (Cartes *et al*., 2013, 2015; Centrón *et al*., 2013; Tuttle *et al*., 2013; Cartes, 2014, 2015; Campos Krauer *et al*., 2015; Altrichter *et al*., 2016; Mandujano, 2017; González *et al*., 2019; Hernández-Sanchez *et al*., 2019). *Bellbird*, published in four volumes between 2006 and 2010 by FAUNA Paraguay, also contains a few mammalogical papers (Smith, 2007; Aguilar Julio, 2008a-c; McBride *et al*., 2010).

Although Paraguay does not have a graduate program dedicated exclusively to the training of mammalogists, some Paraguayan students have carried out postgraduate studies in foreign institutions and have returned to the country. A few biologists have obtained doctoral degrees in Argentina or Brazil, and currently (mid-2023) one is completing a doctoral program at the Instituto "Miguel Lillo" (Tucumán, Argentina) and four at the University of Salamanca (Spain), one of whom has completed her thesis (Weiler, 2023).

In 2008, the Faculty of Exact and Natural Sciences of the National University of Asunción initiated a Master's degree in Biological Sciences with an emphasis in Conservation Biology, and in 2011 an emphasis in Biodiversity and Systematics was added to the program. Through 2022, this program has graduated 35 students (G. González, pers. com.). In addition, the Faculty of Agricultural Sciences now has a Master's degree program in Natural Resource and Environmental Management Planning. Several students in both graduate programs have conducted thesis research pertaining to mammals, under the tutelage of both Paraguayan and international major advisors.

Myers *et al*. (2002) published the first modern comprehensive treatment of the mammals of Paraguay. In it, they also included the first historical review devoted specifically to

mammalogy, providing considerable detail especially of the work in mammalogy during the second half of the 1900s. A small number of books dealing specifically with Paraguayan mammals have been published, most of these in recent years and most non-technical (Azara, 1801, 1802; Rengger, 1830; Villalba and Yanosky, 2000; Esquivel, 2001; Neris *et al.*, 2002; López-González, 2005; Velázquez and Ramírez Pinto, 2014; Villalba *et al.*, 2018; Weiler *et al.*, 2019, 2023; Torres *et al.*, 2022). Other significant publications are worthy of mention. The conservation status of the Paraguayan mammal fauna was first attempted in 1998 (Gamarra de Fox *et al.*, 1998) and this was most recently updated in 2017 (APM / SEAM 2017). López-González *et al.* (2014) provided an extensive review of the written history of mammalogy in Paraguay which we add to and update here.

The latest checklist of Paraguayan mammals was published by de la Sancha *et al.* (2017). Below we outline the recent taxonomic changes that have taken place since that publication, clarifying that the number of extant native species now considered to occur in Paraguay is 183:

Didelphimorphia: Didelphidae

Marmosa constantiae (Thomas, 1904): Paraguayan specimens assigned to this taxon were reidentified as ***Marmosa rapposa*** (Thomas, 1889) by Voss *et al.* (2020).

Metachirus nudicaudatus (É. Geoffroy, 1803): Paraguayan specimens were assigned to ***Metachirus myosuros*** (Temminck, 1824) by Voss *et al.* (2019).

Monodelphis brevicaudis (Erxelben, 1777): Code Compliant objections to the use of this name were presented by Voss *et al.* (2009), Vilela *et al.* (2010) and P. Smith (2024). The name is considered a senior synonym of ***Monodelphis dimidiata*** (Wagner, 1847) which replaces it and *M. brevicaudis* should not be used as an alternative to this long-standing name (Voss, 2022).

Philander frenatus (Olfers, 1818): The taxon that occurs in the Atlantic Forests of eastern Paraguay should now be known as ***Philander quica*** (Temminck, 1824) following Voss *et al.* (2018). The type specimen of *P. frenatus* was collected in Amazonia and is a junior subjective synonym of *P. opossum* (Linnaeus, 1758).

Philander opossum (Linnaeus, 1758): Paraguayan populations previously attributed to this species are assignable to ***P. canus*** (Osgood, 1913), which was formerly treated as a subspecies or synonym (Voss *et al.*, 2018).

Xenarthra: Cingulata

The species assigned to the Dasypodidae subfamilies Euphractinae and Tolypeutinae are now separated in the family Chlamyphoridae following Gibb *et al.* (2015) and Delsuc *et al.* (2016). The Chlamyphoridae consists of three subfamilies: Chlamyphorinae (*Calyptophractus*), Euphractinae (*Euphractus*, *Chaetophractus*), and Tolypeutinae (*Cabassous*, *Tolypeutes*). The family Dasypodidae is represented by a single genus in Paraguay (*Dasypus*).

Dasypus hybridus (Desmarest, 1804): Morphology, morphometrics and molecular phylogeny analyses performed by Feijó *et al*. (2018, 2019) suggested this species should be considered as a **subspecies of *Dasypus septemcinctus*** Linnaeus, 1758.

Cabassous unicinctus (Linnaeus, 1758): The southern subspecies was split as a distinct species, ***Cabassous squamicaudis*** (Lund, 1845) by Feijó and Langguth (2013), and this has been corroborated by molecular studies (Quintela *et al*., 2020).

Lagomorpha: Leporidae

Sylvilagus brasiliensis (Linnaeus, 1758): As correctly surmised by de la Sancha *et al*. (2017) there is a species complex within the populations traditionally referred to this name. This was identified by Ruedas *et al*. (2017, 2019), who confirmed that *S. brasiliensis* refers to populations north of the Amazon. Two names are available for populations south of the Amazon, *S. minensis* Thomas, 1901:535 (from Río Jordão and Lagoa Santa) and *S. paraguensis* Thomas, 1901:549 (type locality: Sapucay, E of Asunción, Paraguay). Ruedas *et al*. (2017:53) state that these are unlikely to represent the same biological species, but recommend the usage of ***S. minensis*** "*pro tempore*, while further studies are being undertaken." However, should these two indeed prove to be distinct the name ***S. paraguensis***, which has a Paraguayan type, may be applicable.

Chiroptera: Molossidae

Molossus rufus (É. Geoffroy, 1805): Southern South American populations of *Molossus rufus* were split as ***M. fluminensis*** Lataste, 1891 by Loureiro *et al*. (2020).

Chiroptera: Vespertilionidae

Lasiurus cinereus (Palisot de Beauvois, 1796): The molecular differentiation of South American populations was demonstrated by Baird *et al*. (2015) who used ***Aeroestes villosissimus*** (É. Geoffroy St.-Hilaire, 1806) for this species.

Lasiurus ega (Gervais, 1856): The species was placed in *Lasiurus* Gray, 1831, until the molecular distinctiveness of ***Dasypterus*** Peters, 1870 was recognized and its usage as a full genus revived by Baird *et al*. (2015).

All New World bats formerly included in ***Eptesicus*** were assigned to a new genus ***Neoeptesicus*** by Claudio *et al*. (2023).

Primates: Callitrichidae

Callithrix jacchus (Linnaeus, 1758): A feral population was reported as established in central Paraguay by P. Smith *et al*. (2021b). Feral species were omitted by de la Sancha *et al*. (2017), but this species had not been previously associated with Paraguay.

Carnivora: Felidae

Puma yagouaroundi (É. Geoffroy Saint-Hilaire, 1803): The latest classification consensus on world Felidae returned this species to the monotypic genus ***Herpailurus*** Severtzov, 1858 while acknowledging that there is no clear resolution to the species placement as yet (Kitchener *et al*., 2017).

Artiodactyla: Tayassuidae

Pecari tajacu (Linnaeus, 1758): Acosta *et al*. (2020) demonstrated that the correct generic name applicable to this species is ***Dicotyles*** Cuvier, 1816 and *Pecari* Reichenbach, 1835 is a junior synonym.

Catagonus wagneri (Rusconi, 1930): In a phylogenetic study of fossil and extant tayassuids, Dutra *et al*. (2017) concluded that the extant Chacoan peccary should be referred to by the binomial ***Parachoerus wagneri***. This taxonomic proposal has not yet been incorporated either by the IUCN Peccary Specialist Group or the online version of Wilson and Reeder (2005).

Artiodactyla: Cervidae

Mazama gouazoubira (G. Fischer von Waldheim, 1814): Bernegossi *et al*. (2023) resurrected the genus ***Subulo*** H. C. Smith, 1827 for this species and designated a Paraguayan neotype.

Rodentia: Cricetidae

Abrawayaomys ruschii Souza Cunha and Cruz, 1979: Reported as a new species and genus for Paraguay by de la Sancha *et al*. (2020).

Delomys dorsalis (Hensel, 1872): Reported as new for Paraguay by Owen *et al*. (2018a).

Holochilus vulpinus (Brants, 1827): Do Prado *et al*. (2021) again employed the name ***Holochilus brasiliensis*** Desmarest, 1819 for the member of the genus occupying the Atlantic Forest and Pampas biomes (including eastern Paraguay).

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5 PARAGUAYAN MAMMALS IN MUSEUMS

Although the Paraguayan mammalian fauna is often described as "understudied" or "poorly known", it is not a fauna which has been poorly collected, at least in terms of numbers of specimens. We are aware of over 31,000 extant mammal specimens from Paraguay, housed in at least 46 collections in 13 countries in Europe and the Americas. The number of Paraguayan mammals housed in those collections ranges from one to over 6,200 specimens. A little over one-third of the specimens are housed in Paraguayan collections, with the remaining two-thirds in other countries (Gamarra de Fox and Barreto, 2017). Over one-half of the specimens (nearly 17,000) are deposited in collections in the USA, which includes 18 collections holding Paraguayan mammals. Other countries housing more than 100 specimens include Argentina, England, Germany, Spain, and Switzerland (**Table 1**, **Fig. 15**).

Table 1. Museum acronyms, names, locations and approximate number of mammal specimens held.

Acronym*	Museum name	Location	# of specimens
AMNH	American Museum of Natural History	New York, NY, USA	1199
ASNHC	Angelo State Natural History Collection	San Angelo, TX, USA	1
BMNH	The Natural History Museum	London, England	350
BW	?	Germany?	78
CBMI–M	Colección Biológica del Museo de Itaipú – Mamíferos	Hernandarias, Paraguay	237
CCCI	Centro Chaqueño para la Conservación y la Investigación	Fortín Toledo, Paraguay	0
CML	Colección Mamíferos Lillo, Universidad Nacional de Tucumán	Tucumán, Argentina	46
CZPLT	Colección Zoológica de la Fundación Para La Tierra	Pilar, Paraguay	1117
DMNS	Denver Museum of Nature and Science	Denver, CO, USA	4
EBD	Estación Biológica de Doñana	Seville, Spain	315
FACEN	Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Asunción	Asunción, Paraguay	176
FCA	Facultad de Ciencias Agrarias, Universidad Nacional de Asunción	Asunción, Paraguay	100
FMNH	Field Museum of Natural History	Chicago, IL, USA	1427
IBIS	Instituto de Bioecología e Investigaciones Subtropicales	Pilar, Paraguay	61
IIBP-M	Instituto de Investigación Biológica del Paraguay, Mammal Collections	Asunción, Paraguay	77

IRSCNB	Royal Belgian Institute of Natural Sciences	Brussels, Belgium	41
JUM	Jakob Unger Museum	Filadelfia, Paraguay	55
KU	University of Kansas Natural History Museum	Lawrence, KS, USA	108
LACM	Natural History Museum of Los Angeles County	Los Angeles, CA, USA	1
LSUMZ	Louisiana State University, Museum of Zoology	Baton Rouge, LA, USA	42
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"	Buenos Aires, Argentina	266
MCNB	Museum of Natural Sciences of Barcelona	Barcelona, Catalonia, Spain	3
MCNM	Museo de Ciencias Naturales de Madrid	Madrid, Spain	6
MCZ	Museum of Comparative Zoology, Harvard University	Cambridge, MA, USA	169
MHA-EBY	Museo Histórico Ambiental, Entidad Binacional Yacyretá	Ayolas, Paraguay	44
MHNG	Swedish Museum of Natural History	Stockholm, Sweden	1
MNHNP	Museo Nacional de Historia Natural del Paraguay	San Lorenzo, Paraguay	6000
MNHNU	Museo Nacional de Historia Natural de Uruguay	Montevideo, Uruguay	9
MJBZA	Museo del Jardín Botánico y Zoológico de Asunción	Asunción, Paraguay	
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro	Rio de Janeiro, Brazil	17
MSB	Museum of Southwestern Biology, University of New Mexico	Albuquerque, NM, USA	259
MTD	Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde	Dresden, Germany	47
MVZ	Museum of Vertebrate Zoology, University of California–Berkeley	Berkeley, CA, USA	1167
MZUSP	Museu de Zoologia da Universidade de São Paulo	São Paulo, Brazil	15
NHMG	Muséum d'histoire naturelle Geneve	Geneva, Switzerland	1645
O	Natural History Museum, University of Oslo	Oslo, Norway	5
OKMNH	Sam Noble Museum of Natural History, University of Oklahoma	Norman, OK, USA	10
RDO	Collection of Robert D. Owen (temporary, to be deposited in other collections)	Asunción, Paraguay	4166
ROM	Royal Ontario Museum	Toronto, Ontario, Canada	7
TCWS	Texas Cooperative Wildlife Collection, Texas A&M University	College Station, TX, USA	2
TTU	Museum of Texas Tech University	Lubbock, TX, USA	6277
UAM	University of Alaska Museum of the North	Fairbanks, AK, USA	97
UCS	University of Connecticut	Storrs, CT, USA	1869
UF	University of Florida, Florida Museum of Natural History	Gainesville, FL, USA	171
UMMZ	University of Michigan Museum of Zoology	Ann Arbor, MI, USA	3223
USNM	National Museum of Natural History, Smithsonian Institution	Washington, DC, USA	931
Total			**31841**

* Most acronyms are from: Sabaj, M.H. 2023. Codes for Natural History Collections in Ichthyology and Herpetology (online supplement). Version 9.5 (10 Nov 2023). Electronically accessible at https://asih.org, American Society of Ichthyologists and Herpetologists, Washington, DC. For museums not listed in this reference, the Vertnet code is used; other acronyms were provided by museum personnel.

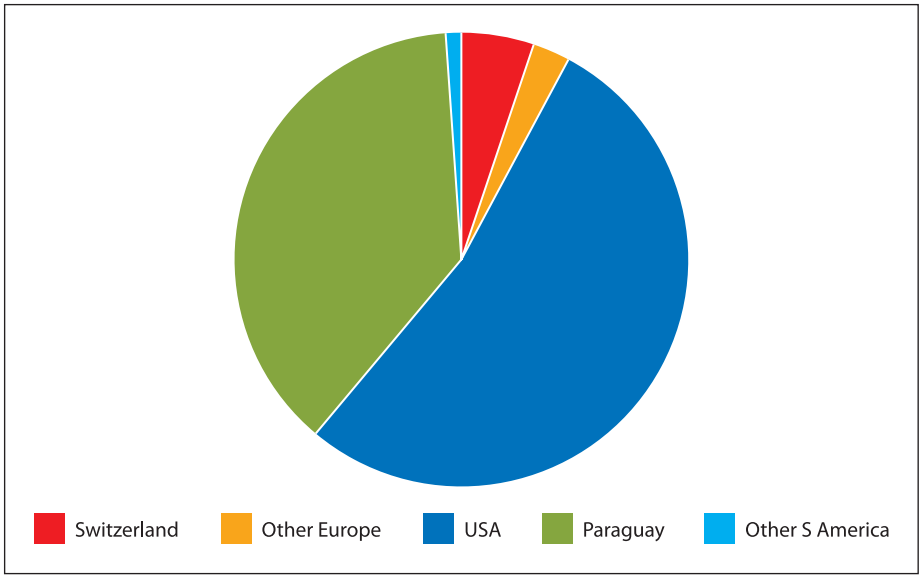

Figure 15. Graph showing numbers of Paraguayan mammal specimens housed in collections in Europe and North and South America. **Other Europe** includes England, Germany, Spain, Belgium, Sweden and Norway. **Other S America** includes Argentina, Uruguay and Brazil. See **Table 1** for detailed information.

More distressing is the number of lost specimens associated with the country, including globally important mammalogical collections amassed by historical naturalists working in Paraguay. These include the vast majority of the specimens and types of Félix de Azara, the entire mammal collection of Johann Rudolph Rengger (which was confiscated by President Rodríguez de Francia and subsequently lost), much of the material from which Arnaldo de Winkelried Bertoni worked (a tiny number of specimens survives in the uncatalogued Monumento Bertoni collection), and the original collections of the Museo Natural de la Sociedad Científica which was founded in 1912 in the Jardín Botánico (Scala, 1987).

Gamarra de Fox and Barreto (2017) provided basic information on eight active mammalogical collections that exist in Paraguay. However, they omitted two significant collections from their listings, that of the Fundación Para La Tierra in Pilar and the remaining Paraguayan collections of the Ungers exhibited in the Jakob Unger Museum in Filadelfia (which holds 55 specimens of 31 medium and large Chaco mammal species). The three largest mammalogy collections in Paraguay are those of the Museo Nacional de Historia Natural del Paraguay, founded in 1980 and based in San Lorenzo and with approximately 6,000 mammal specimens; the Robert D. Owen collection based in Asunción, with around 3,000 specimens; and the Colección Zoológica de Para La Tierra, based in Pilar, founded in 2010 and with around 1,200 specimens. Other Paraguayan collections contain fewer than 300 specimens (Gamarra de Fox and Barreto, 2017).

The Zoological Collection (CZCEN) of the Faculty of Exact and Natural Sciences (FACEN) was established and registered in 2007 with the Secretariat of Environment (now the Ministry of Environment and Sustainable Development – MADES). This collection is

still small but is active and growing, with around 200 mammal specimens, among other vertebrates. Since 2010 the FACEN also publishes a scientific journal, *Reportes Científicos de la FACEN*, which occasionally features mammalogical publications (Cacciali, 2010; Weiler and Nuñez, 2012; Barreto, 2018; Ortega and Weiler, 2018; Sánchez M., 2018; Salinas *et al*., 2022; Zaldivar *et al*., 2022).

The Instituto de Investigación de Paraguay (IIBP), in the city of Asunción, also holds a small mammal research collection (< 200 specimens) mainly consisting of Chiroptera and Didelphids, whilst the Colección Biológica de Itaipú Binacional (231 specimens) in Hernandarias and the Museo Histórico Ambiental de la Entidad Binacional Yacyretá (44 specimens) in Ayolas both contain a mixture of specimens collected locally in the reserve areas established by these hydroelectric entities and those salvaged from the zoological gardens that they established.

The Museo of the Facultad de Ciencias Agrarias (Universidad Nacional de Asunción, in San Lorenzo) was established in 1958 and contains about 100 taxidermied mammal specimens, the majority collected by the Swede Francisco Schade, but it suffers from poor cataloguing and is in a declining state. The Museo del Jardín Botanico y Zoológico de Asunción is another public exhibit, lacking specimen data and with poorly taxidermied specimens.

Reviewing Paraguayan mammal collections

To compile as complete as possible a listing of Paraguayan mammal specimens, we accessed the online databases provided by VertNet, MANiS, and GBIF. In addition, we have over the years, accumulated listings of mammal specimens housed in all collections which we were aware of, which house specimens collected from Paraguay. A number of these are not included in the online databases mentioned above. We also contacted the museums in the Southern Cone of South America from which we thought that collectors might have worked in Paraguay, and we contacted curators of museums (mostly in the USA and Paraguay) from which we were aware collectors had recently worked in Paraguay, to be sure our listing was as current as possible. Nonetheless, it is likely that there are some foreign collections of which we are unaware, and there is one small collection of Paraguayan mammals (Museo del Jardín Botanico y Zoológico de Asunción) for which we were unable to confirm their holdings. Moreover, the numbers reported here reflect digitized records, for the most part. Thus, museums which are currently active in accessioning and cataloging specimens, and digitizing the records, will have their collections of Paraguayan mammals incompletely reported here. These would include Texas Tech University, the Field Museum of Natural History, and several of the collections which are in Paraguay.

A listing of museums housing Paraguayan mammal specimens, and their acronyms, is provided in **Table 1**. This table, compiled in 2023, includes a small number of collections and specimens which were not included in the **Supplemental information tables** which are referenced below and were compiled earlier. For a number of the digital records which we obtained, locality information was not included. Thus, about 12% of our records have no information regarding which department they were collected in (**Table S1**).

Taxonomic patterns of Paraguayan mammalogical collections

Paraguay hosts ten orders of mammals, including native species belonging to 34 families (**Fig. 16**, **Table S2**). 391 records did not have identification information, and could not be assigned to a family (some of these were identified to order), or were species of non-native families (Bovidae and Suidae). Recognizing that mammalian systematics and taxonomy evolves at all taxonomic levels as our understanding of mammalian phylogenetic relationships continues to improve, we will follow Wilson and Reeder (2005) and authors therein, in ordinal and familial taxonomy in this paper. This reference is readily available both as hard copy and online at http://www.departments.bucknell.edu/biology/resources/msw3. The exception to this is that within Order Cingulata we recognize two families, Dasypodidae and Chlamyphoridae.

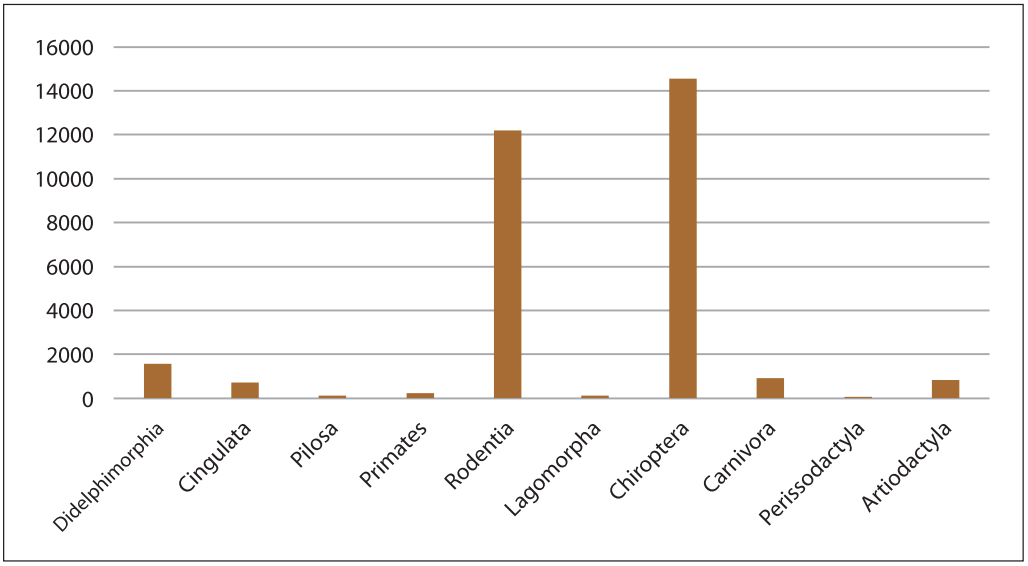

Figure 16. Graph showing numbers of Paraguayan specimens in each of ten mammalian orders represented in Paraguay. See **Supplemental table S2** for detailed information.

Bats (Order Chiroptera) and rodents (Rodentia) are by far the most extensively represented orders among collections, with over 14,500 and 12,100 specimens respectively, whereas anteaters (Pilosa), rabbits (Lagomorpha) and tapirs (Perissodactyla) are each represented with fewer than 100 specimens. Among the rodents, Family Cricetidae has over 11,100 specimens; among bats, Family Phyllostomidae includes about 8,000 specimens. A scarcity of Paraguayan specimens of Carnivores, Primates and Xenarthrans has been highlighted by authors reviewing their distribution (P. Smith and Ríos, 2018; P. Smith *et al.*, 2021b; P. Smith, 2022a, b).

Temporal patterns of collections of Paraguayan mammals

Intensive collections have been conducted only irregularly, and have generally been dependent on the efforts of one or a few individuals, with specimens going to one or a few collections (**Table S3**).

The oldest Paraguayan specimens which we are aware of are the very few surviving specimens collected by Félix de Azara which date from the late 18th century and are housed in the Museo de Ciencias Naturales de Madrid (Cabrera, 1912). Very few other specimens from the 19th century survive. These include a pair of "*Cebus apella*" specimens which were collected in 1846 by an unnamed collector which are housed in the Natural History Museum London, and an *Alouatta caraya* and a *Molossus molossus* collected in 1859 and housed in the USNM. Beginning in the 1890s, specimens were collected in every decade, with numbers ranging from 17 (1890s) to over 12,170 (1990s—**Fig. 17**, **Table S3**).

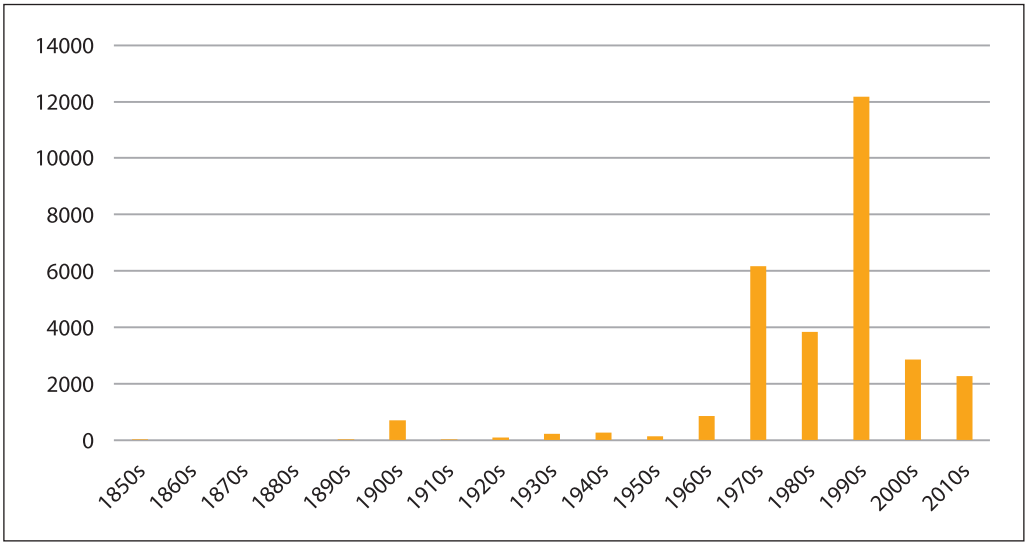

Figure 17. Graph showing numbers of mammalian specimens collected in Paraguay, by decade. See **Supplemental table S4** for detailed information.

In the early 20th century, most of the mammal collecting was by locally-based collectors (notably Guillermo Foster, Arnaldo de Winkelried Bertoni, Francisco Schade and Jakob Unger) who, as well as supplying foreign museums, also established local collections (most of which were subsequently lost). During the 1960s, several hundred specimens (mostly bats) were sent to the AMNH.

The two most productive decades to date for mammal collection were the 1970s (> 6000 specimens collected) and the 1990s (>12,000) representing a combined total of around 60% of Paraguayan mammals collected (**Table S4**). Most of the collecting of the 1970s was by Ralph Wetzel and co-workers (specimens to UCS) and Phil Myers (MVZ and

UMMZ). Although bats and cricetid rodents continued to predominate, these collections also included more didelphids, as well as larger mammals (felids, canids, and tayassuids).

During the 1980s a collaborative effort of the US Peace Corps, US Fish & Wildlife Service, the Smithsonian Institution, and the Paraguayan Ministry of Agriculture established the MNHNP, with over 1,500 specimens, mostly small mammals, being deposited there during that decade. The collecting work was documented in the *Biological Inventory News / Boletín del Inventario Nacional*, of which nine numbers were published between 1981 and 1989. This was a precursor to the *Boletín del Museo Nacional de Historia Natural del Paraguay*, which began publication in 1991 and has featured several mammalogical publications (Wilson and Gamarra de Fox, 1991; Ávila, 2004, 2015; Rumbo, 2010; Ríos Díaz *et al.*, 2014; Gamarra de Fox *et al.*, 2016, 2019; Teta and Ríos, 2017; Airaldi-Wood *et al.*, 2018; Gengler, 2018; Caballero-Gini *et al.*, 2020; Petters *et al.*, 2020; Owen and Cubilla, 2022) and continues to this day.

The large number of specimens in the 1990s was due primarily to Michael Willig, Robert D. Owen, and their students (TTU, MNHNP, FMNH, and RDO). These projects included a survey and inventory of over 30 localities in most of the country's departments, and several ecologically-oriented studies, and resulted in substantial collections of didelphids, cricetids, phyllostomids, molossids, and vespertilionids. Subsequent collections, primarily by Owen, were focused on non-volant small mammals, so fewer bats were collected during the 2000s and 2010s. These collections were first housed in RDO, from which they have been (didelphids and bats) or will be (rodents) deposited into MNHNP, the Colección Zoológica Para La Tierra (CZPLT), the Zoological Collection of the Faculty of Exact and Natural Sciences (CZCEN–Univ. Nacional de Asunción), the Instituto de Investigación Biológica del Paraguay (IIBP), and/or other Paraguayan collections.

Fundación Para La Tierra, a research-based conservation NGO, was founded in 2010, and has developed a significant zoological collection, with increasing holdings of mammalian specimens, particularly didelphids, cricetids, primates, carnivores and phyllostomids, the majority from the under-sampled San Pedro and Ñeembucú departments. The extensive chiropteran portion of the Robert D. Owen collection was also permanently transferred to the Para La Tierra collections.

The Zoological Collection of the Faculty of Exact and Natural Sciences (FACEN) houses specimens from research carried out by faculty and students of Department of Biology and financed mainly with funds from the Rectorate of the National University of Asunción and the National Council of Science and Technology of Paraguay (CONACYT), with support from the Department of Biology, the Directorate of Research and the FACEN (UNA).

Geographical Patterns of Collections of Paraguayan Mammals

A little over half (54%) of the records are from departments in the eastern part of the country (east of the Paraguay River) (**Table S5**). Of these, Canindeyú Department has by far the greatest number of specimens collected, due primarily to the work of Robert D. Owen and Richard Stevens in the Mbaracayú Natural Forest Reserve, as well as earlier work by Phil Myers and his students and colleagues. Other departments in the eastern region

represented by more than one thousand specimens are Itapúa, Paraguarí, and San Pedro. The collecting in San Pedro was primarily by Richard Stevens, collecting in Yaguareté Forest and by Fundación Para La Tierra at Rancho Laguna Blanca. Specimens from the eastern region of the country are heavily biased towards rodents and bats (**Fig. 18**).

In the western region of the country, Alto Paraguay (including Chaco Department, before 1992) is represented by around 2,450 specimens, Presidente Hayes by nearly 3,500, and Boquerón (including Nueva Asunción Department) by over 4,500. The largest collections of specimens from Alto Paraguay are housed at TTU, MNHNP, and RDO. Those from Boquerón are at UCS, FMNH, and RDO. The specimens from Presidente Hayes are distributed among a larger number of collections, with MVZ, TTU, RDO, and UCS all having more than 500, followed by UMMZ, FMNH, and MNHNP, all with over 250. A distinct geographical bias in the number of Paraguayan Carnivore and Xenarthran specimens coming from the Chaco region has been commented upon (P. Smith and Ríos, 2018; P. Smith, 2022a, b).

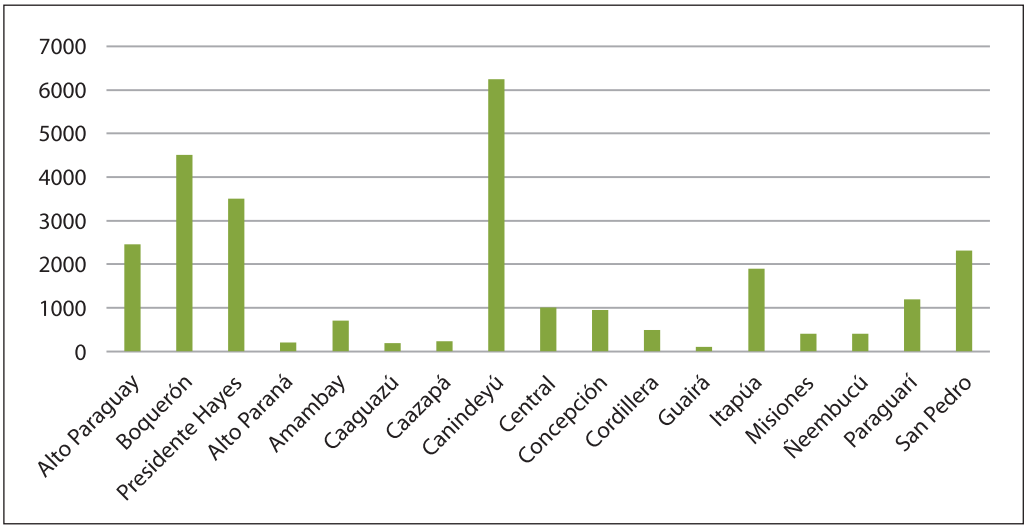

Figure 18. Graph showing numbers of mammalian specimens collected from each of 17 departments in Paraguay. Note: in the graph, Alto Paraguay Department includes specimens collected in Chaco Department, and Boquerón Department includes those collected in Nueva Asunción Department, before 1992, when those departments were merged. Central Department includes the Capital District. See **Supplemental table S1** for detailed information.

6 GAZETTEER OF MAMMAL COLLECTION LOCALITIES IN PARAGUAY

Several gazetteers of Paraguayan localities have appeared over the years, some of known faunal localities and others more general. Naumberg (1935) lists about 34 Paraguayan localities visited in 1930–31 by Emil Kaempfer during his ornithological expedition in Brazil and eastern Paraguay. The US Board on Geographic Names (1957) listed around 2,300 names of places and features in Paraguay, including both "approved standard" and "unapproved variant" names. Besides including geographic information (latitude, longitude, elevation), this list also references the map from which the information was derived for each locality. Paynter (1989) provided an extensive list of localities, based on ornithological specimens housed in the Museum of Comparative Zoology (Harvard University), Field Museum of Natural History, and Museum of Zoology (University of Michigan). This list also includes latitude, longitude and map reference for the localities that could be located. The ornithological work by Hayes (1995) includes a gazetteer listing localities visited by the author, as well as previous ornithological work. This list indicates the department and geographical region for each locality, as well as the latitude and longitude. P. Smith *et al.* (2021a), and Vallotton and P. Smith (2021) provided a gazetteer of ornithological localities with latitude and longitude for two large and previously unpublished ornithological collections that were not included in Hayes (1995). López-González (2005) published a gazetteer of mammal localities for bats, and P. Smith (2024) included a gazetteer of the localities mentioned by Arnaldo de Winkelried Bertoni in his various mammal publications. This list is organized by department, and includes latitude, longitude, and source of the information.

The gazetteer presented here is based entirely on localities recorded for mammal specimens in Paraguay (see Chapter 5). Of the approximately 31,000 specimens which we have encountered, approximately 28,520 have specific localities and/or latitude and longitude recorded. However, many of these did not have a department listed. For this gazetteer, we included only those records (ca. 24,250) which contained both the department and a specific locality. Localities which were written differently (*e.g.*, "12 km S of Santa Rosa" and "Santa Rosa, 12 km S") were standardized (re-written in a standard form, generally "Santa Rosa, 12 km S". Nevertheless, there may be some listed localities which are accidentally duplicated, because we could not confidently determine that they were the same, so we left them listed separately. A list of 558 Paraguayan collecting localities for mammals is given in **Table 2**. Localities determined to be within ca. 10 km of each other are "lumped", *i.e.*, entered as only one of the recorded localities, generally the locality with the greatest number of records or the most centrally-located if more than two localities were included in the lumping, all with only a few records.

This gazetteer is not presented as a precise reference to collecting localities within the county. Rather it is intended to provide an overview of areas which have been collected, the period during which the collections were made, how many specimens were collected there, and how many species are represented among those collections.

Where coordinates were provided in the digitized data we received, we include those in the gazetteer. We report them in decimal degrees, to two decimal places, which in this latitudinal region is the equivalent of approximately one kilometer in both latitude and longitude. The coordinates were checked to ensure that they appear to be correct, and those that were clearly erroneous were omitted from the listing. In a few cases, the department of the reference point was listed as the department of the actual collecting locality; where these were detected, they were changed to reflect the department of the collecting locality. In other cases, a named locality was on the border between two departments, and separate coordinate sets were provided for the specific localities within the two departments. These were left as two separate localities (although with the same name), falling within two departments, with two sets of coordinates listed. Similarly, there are localities, such as "Rio Tebicuary", listed in several different departments. These were left as separately listed. Finally, we note that only in recent decades have good maps and/or GPS been available. Therefore, earlier records may have a reasonably accurate locality description, but an incorrectly designated department.

For each of the localities listed, we indicate the first and last year known for collections from that locality, the number of specimens collected there, and the number of species. The number of species is in many cases an overestimate of the number actually collected at the locality, because we generally left species identifications as they were provided to us from the various museum collections, rather than correcting or updating taxonomy and nomenclature without access to the specimens. The number of specimens collected at a locality ranges from one (147 localities listed) to 1,175 (Reserva Natural del Bosque Mbaracayú, Canindeyú Department). The number of species recorded ranges from one (201 localities) to 59 (Juan de Zalazar, Presidente Hayes Department).

Table 2. Reported collecting localities of Paraguayan mammals. Localities are listed alphabetically, and the department, latitude and longitude (where available, in decimal degrees), year of earliest and most recent collection, number of specimens, and number of species is given.

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
24°0'S, 58°30'W	Presidente Hayes	-24.00	-58.50	1986	1986	1	1
Aca Poí	San Pedro			1950	1950	4	3
Acaray Dam, 03 km S	Alto Paraná			1973	1973	1	1
Acosta Ñu	Cordillera			1986	1987	5	2
Agua Dulce	Alto Paraguay	-20.02	-59.77	1977	1984	35	17
Agua Dulce, 11 km W	Alto Paraguay	-20.30	-60.22	1980	1983	5	4
Agua Dulce, 35 km E	Alto Paraguay			1981	1981	3	2

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Agua Dulce, 54 km E	Alto Paraguay			1981	1981	5	3
Agua Rica	Alto Paraguay			1980	1980	1	1
Aguada Lidia	Boquerón			1981	1981	1	1
Altos, 20 km N	Cordillera	-25.07	-57.07	1973	1973	24	12
ANDE	Alto Paraná			1980	1980	1	1
Antebi	Concepción	-22.65	-57.52	1999	1999	57	20
Antequera, 2 km NNW	Presidente Hayes	-24.07	-57.23	1988	1988	1	1
Ape Aime, 3 km N	Itapúa	-26.54	-54.84	1998	1998	163	13
Arroyo Acaray mi	Alto Paraná			1979	1979	1	1
Arroyo Bandera	Canindeyú			1996	1996	1	1
Arroyo Dos Hermanas	Alto Paraná			1980	1980	1	1
Arroyo Ñacunday	Alto Paraná			1981	1981	1	1
Arroyo Tagatija mi	Concepción	-22.65	-57.54	2002	2002	84	8
Arroyos y Esteros	Cordillera			1969	1969	1	1
Asunción	Capital	-25.27	-57.67	1902	2008	167	35
Asunción, 53 km NW, Río Manduvira	San Pedro			1988	1988	2	1
Asunción, Barrio Santisima Trinidad	Central			1982	1982	6	3
Asunción, Catedral	Central			1963	1963	24	5
Asunción, Cerro Lambaré	Central			2005	2007	2	2
Asunción, Jardín Botánico	Central	-25.27	-57.67	1976	1976	3	1
Asunción, Mariscal López and General Santos	Central			1995	1995	4	1
Asunción, Recoleta	Central	-25.27	-57.67	1972	1979	343	23
Asunción, San Roque	Central			1963	1963	25	4
Asunción, Universidad Católica	Central	-25.33	-57.64	1996	1998	6	3
Asunción, Villa Morra	Central	-25.27	-57.67	1973	1973	2	2
Ayolas, 5 km ENE	Misiones	-27.37	-56.82	1977	1979	48	14
Ayolas, Arroyo Atinguy	Misiones			1982	1996	22	5
Ayolas, Barrio San Antonio	Misiones	-27.39	-56.84	1995	1996	17	5
Ayolas, Barrio Villa Permanente	Misiones			1996	1996	1	1
Bahía Negra	Alto Paraguay	-20.18	-58.16	1983	2002	348	27
Bahía Negra, 17 km N, Estancia Immaculada Concepción	Alto Paraguay	-20.08	-58.17	1983	1988	44	4
Bahía Negra, Naval Base	Alto Paraguay			1983	1983	6	1

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Base Aerea Nueva Asunción	Boquerón	-20.71	-61.92	1986	2002	13	6
Base Aerea Teniente Pratt Gill	Boquerón			1978	1986	5	4
Base Aerea Teniente Pratt Gill, 40 km NW	Boquerón			1978	1978	14	11
Base Aerea, 57 km NE	Boquerón			1982	1982	1	1
Bella Vista, 3 km E, Colonia Sargento Dure	Amambay	-22.17	-56.42	1979	1992	34	11
Benjamín Aceval, 67 km NW	Presidente Hayes	-24.54	-58.04	1979	1979	4	3
Buena Vista	Presidente Hayes	-22.60	-59.71	1995	1995	8	1
Caaguazú	Caaguazú			1950	1950	1	1
Campo 9	Caaguazú	-25.47	-56.00	1995	1995	48	7
Campamento Leite	Boquerón			1982	1982	2	1
Campo Loro	Boquerón			1999	1999	1	1
Campo María	Presidente Hayes					3	3
Campo Rosa	Boquerón			1995	1995	1	1
Cañada el Carmen	Boquerón			1975	1978	2	1
Capitán Bado	Amambay			1981	1981	1	1
Capitán Meza	Itapúa			1932	1948	171	38
Capitán Pablo Lagerenza	Alto Paraguay	-18.87	-60.74	1997	1997	2	1
Carapá	Canindeyú			1978	1978	3	3
Carapeguá	Paraguarí			1991	1991	1	1
Carayaó, 24 km NNW, Estancia San Ignacio	San Pedro	-24.97	-56.52	1979	1979	67	16
Caroneny	Guairá			1933	1933	8	4
Cato de Mora's property	Itapúa	-26.52	-55.80	2001	2001	59	7
Centro de Desarrollo Forestal	Itapúa			1983	1983	4	1
Centu Cu	Misiones	-26.42	-57.03	1999	1999	77	8
Centu Cué	Paraguarí	-26.42	-57.03	1999	1999	77	8
Cerro Casilda	Alto Paraguay			1944	1944	2	1
Cerro Colorado	San Pedro			1944	1944	1	1
Cerro Corá, 4 km SW	Amambay	-22.62	-55.98	1977	1977	67	14
Cerro Pero	Itapúa	-26.76	-55.86	1996	1996	5	23
Chaco-i, 15 km NNW	Presidente Hayes	-25.12	-57.69	1978	1978	19	3
Choré	San Pedro			1987	1987	42	6
Chovoreca	Alto Paraguay	-19.59	-58.70	1995	2002	9	8
Chupa Pou	Canindeyú	-24.16	-55.71	1999	2001	27	5

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Ciudad del Este	Alto Paraná			1978	1981	3	3
Colonia 14	Boquerón	-22.31	-59.91	1995	1995	2	1
Colonia 8 de Diciembre	San Pedro			1987	1987	1	1
Colonia Alto Verá	Itapúa			1988	1988	1	1
Colonia Fernheim, Estancia Laguna Pora	Presidente Hayes			1978	1978	12	5
Colonia Lapachal	Itapúa			1989	1989	16	4
Colonia Lolita	Boquerón			1998	1998	13	4
Colonia Mayor Otaño	Itapúa			1982	1982	2	2
Colonia Mboi Cué	Itapúa	-26.72	-55.57	1999	1999	1	1
Colonia Orloff	Boquerón			1945	1948	25	14
Colonia Paratodo	Presidente Hayes					1	1
Colonia Taruma	Itapúa			1987	1988	36	7
Colonias Unidas	Itapúa			1989	1989	36	4
Concepción, 8 km E	Concepción	-23.36	-57.39	1972	1992	72	26
Concepción, 11 km S	San Pedro			1988	1988	1	1
Concepción, 40 km E	Concepción	-23.38	-57.17	1979	1979	3	2
Copagro	Boquerón			1976	1978	182	24
Copagro, 25 km SW	Boquerón			1977	1977	1	1
Corateí, 4 km W	Misiones	-27.42	-56.95	1986	1989	18	1
Cordillera de los Altos	Paraguarí			1987	1987	7	4
Coronel Oviedo	Caaguazú			1981	1981	5	1
Coronel Oviedo, 22 km N	Caaguazú	-25.25	-56.50	1976	1976	7	6
Coronel Oviedo, 50 km N	San Pedro			1981	1981	1	1
Coronel Oviedo, 194 km N	San Pedro	-23.72	-56.45	1972	1972	2	1
Corrales	Boquerón	-22.43	-60.37	1997	1997	93	11
Cruce 4 de mayo	Alto Paraguay			1988	1988	2	1
Curuguaty	Canindeyú			1982	1982	1	1
Curuguaty, 6 km NE	Canindeyú			1976	1976	85	22
Curuguaty, 13 km N	Canindeyú	-24.45	-55.65	1978	1979	428	36
Curupaytu, Estancia Paso Pucú	Ñeembucú			1993	1993	4	1
Destacamento Militar Gabino Mendoza	Alto Paraguay	-20.05	-61.85	1996	1997	100	13
Destacamento Militar Gabino Mendoza, 15 km E	Alto Paraguay	-20.09	-61.79	1996	1996	177	13

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Destacamento Militar Sargento Rodríguez	Boquerón			1975	2002	40	13
Destacamento Militar Teniente Americo Picco	Boquerón	-21.09	-60.55	1982	1997	143	30
Destacamento Militar Teniente Americo Picco, 52 km N	Boquerón			1982	1982	7	11
Distrito Hernandarias, Bosque de la ANDE, al lado del Zoológico	Alto Paraná			1995	1995	1	1
Distrito Hernandarías, Pikyry, Ex Seminario Verbo Divino	Alto Paraná			1995	1995	2	1
Distrito Mbaracayú, Reserva Biológica Itabó	Alto Paraná			1988	1988	1	1
Distrito San Alberto, Res. Biol. Limoy	Alto Paraná			1995	1995	1	1
Doctor Pedro P. Peña	Boquerón	-22.38	-62.26	1965	2017	247	28
Doctor Pedro P. Peña, 15 km NE	Boquerón			1978	1978	1	1
Don Bosco, Ciudad del Este	Alto Paraná			1979	1979	1	1
Dos Estrellas, 04 km NW	Alto Paraguay			1983	1983	1	1
Dourados	Misiones			1965	1965	1	1
El Tirol	Itapúa	-27.17	-55.83	1976	1983	63	9
Emboscada	Cordillera	-25.09	-57.27	2001	2001	1	1
Emboscada, Colonia Minas Cué	Cordillera			2001	2001	11	4
Empresa San Agustín	Cordillera	-25.09	-57.40	2004	2004	1	1
Encarnación	Itapúa	-27.33	-55.98	1905	2012	19	10
Encarnación, 20 km NNE	Itapúa	-27.17	-55.77	1973	1980	15	8
Escuela Agropecuaria y Forestal	Canindeyú			1984	1984	4	2
Escuela Técnica Forestal	Alto Paraná			1981	1981	24	6
Estacion Biológica Tres Gigantes	Alto Paraguay	-20.08	-58.16	2012	2012	3	3
Estancia Agro Chaco, 15 km NW	Boquerón			1981	1981	1	1
Estancia Arakangy	Caaguazú			2009	2009	1	1
Estancia Campo Grande	Alto Paraguay			2003	2003	2	1
Estancia Cañada Mil	Boquerón	-22.38	-62.26	1996	1996	114	10
Estancia Casilda	Alto Paraguay			1944	1944	2	1
Estancia Cerrito	Concepción	-23.25	-57.49	1995	1995	33	11
Estancia Chacoite	Boquerón	-21.19	-61.70	1997	1998	174	11
Estancia Dos Marías, 12 km S, Río Tebuicuary	Itapúa	-26.80	-56.55	2001	2001	3	3
Estancia El 43	Boquerón	-21.94	-60.24	1995	1995	18	6

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Estancia Felicidad	Canindeyú	-24.16	-55.70	1999	2001	43	11
Estancia Garay Cue	Concepción	-22.67	-57.35	1996	2009	73	18
Estancia Golondrina	Caazapá	-25.54	-55.48	1996	1996	55	11
Estancia González	Itapúa			1993	1993	3	1
Estancia Guajho	Alto Paraguay			1944	1944	16	4
Estancia Guyra Toro	Alto Paraguay	-19.81	-58.62	2002	2002	36	14
Estancia Iparoma	Boquerón			1978	1978	71	22
Estancia Itabó	Canindeyú	-24.44	-54.66	1996	1997	109	8
Estancia Kamba Aka	Alto Paraguay	-19.84	-58.76	2002	2003	6	3
Estancia La Escondida	Cordillera			1991	1991	2	1
Estancia La Gama	Boquerón			1982	1991	18	10
Estancia La Golondrina	Presidente Hayes	-25.08	-57.75	1979	1998	303	25
Estancia La Victoria	Presidente Hayes	-23.67	-58.60	1995	1996	203	26
Estancia Las Mañanitas	San Pedro	-23.69	-56.22	2011	2012	5	2
Estancia Loma Pora	Presidente Hayes	-23.49	-57.58	1996	1997	414	23
Estancia Loma Pora, Retiro Alegría	Presidente Hayes	-23.46	-57.78	1996	1996	13	3
Estancia Loma Pora, Retiro Algarrobo	Presidente Hayes	-23.53	-57.74	1996	1996	1	1
Estancia Loma Pora, Retiro Chimo Cué	Presidente Hayes	-23.45	-57.58	1996	1996	9	5
Estancia Melgarejo	Misiones			1992	1992	5	2
Estancia Paicuara	Amambay			1981	1982	8	2
Estancia Palo Santo	Boquerón					21	9
Estancia Palo Santo	Presidente Hayes			1944	1991	3	3
Estancia Parabel, 6 km S of house	Itapúa	-26.39	-55.54	1998	1998	34	12
Estancia Parabel, near house	Itapúa	-26.35	-55.52	1998	1998	298	18
Estancia Parra Cué	Alto Paraguay	-21.10	-57.89	1995	1995	44	8
Estancia Pirizal	Boquerón			1978	1991	8	5
Estancia Punto Alto	Alto Paraguay	-19.69	-58.70	2002	2002	13	8
Estancia Pytere, margin of Río Tebicuary	Caazapá	-26.49	-55.90	1999	1999	11	3
Estancia Rama III	Canindeyú	-24.16	-55.57	2004	2006	63	6
Estancia Rivas	Canindeyú	-24.44	-54.67	1996	1996	110	10
Estancia Rojas Silva	Presidente Hayes					2	2
Estancia Samaklay	Presidente Hayes	-23.51	-59.82	1995	2005	579	31

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Estancia San Antonio	Ñeembucú			1992	1992	1	1
Estancia San Felipe	Ñeembucú	-27.17	-58.39	1998	1998	32	13
Estancia San Gabriel	Presidente Hayes	-23.36	-59.54	2005	2005	2	2
Estancia San Isidro, 5 km NW of houses	Itapúa	-26.49	-55.90	1999	1999	47	6
Estancia San Jorge	Boquerón	-22.04	-60.33	1995	1996	10	4
Estancia San José	Alto Paraguay	-19.56	-60.52	1997	1997	115	9
Estancia San José, 5 km E of house	Ñeembucú	-27.18	-58.42	1998	1998	35	12
Estancia San Juan	Amambay			1984	1984	2	2
Estancia San Luis	Concepción	-22.39	-57.48	1999	1999	25	7
Estancia San Rafael	Itapúa	-26.76	-55.86	1996	1996	1	1
Estancia San Roque	Presidente Hayes					4	4
Estancia Santa Ana	Misiones	-27.37	-56.93	1993	1996	10	9
Estancia Santa Carolina	Presidente Hayes			1999	1999	1	1
Estancia Santa Clara	Concepción	-23.22	-57.53	1995	1995	34	14
Estancia Santa Teresa	Alto Paraguay	-21.07	-59.16	1996	1998	99	9
Estancia Santa Teresa, Puesto Anastácio, 4 km S	Ñeembucú	-26.58	-58.14	1999	1999	8	4
Estancia Sofía	Presidente Hayes			1991	1991	1	1
Estancia Sombrero	Cordillera	-25.07	-56.60	1995	2001	187	26
Estancia Tinfunke	Presidente Hayes			1983	1983	2	2
Estancia Toro 1	Alto Paraguay	-20.38	-59.58	1995	1995	1	1
Estancia Toro Pampa	Alto Paraguay	-20.38	-59.58	1997	1998	8	4
Estancia Tres Marías	Alto Paraguay	-21.28	-59.55	1996	1997	116	27
Estancia Villa Rey	Canindeyú			1996	1996	3	1
Estancia Waldbrunner	Boquerón			1988	1988	8	1
Estancia Yacaré	Ñeembucú	-26.62	-58.07	1996	1997	232	31
Estancia Yacaré, Puesto San Fernando	Ñeembucú	-26.58	-58.15	1999	1999	11	5
Estancia Ype Kua	Cordillera	-25.03	-57.32	2001	2001	4	3
Estancia Ypoá	Paraguarí	-26.04	-57.43	1995	1995	7	6
Estancia Zapag, Vy'a renda	San Pedro	-24.47	-56.27	2008	2008	2	2
Estrella	Boquerón			1972	1972	1	1
Filadelfia	Boquerón	-22.35	-60.03	1953	1995	50	21
Filadelfia, 16 km W, Colonia Fernheim	Boquerón	-17.28	-59.98	1945	1997	188	18

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Filadelfia, 29 km N	Boquerón			1974	1988	8	4
Filadelfia, 50 km N	Boquerón	-22.20	-59.95	1974	1979	58	9
Filadelfia, 65 km N	Boquerón	-22.10	-59.90	1976	1980	6	5
Filadelfia, 100 km N	Alto Paraguay	-21.45	-60.03	1974	1980	4	4
Filadelfia, 119 km N	Boquerón	-22.40	-59.80	1977	1977	2	2
Filadelfia, 144 km NE	Alto Paraguay			1978	1978	7	4
Filadelfia, 150 km N	Boquerón			1981	1981	1	1
Filadelfia, 165 km N	Alto Paraguay	-20.97	-59.80	1978	1980	2	2
Fort Wheeler	Presidente Hayes			1919	1919	7	2
Fortín Casanillo	Boquerón			1991	1991	1	1
Fortín Gloria Meyers, 12 km SW	Presidente Hayes			1978	1978	3	3
Fortín Gloria Meyers, 22 km SW	Presidente Hayes			1978	1978	2	2
Fortín Orihuela	Presidente Hayes			1940	1940	1	1
Fortín Pikyrenda	Alto Paraguay	-20.99	-61.79	1997	1997	58	10
Fortín Teniente Acosta	Boquerón			1988	1991	8	6
Fortín Teniente Montanía	Boquerón	-22.02	-59.95	1974	2005	36	8
Fortín Teniente Montanía, 12 km W	Boquerón			1974	1974	1	1
Fortín Teniente Montanía, 25 km N	Alto Paraguay			1978	1978	1	1
Fortín Teniente Montanía, 28 km W	Boquerón			1974	1974	6	3
Fortín Teniente Montanía, 40 km W	Boquerón			1974	1974	1	1
Fortín Teniente Montanía, 65 km N, Agua de Linda	Alto Paraguay			1978	1978	1	1
Fortín Teniente Montanía, 80 km N	Alto Paraguay			1978	1978	1	1
Fortín Teniente Ochoa	Boquerón			1972	1976	126	24
Fortín Teniente Ochoa, 8 km W	Presidente Hayes			1974	1974	1	1
Fortín Teniente Ochoa, 32 km W	Boquerón			1974	1974	3	2
Fortín Teniente Ochoa, 57 km W	Boquerón			1974	1974	1	1
Fortín Toledo	Boquerón	-22.36	-60.34	1945	1997	524	22
Fuerte Olimpo	Alto Paraguay	-21.04	-57.87	1991	1995	166	23
Fuerte Olimpo, 100 km W, Estancia General Díaz	Alto Paraguay			1991	1991	16	6
Ganadera Jejuí, 2 km SE from houses	San Pedro	-24.12	-56.42	2001	2001	17	4

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Ganadera La Carolina, 1 km W from houses	San Pedro	-24.10	-56.42	2001	2001	11	5
General Bruguez	Presidente Hayes			2003		1	1
General Díaz	Presidente Hayes			1990	1990	2	1
General Díaz, 2 km E	Neembucú	-27.19	-58.35	1998	1998	21	1
General Eugenio Garay	Boquerón			1976	1976	1	1
Guachalla	Boquerón			1945	1965	78	16
Heriberta Stroessner de Iglesias	Itapúa			1988	1996	7	4
Hernandarias	Alto Paraná			1978	1981	6	5
Hernandarias, ITAIPU	Alto Paraná			1988	1988	1	1
Hernandarias, Pira Pyta	Alto Paraná			1987	1987	1	1
Hernandarias, Puerto Palma	Alto Paraná			1980	1980	1	1
Hernandarias, Refugio Biológico Tati Yupi	Alto Paraná			1982	1982	2	2
Hernandarias, Refugio Fauna	Alto Paraná			1981	1985	9	8
Hernandarias, Vivero Forestal ITAIPU	Alto Paraná			1978	2004	60	33
Hito IV	Boquerón	-20.09	-61.92	1996	1996	1	1
Hohenau	Itapúa			1989	1989	2	2
Horqueta	Concepción	-23.40	-56.88	1932	1988	11	4
Hostettler property	Itapúa	-26.64	-55.66	2002	2002	57	5
Igatuiui	Caaguazú			1967	1967	1	1
Iguazú	Ñeembucú			1932	1932	1	1
Isla Poí	Presidente Hayes	-22.50	-59.73	1996	1997	15	5
Isla Talavera	Itapúa			1992	1992	25	5
Isla Yacyretá	Misiones	-27.45	-56.81	1992	1996	104	29
Itabó	Alto Paraná			1979	1979	1	1
Itacurubí del Rosario, Ruchenau	San Pedro	-24.54	-56.83	1962	1962	12	7
Itacurubí del Rosario, Village No. 8	San Pedro	-24.54	-56.83	1962	1962	1	1
Itauguá	Central			1984	1984	1	1
Itaipú Binacional	Alto Paraná			1987	1995	30	6
Itambey	Alto Paraná			1980	1980	1	1
Itambey, San Alberto	Alto Paraná			1980	1980	1	1
Itanará, 17 km SE	Canindeyú			1988	1988	1	1
Jesudí	Boquerón			2003	2003	1	1

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Juan de Mena	Cordillera	-24.92	-56.73	1981	1984	45	9
Juan de Zalazar	Presidente Hayes	-23.88	-59.24	1952	1997	458	59
Juan de Zalazar, Guest House, 25 km N	Presidente Hayes			1973	1973	1	1
Juan de Zalazar, Río Verde	Presidente Hayes	-23.05	-59.20	2004	2004	80	8
Junction Route 3 and Route 5, 28 km S	Amambay	-22.72	-56.30	1972	1972	4	2
La Lomita	Boquerón	-22.48	-62.31	1996	1996	9	3
La Urbana	Alto Paraguay			1925	1925	1	1
Lago Ypoá	Paraguarí	-25.95	-57.45	1995	1995	44	13
Laguna Capitán	Presidente Hayes					2	1
Laguna General Bogado	Boquerón			1982	1982	93	12
Laguna General Díaz	Alto Paraguay			1944	1991	2	2
Laguna He'e	Presidente Hayes			1982	1982	1	1
Laguna Placenta	Alto Paraguay	-21.13	-59.35	1996	1996	81	9
Lake Caruchi	Presidente Hayes			1973	1973	6	5
Limoy	Canindeyú			1975	1979	3	3
Linea 101	Boquerón			1982	1982	1	1
Loma Plata	Boquerón	-22.38	-59.85	1962	1995	20	11
Loma Plata, 85 km E, Estancia Laguna Pora	Presidente Hayes			1978	1993	107	22
Loma Valerolisca	Guairá			1933	1933	1	1
Luque	Central			1985	1985	1	1
Luque, 17 km E	Central	-25.25	-57.35	1972	1978	50	11
Madrejón	Alto Paraguay	-20.63	-59.87	1978	1995	39	13
Madrejón, 17 km W	Boquerón	-20.70	-60.00	1976	1976	1	1
Madrejón, 25 km N	Alto Paraguay			1977	1977	1	1
Madrejón, 30 km S	Boquerón	-20.95	-59.75	1977	1983	3	3
Madrejón, 50 km WSW	Boquerón			1977	1977	49	16
Madrejón, 65 km N	Alto Paraguay			1977	1977	9	2
Madrejón, 67 km WSW	Boquerón			1977	1977	1	1
Marangatu	Canindeyú			1980		2	2
Marcial Concha's property	Concepción	-23.24	-57.49	1995	1995	16	7
Mariscal Estigarribia	Boquerón	-22.07	-60.55	1965	1997	24	15
Mariscal Estigarribia, 14 km E, Cañada Elisa	Boquerón	-22.03	-60.48	1974	1995	46	15

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Mariscal Estigarribia, 24 km E	Boquerón	-22.05	-60.37	1978	1996	5	3
Mariscal Estigarribia, 39 km N	Alto Paraguay			1982	1982	1	1
Mariscal Estigarribia, 45 km W	Boquerón			1974	1996	3	3
Mariscal Estigarribia, 90 km W, Estancia Moutureta	Boquerón			1978	1978	1	1
Mayor Martínez	Ñeembucú			1983	1983	1	1
Mbopi Kua	Concepción			1999	1999	2	1
Mborero	Guairá			1933	1933	8	3
Mbutuy, 46 km ENE	San Pedro	-24.62	-56.42	1979	1979	1	1
Minas	Cordillera	-25.86	-57.33	2004	2004	1	1
Misión	Alto Paraguay			1920	1920	1	1
Misión Faro Moro	Boquerón			1982	1982	1	1
Monday	Alto Paraná			1981	1981	1	1
Monte Palma	Presidente Hayes	-22.61	-59.53	1995	1995	28	8
Montelindo, 5 km NW	Presidente Hayes			1995	1995	1	1
Mount Bogarín	Paraguarí			1967	1967	5	2
Movat, Tanja	Presidente Hayes			1930	1930	1	1
Naranhaty	Presidente Hayes			2004	2004	4	4
Neuland	Boquerón			1984	1991	35	10
Neuland, 48 km W, Estancia San Ramón	Boquerón			1988	1990	25	5
Neuland, 80 km SW, Estancia Pirizal	Boquerón			1978	1978	17	8
Ñu Guazu	Central			1987	1987	1	1
Nueva Asunción	Boquerón	-20.52	-62.14	1982	2007	3	3
Nueva Asunción, 57 km NE	Boquerón			1982	1982	2	1
Nueva Italia	Central			1942	1945	24	10
Nuevo Retiro, 10 km E	Presidente Hayes			1986	1986	2	1
Obrasen, San Miguel	Boquerón			1982	1982	2	2
Palmar de las Islas	Alto Paraguay	-19.62	-60.57	1997	1998	157	22
Paraguarí	Paraguarí	-25.63	-57.12	1901	1987	15	5
Parque Cué	Boquerón	-20.13	-61.76	1996	1997	151	8
Parque Nacional Caaguazú	Caazapá			1986	1993	31	5
Parque Nacional Cerro Corá	Amambay	-22.65	-56.04	1979	2002	473	56
Parque Nacional Cerro Corá, 19 km NNW of Administration Building	Amambay			1982	1982	8	1

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Parque Nacional Defensores del Chaco	Alto Paraguay			1979	1998	265	46
Parque Nacional San Rafael	Itapúa	-26.76	-55.86	1995	1996	86	17
Parque Nacional San Rafael, Guyra Reta	Itapúa			2009	2009	3	3
Parque Nacional San Rafael, Parabel	Itapúa	-26.35	-55.52	2000	2000	63	12
Parque Nacional San Rafael, San Pedro mi	Itapúa	-26.52	-55.81	1996	2000	56	10
Parque Nacional Serranía San Luis	Concepción	-22.63	-57.36	1995	1996	436	42
Parque Nacional Teniente Enciso	Boquerón	-21.21	-61.66	1972	2012	416	51
Parque Nacional Teniente Enciso, 15 km S	Boquerón			1983	1983	2	2
Parque Nacional Teniente Enciso, 25 km W	Boquerón			1975	1975	2	2
Parque Nacional Ybycuí	Paraguarí	-26.09	-56.84	1976	1997	821	47
Parque Nacional Ybycuí, 25 km SE	Paraguarí	-26.08	-56.80	1991	1997	3	2
Parque Nacional Ybycuí, Arroyo Corrientes	Paraguarí	-26.02	-57.05	1981	1981	1	1
Parque Nacional Ybycuí, Arroyo Minas	Paraguarí	-26.02	-57.05	1980	1981	11	5
Parque Nacional Ybycuí, Monumento La Rosada	Paraguarí			1997	1997	26	6
Patino	Central			1927	1927	2	2
Pedro Juan Caballero	Amambay			1977	1977	2	2
Pedro Juan Caballero, 28 km SW	Amambay	-22.75	-55.81	1976	1977	71	15
Pilar, 4 km E	Ñeembucú	-26.82	-58.27	1979	2017	13	4
Pirapó	Itapúa			1974	1983	10	4
Piribebuy, 10 km S	Paraguarí	-25.55	-57.05	1973	1973	7	3
Piribebuy, 16 km NE	Cordillera			1991	1991	1	1
Piribebuy, 17 km SW, Saltos de Piraretá	Paraguarí	-25.73	-57.24	1976	1979	29	10
Piribebuy, 27 km SW	Paraguarí	-25.81	-57.32	1976	1976	2	2
Pozo Colorado	Presidente Hayes	-23.47	-58.82	1974	1997	35	11
Pozo Hondo	Boquerón			1981	1981	3	2
Pozuelo	Canindeyú			1979	1980	9	9
Puente Remanso, 2 km S	Presidente Hayes			1973	1982	2	2
Puerto Bertoni	Alto Paraná			1920	1981	10	4

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Puerto Carmelo Peralta	Alto Paraguay	-21.60	-57.95	1988	1998	2	2
Puerto Carmelo Peralta, Isla Alta	Alto Paraguay			1998	1998	38	4
Puerto Casado	Alto Paraguay			1940	1998	50	15
Puerto Casado, 30 km W	Alto Paraguay			1945	1945	7	6
Puerto Diana, 12 km W	Alto Paraguay			1983	1983	2	2
Puerto Dorila	Alto Paraná			1978	1978	1	1
Puerto Esperanza	Alto Paraguay	-20.40	-58.03	1988	1988	8	1
Puerto Falcón, 83 km NW	Presidente Hayes			1979	1979	1	1
Puerto Fonciere, 4 km NW	Presidente Hayes	-22.42	-57.87	1988	1990	50	3
Puerto Gisela	Itapúa	-27.02	-55.45	1924	1924	1	1
Puerto Guaraní	Alto Paraguay			1928	1928	1	1
Puerto Indio	Alto Paraná			1978	1978	3	2
Puerto Marangatu, Nueva Esperanza	Canindeyú			1979	1979	1	1
Puerto Mihanovich, 5 km NNE, Estancia María Elena	Alto Paraguay	-20.71	-57.95	1988	1988	6	1
Puerto Palma	Alto Paraná			1980	1980	2	2
Puerto Presidente Stroessner	Alto Paraná			1977	1985	3	2
Puerto Sastre	Alto Paraguay			1978	1978	2	2
Puerto Sastre, 14 km W	Alto Paraguay			1978	1978	1	1
Puerto Sastre, 64 km W	Alto Paraguay	-22.10	-58.60	1978	1978	1	1
Puerto Sastre, 139 km W	Alto Paraguay			1978	1978	3	3
Puerto Sauce	Alto Paraná			1978	1979	5	4
Puerto Turi	Misiones			1996	1996	1	1
Puerto Ybapobo	San Pedro			1926	1926	6	4
Puerto Ybapobo, Laguna Vera	San Pedro			1926	1926	4	2
Puesto Santo Domingo	Boquerón					1	1
Puesto Taruma	Paraguarí			1986	1987	4	2
Quiindy	Paraguarí			1986	1987	4	2
Rancho Quemado	Boquerón			1981	1987	6	3
Refugio Biológico Carapá	Canindeyú			1978	1978	1	1
Refugio Biológico Pikyry	Alto Paraná			2009	2010	2	2
Refugio Biológico Tati Yupi	Alto Paraná			1982	1982	1	1
Reserva Biológica Itabó	Canindeyú	-24.47	-54.64	1987	2008	195	15
Reserva Biológica Limoy, 11 km N	Alto Paraná			1987	1987	1	1

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Reserva Faunística Atinguy	Misiones	-27.34	-56.68	1993	1996	31	17
Reserva Maharishi	Alto Paraná			2009	2009	1	1
Reserva Natural del Bosque Mbaracayú	Canindeyú	-24.13	-55.53	1983	2014	1175	48
Reserva Natural del Bosque Mbaracayú, Aguara Ñu	Canindeyú	-24.19	-55.28	1996	2015	189	27
Reserva Natural del Bosque Mbaracayú, Arroyo Guyra Keha	Canindeyú			1997	1997	16	3
Reserva Natural del Bosque Mbaracayú, Arroyo Moroti	Canindeyú			1997	2003	31	7
Reserva Natural del Bosque Mbaracayú, Horqueta mi	Canindeyú	-24.13	-55.32	1997	2005	519	18
Reserva Natural del Bosque Mbaracayú, Jejui mi	Canindeyú	-24.23	-55.53	1996	2005	576	21
Reserva Natural del Bosque Mbaracayú, Karapa	Canindeyú	-24.00	-55.35	1984	2009	50	17
Reserva Natural del Bosque Mbaracayú, La Morena	Canindeyú	-24.24	-55.53	1991	2003	96	11
Reserva Natural del Bosque Mbaracayú, Lagunita	Canindeyú	-24.13	-55.43	1996	2003	119	14
Reserva Natural del Bosque Mbaracayú, Maria Auxiliadora	Canindeyú	-24.10	-55.53	2005	2005	8	1
Reserva Natural del Bosque Mbaracayú, Nandurokai	Canindeyú	-24.00	-55.48	1997	2003	85	10
Reserva Natural Laguna Blanca	San Pedro	-23.80	-56.28	2007	2016	505	48
Reserva Natural Privada Morombí	Caaguazú			2006	2009	30	2
Reserva Natural Privada Ypetí	Caazapá	-25.64	-55.51	1996	2008	118	14
Reserva Natural Tayptá	Caazapá			2009	2009	1	1
Reserva Yabebyry	Misiones			1993	1993	1	1
Retiro	Boquerón			1973	1973	1	1
Retiro Alegre	Concepción	-22.45	-57.59	1999	1999	3	1
Retiro, 2 km SW	Presidente Hayes			1973	1973	11	1
Riacho Yacaré	Alto Paraguay			1958	1959	8	4
Rio Aguaray Guazu, 1 km N	San Pedro			1979	1979	7	3
Rio Aguaray Guazu, at road crossing	San Pedro			1979	1979	7	4
Rio Aqudabán at Paso Horqueta	Concepción			1979	1979	7	4
Rio Atinguy	Misiones	-27.34	-56.68	1996	1996	20	4
Rio Corrientes	Canindeyú			1984	1984	2	2

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Rio Jejuí Guazu	Canindeyú	-24.24	-55.67	2001	2001	3	1
Rio Jejuí mi	Canindeyú			1996	1996	33	4
Rio Negro	Presidente Hayes			1913	1999	14	9
Rio Negro, 8 km above mouth	Alto Paraguay	-20.08	-58.13	1999	1999	1	1
Rio Paraná	Itapúa			1974	1974	84	10
Rio Pilcomayo	Presidente Hayes			1995	1995	3	3
Rio Pilcomayo, 15 km W of Asunción	Presidente Hayes			1982	1982	1	1
Rio Pilcomayo, 15 mi W of Rio Paraguay	Presidente Hayes			1944	1944	20	3
Rio Tebicuary	Itapúa	-26.76	-56.56	2001	2001	2	2
Rio Tebicuary	Misiones	-26.52	-57.24	1999	2001	10	7
Rio Tebicuary	Ñeembucú			1932	1932	4	1
Rio Tebicuary	Paraguarí	-26.51	-57.24	1999	2001	16	6
Río Verde	Presidente Hayes			1983	1983	4	2
Rio Verde, Estancia Kent	Presidente Hayes			1972	1972	1	1
Rosario, 10 km NW	San Pedro	-24.32	-57.17	1988	1988	9	3
Rosario, 10 km NW, island in Rio Paraguay	San Pedro	-24.32	-57.17	1988	1990	111	1
Rosario, 22 km SSW	San Pedro	-24.62	-57.15	1988	1988	5	2
Ruta 10, Tapiracuai	San Pedro			1999	1999	1	1
Ruta 3, Rio Jejuí	San Pedro	-24.08	-56.44	2001	2001	1	1
Ruta General Díaz, km 70	Presidente Hayes			1996	1996	1	1
Ruta Trans-Chaco, border of Boquerón and Presidente Hayes, 4 km N	Boquerón			1982	1982	1	1
Ruta Trans-Chaco, intersection Concepción road, 35 km E	Presidente Hayes			1995	1995	2	1
Ruta Trans-Chaco, km 10	Presidente Hayes			1975	1975	1	1
Ruta Trans-Chaco, km 55	Presidente Hayes			1975	1982	2	2
Ruta Trans-Chaco, km 64	Presidente Hayes			1977	1977	5	2
Ruta Trans-Chaco, km 75	Presidente Hayes			1975	1998	3	3
Ruta Trans-Chaco, km 84	Presidente Hayes			1977	1977	2	1
Ruta Trans-Chaco, km 94	Presidente Hayes			1975	1982	2	2
Ruta Trans-Chaco, km 100	Presidente Hayes			1973	2001	4	4
Ruta Trans-Chaco, km 139	Presidente Hayes			1976	2007	4	4
Ruta Trans-Chaco, km 165	Presidente Hayes	-24.25	-58.28	1976	1997	2	2

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Ruta Trans-Chaco, km 194	Presidente Hayes			1975	1975	1	1
Ruta Trans-Chaco, km 200	Presidente Hayes			1974	1977	3	2
Ruta Trans-Chaco, km 205, 20 km SW, Retiro Mandeyu	Presidente Hayes			1972	1972	37	7
Ruta Trans-Chaco, km 226	Presidente Hayes			1975	1981	2	2
Ruta Trans-Chaco, km 247, Pirahú Bridge	Presidente Hayes	-23.66	-58.70	2012	2013	7	1
Ruta Trans-Chaco, km 250	Presidente Hayes			1967	1967	27	8
Ruta Trans-Chaco, km 275	Presidente Hayes			1973	1975	3	3
Ruta Trans-Chaco, km 295, Chaco Experiment Station	Presidente Hayes	-23.20	-59.18	1972	1973	80	13
Ruta Trans-Chaco, km 305, Retiro	Presidente Hayes			1973	1983	57	11
Ruta Trans-Chaco, km 315, Río Sombrero	Presidente Hayes			1973	1981	12	2
Ruta Trans-Chaco, km 320, 50 km E	Boquerón	-22.67	-61.00	1973	1973	13	4
Ruta Trans-Chaco, km 325	Presidente Hayes			1973	1973	1	1
Ruta Trans-Chaco, km 361	Presidente Hayes			1975	1975	1	1
Ruta Trans-Chaco, km 384	Presidente Hayes			1977	1977	3	1
Ruta Trans-Chaco, km 412, Cruce Pioneros, 2 km W, Experimental Farm	Presidente Hayes	-22.69	-59.78	1996	1997	325	16
Ruta Trans-Chaco, km 483	Boquerón			1976	1976	2	2
Ruta Trans-Chaco, km 545	Boquerón			1972	1975	10	4
Ruta Trans-Chaco, km 570	Boquerón			1972	1977	12	5
Ruta Trans-Chaco, km 585	Boquerón			1976	1977	24	7
Ruta Trans-Chaco, km 588, 09 km WSW	Boquerón			1978	1978	25	1
Ruta Trans-Chaco, km 588, 19 km SW	Boquerón	-21.75	-61.20	1978	1978	102	9
Ruta Trans-Chaco, km 588, 30 km SW	Boquerón			1977	1977	1	1
Ruta Trans-Chaco, km 589	Boquerón	-21.70	-60.85	1975	1977	27	9
Ruta Trans-Chaco, km 589, 13 km S	Boquerón			1976	1977	6	4
Ruta Trans-Chaco, km 607	Boquerón			1975	1996	12	6
Ruta Trans-Chaco, km 620, Garrapatal-i	Boquerón	-21.55	-61.15	1975	1978	56	16
Ruta Trans-Chaco, km 652	Boquerón			1975	1975	1	1

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Ruta Trans-Chaco, km 674	Boquerón			1972	1975	3	3
Ruta Trans-Chaco, km 675, 29 km SW	Boquerón			1975	1975	2	2
Ruta Trans-Chaco, km 697	Boquerón			1981	1981	1	1
Ruta Trans-Chaco, km 715	Boquerón			1997	1997	1	1
Ruta Trans-Chaco, km 751	Boquerón			1975	1975	1	1
Ruta Trans-Chaco, Río Verde	Presidente Hayes			1972	1973	2	2
Ruta Trans-Chaco, Río Verde, 4 km downstream	Boquerón			1973	1973	2	1
Salto de Piribebuy	Cordillera			1981	1981	2	2
Salto Tembey	Itapúa			1981	1981	2	2
San Alberto, Reserva Biológica Limoy	Alto Paraná			1979	1979	1	1
San Alfredo	Alto Paraguay			1982	1982	2	2
San Alfredo, 15 km W	Alto Paraguay			1982	1982	1	1
San Alfredo, 65 km S	Boquerón			1982	1982	1	1
San Alfredo, 65 km SE	Alto Paraguay			1981	1982	4	4
San Antonio, 3 km N	Ñeembucú	-27.16	-57.65	1976	1976	74	14
San Bonito, 2 km S	Itapúa	-26.81	-55.72	2017	2017	1	1
San Ignacio	Misiones			1965	1965	24	5
San Ignacio, 20 km W	Misiones			1965	1965	22	3
San Ignacio, 36 km NE	Misiones			1965	1965	14	6
San Ignacio, 40 km S	Misiones	-27.15	-57.05	1967	1979	20	7
San Ignacio, Maru	Misiones			1965	1965	2	1
San José de los Arroyos	Cordillera			1987	1987	1	1
San Lázaro	Concepción	-22.17	-57.92	1939	1997	67	5
San Lorenzo	Central			1966	1982	79	15
San Lorenzo	Itapúa			1982	1982	10	7
San Rafael del Paraná, 4 km E	Itapúa	-27.12	-56.39	1978	1998	290	31
San Salvador	Guairá			1925	1925	4	1
Santa Fé, Refugio Biológico Pikyry	Alto Paraná			1977	1977	1	1
Santiago, 15 km SSW, Estancia Sarandy	Misiones	-27.21	-56.79	1986	1986	1	1
Sapucay	Paraguarí			1900	2001	96	29
Serranía de Acahay	Paraguarí			1986	1986	1	1
Sommerfeld Colony No. 11	Caaguazú			1950	1950	18	9

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Super Carretera Itaipú, 24°40'30.3"S, 54°52'19.3"W	Alto Paraná			2010	2010	1	1
Tacuaral	Misiones			1900	1900	5	2
Tacuaral (Tacuaras?)	Ñeembucú	-26.82	-57.95	1900	1976	6	3
Taquate	San Pedro			1950	1950	1	1
Teniente Martínez	Boquerón			1981	1981	1	1
Teniente Martínez, 10 km S	Boquerón	-21.06	-59.80	1980	1980	1	1
Tobatí, 2 km S	Cordillera	-25.28	-57.10	1972	1979	170	40
Tobatí, 12 km N	Cordillera	-25.14	-57.07	1973	1974	24	11
Toro Mocho	Boquerón	-23.53	-60.53	2004	2004	74	8
Tribu Nueva	Alto Paraguay			1983	1983	4	1
Valle Apu-á	Ñeembucú			1994	1994	1	1
Valle mi, 2 km SW	Concepción	-22.25	-57.97	1988	1988	15	1
Villa Hayes	Presidente Hayes			1975	1985	8	3
Villa Hayes, 30 km W	Presidente Hayes	-25.10	-57.86	1986	1986	1	1
Villa Hayes, 69 km NW	Presidente Hayes	-24.70	-57.90	1973	1973	5	3
Villa Hayes, 107 km NW	Presidente Hayes	-24.38	-58.12	1973	1973	4	1
Villa Hayes, 130 km NW	Presidente Hayes	-24.28	-58.25	1973	1973	1	1
Villa Hayes, 213 km NW	Presidente Hayes	-23.78	-58.52	1972	1979	19	8
Villa Hayes, 226 km NW	Presidente Hayes	-23.63	-58.68	1972	1973	148	14
Villa Hayes, 275 km NW	Presidente Hayes	-23.37	-59.00	1973	1979	245	19
Villa Hayes, 295 km NW	Presidente Hayes	-23.22	-59.15	1972	1973	78	17
Villa Hayes, 300 km NW, Río Verde	Presidente Hayes	-23.18	-59.20	1972	1973	24	12
Villa Hayes, 320 km NW	Presidente Hayes	-23.05	-59.27	1972	1973	15	4
Villa Hayes, 345 km NW	Presidente Hayes	-22.87	-59.47	1973	1973	2	2
Villa Hayes, 390 km NW	Presidente Hayes	-22.67	-59.73	1973	1973	1	1
Villa Hayes, 410 km NW	Boquerón	-22.55	-59.90	1973	1973	12	8
Villa Hayes, 419 km NW	Boquerón	-22.48	-59.98	1973	1977	32	11
Villa Hayes, 460 km NW	Boquerón	-22.32	-60.32	1953	1973	27	10
Villa Hayes, 474 km NW	Boquerón	-22.30	-60.33	1973	1973	9	5
Villa Militar	Presidente Hayes			1945	1945	1	1
Villa Militar, 30 km NE	Presidente Hayes			1945	1945	1	1
Villa Rica	Guairá			1930	1954	21	13
Villa Ygatimí	Canindeyú			1987	1989	9	6

Locality	Department	Latitude	Longitude	First year	Last year	# of records	# of species
Villa Ygatimí, 17 km SE	Canindeyú			1988	1988	12	4
Villeta	Central			1981	1982	3	3
Villeta, Nueva Italia	Central			1940	1940	4	4
Vivero Servicio Forestal Nacional	Amambay			1981	1981	3	2
Yaguarete Forests	San Pedro	-23.81	-56.13	1996	1996	89	18
Yaguarete Forests, Aguaray Guasu	San Pedro			1996	1996	2	1
Yaguarete Forests, Aserradero, 2 km SE	San Pedro			1997	1997	3	1
Yaguarete Forests, Campamento	San Pedro			1997	1997	208	7
Yaguarete Forests, Confluencia Río Verde	San Pedro			1997	1998	389	9
Yaguarete Forests, Headquarters	San Pedro			1996	1998	286	18
Yaguarete Forests, Puente Aguaray	San Pedro			1996	1996	1	1
Yaguarete Forests, Puente Río Verde	San Pedro			1997	1998	159	6
Yaguarete Forests, Puesto Céspedes, 2 km N	San Pedro			1997	1997	19	3
Yaguarete Forests, Puesto Martillo, 1 km W	San Pedro			1997	1998	259	14
Yalve Sanga	Boquerón			1989	1989	1	1
Yataity	Ñeembucú			1991	1994	24	1
Yby Yaú, 12 km S	Concepción	-23.05	-56.50	1979	1979	1	1
Ybycuí, 07 km SSW	Paraguarí	-26.13	-57.10	1976	1976	2	2
Ypacaraí	Central			1991	1991	3	1
Zoológico ITAIPU, Jaula Nº12	Alto Paraná			2010	2010	1	1

7 KEYS TO THE ORDERS AND FAMILIES OF PARAGUAYAN MAMMALS

In this section we provide two keys to the orders and families of Paraguayan mammals. The first of these is based on external characters, which can be observed with the animal close at hand, either alive or recently dead (*e.g.*, a roadkill in reasonably good shape). Some steps in this key include incisor and canine teeth. Although these are craniodental characters, they should also be observable as external characters. The second key is based on cranial and dental characteristics, and assumes that a reasonably clean and intact skull is available, preferably from an adult animal. For an order in which only one family is represented among Paraguayan mammals, that family is listed with the order. Further, if only one species represents the order or family in Paraguay, that species is also listed. These keys are designed to be used specifically for Paraguayan mammals. They are not necessarily applicable outside of the country.

In addition, the keys to craniodental characters include humans and the more common domestic and potentially feral species, as skulls of these may also be encountered, and need to be identified. Domestic species are not included in the key to external characters, as we assume that the reader of this book will be familiar with their general appearance. We provide pen-and-ink illustrations of key features where we think they may be useful. All such drawings were done by PS, some with modifications by Gabriela Ruellan. They are numbered sequentially, separately from the other figures in this paper with the understanding that this key may be used separately in the field or laboratory by colleagues or others interested in identifying the mammalian fauna which they encounter or work with.

In constructing these keys, we borrowed heavily from others, especially the excellent keys of Pine (1973), DeBlase and Martin (1974), Husson (1978), Langguth and Anderson (1980), Emmons and Feer (1990), Anderson (1993, 1997), Martin *et al*. (2001), López-González (2005), González and Martínez Lanfranco (2010), Patton *et al*. (2015) and Diaz *et al*. (2021).

Key to orders and families of living mammals of Paraguay, using external characters

1(1) Front limbs modified as wings; bones of hand and fingers greatly elongated. Wing membranes connect fingers with each other and with body..... ..... **Order Chiroptera (6 families)**

1(1)a Tail rat-like and extending free of the uropatagium (**Fig. 1**)..... ..... **Family Molossidae (17 species)**

Tail either absent or mostly contained within the uropatagium (**Fig. 2**).....**1(1)b**

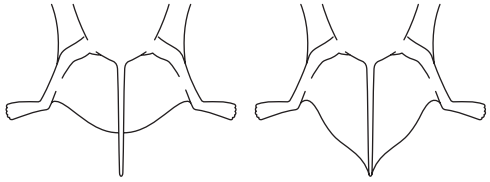

Fig. 1 **Fig. 2**

1(1)b Prominent nose leaf in all species (**Fig. 3**) except the vampire bats, in which the nose leaf is greatly reduced but dentition shows sharply-pointed incisors..... ..... **Family Phyllostomidae (20 species)**

No prominent nose leaf and incisors not sharply-pointed..... **1(1)c**

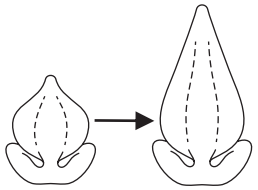

Fig. 3

1(1)c A small sac present on the anterior part of the propatagium (**Fig. 4**, ***Saccopteryx* left, *Peropteryx* right**). Posterior limbs elongated.... **Family Emballonuridae (2 species)**

No sac present on the anterior part of the propatagium. Posterior limbs may or may not be elongated.....**1(1)d**

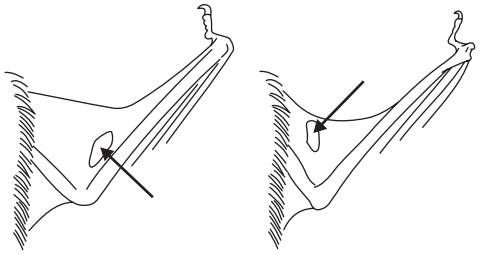

Fig. 4

1(1)d Body fur usually reddish or yellowish in color. Upper lip deeply cleft reaching to the nose (**Fig. 5**). Feet extremely large with long laterally-compressed claws..... ..... **Family Noctilionidae (2 species)**

Lacks deeply cleft upper lip. Feet not noticeably large or with long, hooked claws.... ..... **1(1)e**

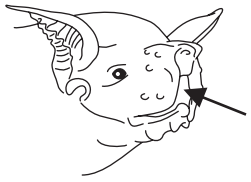

Fig. 5

1(1)e Head rounded with steeply-elevated braincase. Funnel-shaped ears. Snout when viewed laterally almost beak-like. Wing membrane joins the legs at the tibia (**Fig. 6, right**). Tail vertebrae extremely elongated..... ..... **Family Natalidae (1 species: *Natalus macrourus*)**

Head with gently-elevated brain case, so as not to appear particularly rounded. Ears pointed or rounded (not funnel-shaped). Snout not beak-like. Wing membrane joins the legs at or near the base of the toes (**Fig. 6, left**). Tail vertebrae not extremely elongated ..... **Family Vespertilionidae (16 species)**

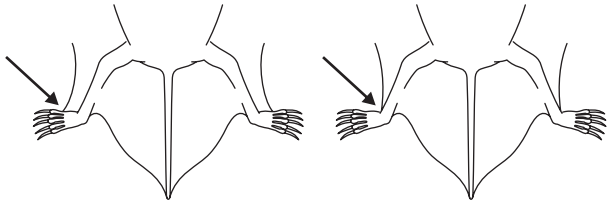

Fig. 6

1(2) Front limbs not winged.....**2**

2(1) First hind toe projecting laterally (in one species connected by web) and without claw or nail (**Fig.** 7)....**Order Didelphimorphia, Family Didelphidae (18 species)**

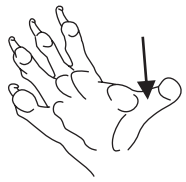

Fig. 7

2(2) First hind toe present or not; if present, with claw or nail.....**3**

3(1) Dorsal surface of body with a bony carapace possessing movable bands. Naked or sparsely haired with stiff bristles. Limbs relatively short and stout. Claws heavily built for digging. Teeth peg-like..... **Order Cingulata (2 families)**

3(1)a Head elongated, somewhat conical. Ears long, protruding well above the head (**Fig. 8**). Scutes of the scapular shield small, granular, of variable size (so that they do not fit together tightly) and vaguely rounded. Forefoot with 4 toes .... **Family Dasypodidae (2 species)**

Head not particularly conical or elongated. Ears may or may not protrude above the head. Scutes of scapular shield small or large, often rectangular and typically fitting together tightly. Forefoot with 4 or 5 toes .... **Family Chlamyphoridae (9 species)**

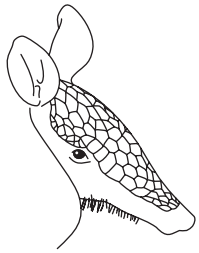

Fig. 8

3(2) Dorsal surface totally furred and without armor of plates **4**

4(1) Claws (especially on front feet) extremely well-developed, long, strong and scythe-like for tearing open termite nests. Head elongated, lacking teeth and with long, narrow tongue..... **Order Pilosa, Family Myrmecophagidae (2 species)**

4(2) Claws on front feet (if present) not especially well-developed or scythe-like. Teeth present **5**

5(1) One or more toes of each foot have a conspicuous hoof or (in camelids, **Fig. 9**) foot with two large pad-like toes, each with a nail-like hoof at the front **6**

Fig. 9

5(2) No toe has a conspicuous hoof (but toes usually have claws or nails), never with only two conspicuous toes **7**

6(1) Main axis of foot lies in middle of central toe that is larger than other toes. More than one conspicuous hoof on each foot (four front, three rear, **Fig. 10**). Nose elongated

and trunk-like. Upper incisor teeth present .....
.....**Order Perissodactyla, Family Tapiridae (1 species: *Tapirus terrestris*)**

Fig. 10

6(2) Main axis of foot lies between two toes of about equal size (**Cervidae left, Tayassuidae right, Fig. 11**). Some species have no upper incisors .....
..... **Order Artiodactyla (3 families)**

Fig. 11

6(2)a Snout pig-like, flattened, with rim, and somewhat rounded. Two or three toes on hind feet. Tail scarcely evident externally..... **Family Tayassuidae (3 species)**

Snout not "pig-like". Tail evident externally .....**6(2)b**

6(2)b No horns or antlers at any time. Hind part of body contracted, knee-joint low, thigh appears distinct from body (**Fig. 12**). Cutaneous pad on each of two toes. Nails on upper surfaces (rather than hoof encasing the last bone of each toe) (**Fig. 9**) .....
.....**Family Camelidae (1 species: *Lama guanicoe*)**

Antlers of bony material and with no permanent covering, present in males at least part of year, sometimes branched. Thigh not so distinctly separate from body (**Fig. 13**)..... **Family Cervidae (5 species)**

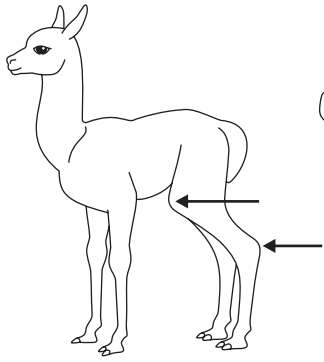

Fig. 12

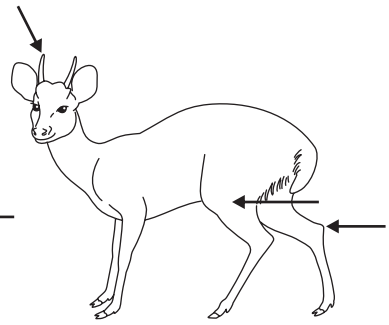

Fig. 13

7(1) Canines absent. Incisors strongly enlarged and chisel-like **8**

7(2) Canines present, longer than the incisors **9**

8(1) Four incisors in the upper jaw, the second pair much reduced, directly behind the first pair. Hind foot with three toes and densely haired on ventral surface (no paw pads). Ears long, extending well above the head .... **Order Lagomorpha, Family Leporidae (2 species, 1 introduced)**

8(2) Two incisors in the upper jaw. If the hind foot has three toes, it is not densely haired. Soles of feet not covered with hair (visible paw pads) .... **Order Rodentia (11 families)**

8(2)a Body covered with thick, keratinous spines .....**Family Erethizontidae (2 species)**

Body not covered with thick, keratinous spines.....**8(2)b**

8(2)b Body pelage brown with large and profuse white spots. Tail extremely short ....**Family Cuniculidae (1 species: *Cuniculus paca*)**

Body without profuse white spotting ..... **8(2)c**

8(2)c Claws on forefeet greatly enlarged for digging. Incisors extremely large, orange in colour and visible externally even when mouth is closed (**Fig. 14**). Eyes small, located high on the head.....**Family Ctenomyidae (4 species)**

Not as above .....**8(2)d**

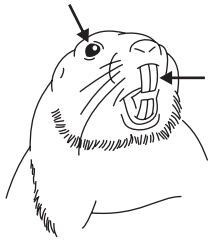

Fig. 14

8(2)d Tail long and bushy. Arboreal behavior ..... **Family Sciuridae (3 species)**

Tail not long and bushy. Arboreal or terrestrial behavior ..... **8(2)e**

8(2)e Bold black-and-white head markings. Body pelage grey. Tail long and with prominent tuft. Dry Chaco only..... .....**Family Chinchillidae (1 species: *Lagostomus maximus*)**

Not as above .....**8(2)f**

8(2)f Tail present and long or of medium-length. (**Fig. 15**).....**8(2)g**

Tail absent or extremely short so as to appear almost tail-less. (**Fig. 16**).....**8(2)j**

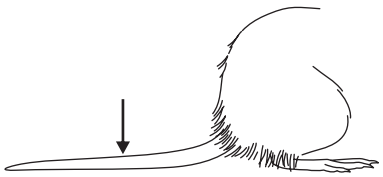

Fig. 15

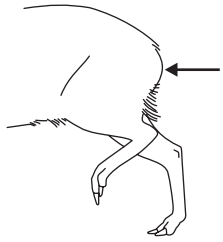

Fig. 16

8(2)g General appearance "beaver-like". Hind foot with prominent webbing. (**Fig. 17**) ....**Family Myocastoridae (1 species: *Myocastor coypus*)**

General appearance "mouse/rat-like". Hind foot without prominent webbing in most species.....**8(2)h**

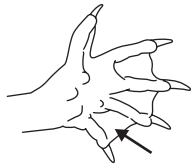

Fig. 17

8(2)h Diverse family with few uniting characteristics. Pelage with stiff guard hairs (in most species). Large size, HBL usually >13 cm. Hind foot never webbed. Genera can be characterised with following combinations:

Large species with soft fur: 1) Large (HBL > 22 cm). Tail furred, longer than HBL with conspicuous tuft. Pelage buffy yellowish. Digits of forefeet elongate and slender, no obvious plantar pad. Atlantic Forest usually in bamboo stands. (*Kannabateomys amblyonyx*). 2) Large (HBL > 22cm). Tail furred, approximately equal to head and body length with conspicuous tuft. Pelage greyish. Conspicuous white crescents around eyes. Usually in rocky areas. (*Thrichomys fosteri*).

Cavy-like species: 3) Medium-sized (HBL >15cm) and cavy-like. Dorsal pelage stiff. Forefeet and hindfeet elongated with strong, digging claws. Pelage yellowish-brown. Semi-fossorial behaviour. Tail much shorter than HBL. Open Cerrado savannas. (*Clyomys laticeps*). 4) Medium-sized (HBL >15cm) and cavy-like. Dorsal pelage stiff. Forefeet and hindfeet elongated with strong, digging claws. Pelage dark brown. Semi-fossorial behaviour. Tail much shorter than HBL (< 50%). Forest habitats. (*Euryzygomatomys spinosus*).

Rat-like species: 5) Medium-sized (HBL >18 cm) and rat-like. Dorsum with stiff hairs and rich chestnut-orange in colour, clearly demarcated from white underparts. Tail shorter than HBL length (*Proechimys longicaudatus*) .... **Family Echimyidae (5 species)**

Not as above. Hind foot webbed in a small number of genera. Pelage without spiny guard hairs. Size variable, HBL often <13cm (greater in a few species). Tail sometimes naked and usually without conspicuous tuft (present in some species). (**Note:** we are unaware of any external characters which reliably and consistently distinguish between Paraguayan species of the families Cricetidae and Muridae, and have thus included dental characters in this section of the key to external characters) .....**8(2)i**

8(2)i Molar cusps arranged in two parallel longitudinal rows (**Fig. 29, right**). Tail length may be less than, equal to or longer than head and body length. Hind foot webbed in a small number of semi-aquatic genera (*Holochilus*, *Nectomys*, *Scapteromys*) ....**Family Cricetidae (36 species)**

Molar cusps arranged in three parallel longitudinal rows (**Fig. 29, left**). Tail always longer than head and body length. Hind foot never webbed ....**Family Muridae (3 introduced species)**

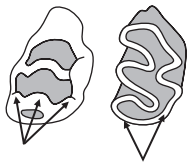

Fig. 29 (from craniodental keys, provided here as a convenience)

8(2)j Limbs elongated. Head small and rounded. Ears short and rounded (**Fig. 18**). No white periocular markings. Head and body length does not exceed 700 mm..... .....**Family Dasyproctidae (1 species: *Dasyprocta azarae*)**

Limbs short (**Subfamily Caviinae, 2 species**) or elongated. When legs are elongated, ears are long, and eyes with bold white periocular markings (**Fig. 19**) (**Subfamily Dolichotinae, 1 species**); or head large and rectangular, with eye, ear and nose located high on the head (**Fig. 20**), and head and body length of adults can greatly exceed 700 mm (**Subfamily Hydrochoerinae, 1 species**) ..... **Family Caviidae (4 species)**

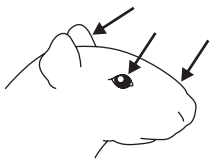

Fig. 18

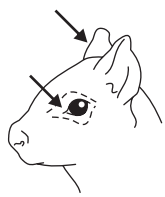

Fig. 19

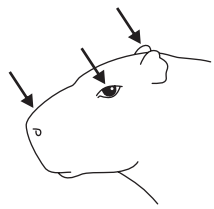

Fig. 20

9(1) Muzzle may be short or long. Teeth pointed for flesh-eating, canines enlarged. Total number of upper and lower incisors = 12 (3 pairs above, 3 pairs below) and outer upper incisors (I3) larger than other pairs (I1 or I2); neither pair of limbs especially elongated (except in *Chrysocyon*), tail long or short and never prehensile .... **Order Carnivora (5 families)**

9(1)a Tail more or less distinctly ringed with black or brown, and face "masked" ....**Family Procyonidae (2 species)**

Tail not ringed, or tail ringed and face not masked.....**9(1)b**

9(1)b Dorsal coat pattern of dark spots on paler background, or relatively uniformly brownish, reddish or blackish dorsally (in two species). Melanism common but pattern of spotted species still visible. Claws sharp and retractable (most noticeably on front feet); tail typically slender, often kinked. One non-native species commensal with humans..... **Family Felidae (8 native species)**

Dorsal coat pattern never spotted. Claws bluntish-ended and not retractable (always visible externally). Tail bushy, even when extremely short..... **9(1)c**

9(1)c Tail long, bushy and mostly white. Dorsal pelage consisting of contrasting white markings on a black background. Very strong musky ("skunky") smell. Claws of forefoot very long and strong (**Fig. 21**), the longest more than 14 mm..... ..... **Family Mephitidae (1 species: *Conepatus chinga*)**

Tail not long, bushy or white. Claws of forefeet not noticeably long .....**9(1)d**

Fig. 21

9(1)d Relatively long legs, height at shoulders usually more than 40% of length of head and body, or if not, then tail less than 40% of length of head and body). Ears often relatively large, triangular and erect (except *Speothos venaticus*). Face relatively long, eye usually about mid-way between end of nose and ear opening (**Fig. 22, right**). One species a non-native human commensal .... **Family Canidae (4 native species)**

Relatively shorter legs, height at shoulders usually less than 40% of head and body length, or if not, then tail is more than 40% of length of head and body. Ears relatively short and rounded, barely or not at all protruding above the top of the head. Face relatively flattened, eye usually nearer to end of nose than to ear opening. (**Fig. 22, left**) .....**Family Mustelidae (5 species)**

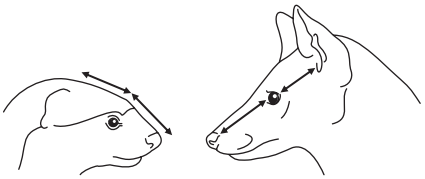

Fig. 22

9(2) Muzzle short, and nose set on flat face. Teeth not pointed, though canines may be enlarged. Total number of upper and lower incisors: 8 (2 pairs above, 2 pairs below) and I2 smaller than I1. One pair or both pairs of limbs noticeably elongate. Tail long and sometimes prehensile..... **Order Primates (5 native families)**

9(2)a Very large. Male with enlarged hyoid region (so as to appear "bearded") (**Fig. 23**). Strongly sexually dimorphic in coloration, black male and straw-coloured female. Tail strongly prehensile. Widespread ..... **Family Atelidae (1 species: *Alouatta caraya*)**

Not as above .....**9(2)b**

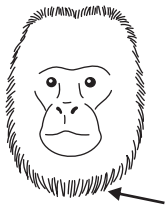

Fig. 23

9(2)b Nocturnal or crepuscular. Extremely large eyes occupying much of the face and bold markings on the head (**Fig. 24**). Coloration strongly bicolored between grizzled greyish dorsum and uniformly bright orange ventrum. Tail not prehensile. Chaco region only ..... **Family Aotidae (1 species: *Aotus azarae*)**

Not as above ..... **9(2)c**

Fig. 24

9(2)c Very small (<500 g). Nails claw-like on all digits except large toe (**Fig. 25**). Large white ear tufts, or nose clearly paler than the rest of the face .... **Family Callitrichidae (2 species, 1 introduced)**

Medium to large (> 800 g). Nails not claw-like. Nose concolorous with the rest of the face and no large white ear tufts present .....**9(2)d**

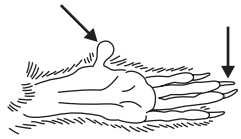

Fig. 25

9(2)d Pelage brownish or yellowish-brown with darker markings on the head (which bears furred protruberances in adults). Tail semi-prehensile. Mainly in the Oriental region, with marginal occurrence in the northern Chaco .... **Family Cebidae (1 species: *Sapajus cay*)**

Pelage uniformly pale grizzled-grey to whitish. No furred protruberances on the head. Appears rather "woolly." Tail not prehensile. Chaco region only..... .....**Family Pitheciidae (1 species: *Plecturocebus pallescens*)**

Key to orders and families of living mammals of Paraguay, using craniodental characters

1(1) Incisor teeth reduced to a single large and persistently growing pair in both upper and lower jaws. No small secondary pair behind the upper pair. Wide gap between incisors and grinding teeth (**Fig. 26**) .....**Order Rodentia (11 families)**

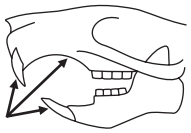

Fig. 26

1(1)a Zygomatic plate anterior to zygomatic arch well-defined. Infraorbital foramen small. Lower jaw with origin of angular process directly ventral to sheath of lower incisor .....**1(1)b**

No zygomatic plate. Infraorbital foramen greatly enlarged (**Fig. 27**). Lower jaw with root of angular process deflected lateral to sheath of lower incisor .... **Hystricomorpha (8 families) 1(1)d**

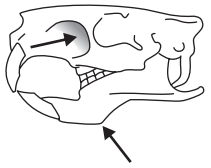

Fig. 27

1(1)b Zygomatic plate oriented laterally. Maxillary teeth 3 or less. Infraorbital foramen pierces zygomatic plate (**Fig. 28, left**) ....**Suborder Sciuromorpha, Family Sciuridae (3 species)**

Zygomatic plate oriented anteriorly. Maxillary teeth 4 or 5. Infraorbital foramen narrow and usually expanded dorsally (**Fig. 28, right**) .... **Suborder Myomorpha (2 families) 1(1)c**

Fig. 28

1(1)c Molar cusps arranged in two parallel longitudinal rows (**Fig. 29, right**)..... .....**Family Cricetidae (36 species)**

Molar cusps arranged in three parallel longitudinal rows (**Fig. 29, left**) ....**Family Muridae (3 species, introduced)**

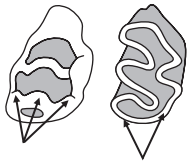

Fig. 29

1(1)d Dentary with prominent ridge and groove on lateral side of dentary below and parallel to cheek teeth (**Fig. 30**) ..... **Family Caviidae (4 species)**

No prominent ridge and groove on lateral side of dentary..... **1(1e)**

Fig. 30

1(1)e Zygomatic arch greatly expanded, forming thickened and rugose cheekplate (**Fig. 31**). Skull length of adult >100 mm ....**Family Cuniculidae (1 species: *Cuniculus paca*)**

Zygomatic arch normally developed, without thickened cheekplate. Skull length variable .....**1(1)f**

Fig. 31

1(1)f Cheek teeth composed of two to four simplified transverse plates (**Fig. 32**)..... .....**Family Chinchillidae (1 species: *Lagostomus maximus*)**

Cheek teeth with more complex occlusal surfaces.....**1(1)g**

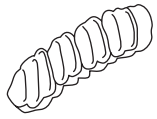

Fig. 32

1(1)g Cheek teeth either with very wide reentrant folds or nearly laminate, rooted and paroccipital process not greatly lengthened (**Fig. 33**) ....**Family Erethizontidae (2 species)**

Not as above .....**1(1)h**

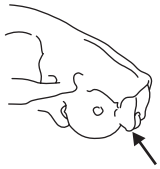

Fig. 33

1(1)h Cheek teeth semirooted, reentrant folds isolating as narrow islands on crown surfaces in adults (**Fig. 34**) .....**Family Dasyproctidae (1 species: *Dasyprocta azarae*)**

Cheek teeth with occlusal surfaces rather simplified when growing. Occlusal surface shows pattern of isolated islands when rooted .....**1(1)i**

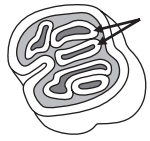

Fig. 34

1(1)i Cheek teeth greatly simplified, labial side of upper series with only one reentrant fold. Occlusal surfaces of cheek teeth weakly kidney shaped, size decreasing notably from front to back (**Fig. 35**). Skull heavily ridged. Elongated rostral tubes extend dorsolaterally from the auditory bullae (**Fig. 36**) ....**Family Ctenomyidae (4 species)**

Cheek teeth more complex, labial side of upper series always with at least two, typically three, sometimes more reentrant folds. Jugal does not contact lacrimal ....**1(1)j**

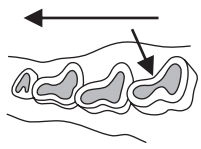

Fig. 35

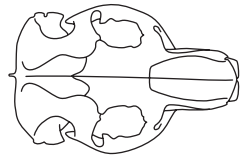

Fig. 36

1(1)j Maxillary teeth with two to three labial and three lingual flexi. Teeth increasing in size from front to back (**Fig. 37**). Paroccipital process greatly elongated, vertical, and completely free from the auditory bulla (**Fig. 38**). Rostrum long and deep..... .....**Family Myocastoridae (1 species: *Myocastor coypus*)**

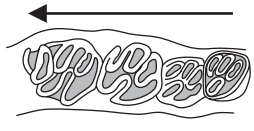

Fig. 37

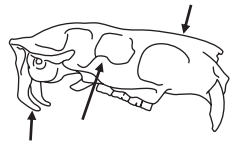

Fig. 38

Maxillary teeth with typically only one lingual flexus with labial flexi varying from two to four (**Fig. 39**); teeth either uniform or decreasing in size from front to back. Paroccipital process short and curved to follow contour of the auditory bulla (**Fig. 40**)..... **Family Echimyidae (5 species)**

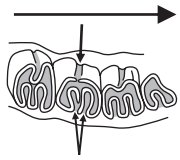

Fig. 39

Fig. 40

1(2) Incisor teeth range in number from none to five upper and none to four lower pairs, but are never a single pair as described above.....**2**

2(1) Bones of skull relatively thin and fused so that few sutures are visible; skull shorter than 54 mm..... **Order Chiroptera (6 families)**

2(1)a Postorbital processes present (**Fig. 41**). Palatal branch of premaxilla reduced (incomplete anterior palate). Premaxillae movable, not fused to maxillae. Dental formula i1/3, c1/1, p2/2, m3/3 × 2 = 32 ..... **Family Emballonuridae (2 species)**

No postorbital processes (**Fig. 42**). Palatal branch of premaxilla may or may not be reduced (complete or incomplete anterior palate). Premaxillae fused to maxillae..... .....**2(1)b**

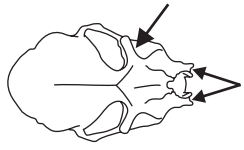

Fig. 41

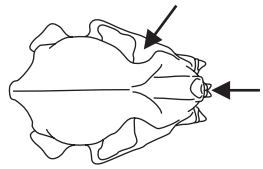

Fig. 42

2(1)b Skull broad and massive with high sagittal crest (**Fig. 43**) and anterior palate complete. Dental formula i2/1, c1/1, p1/2, m3/3 × 2 = 28..... ..... **Family Noctilionidae (2 species)**

Not as above ..... **2(1)c**

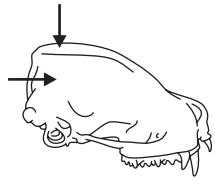

Fig. 43

2(1)c Premaxillae separate (**Fig. 44**). Palate emarginated anteriorly..... ..... **Family Vespertilionidae (16 species)**

Premaxillae complete and fused with each other (**Fig. 45**) .....**2(1)d**

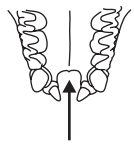

Fig. 44

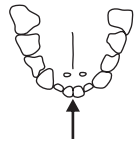

Fig. 45

2(1)d Elongated snout and small, rounded braincase (**Fig. 46**). Dental formula i2/3, c1/1, p3/3, m3/3 × 2 = 38 ..... **Family Natalidae (1 species: *Natalus macrourus*)**

Not as above and total number of teeth 34 or less ..... **2(1)e**

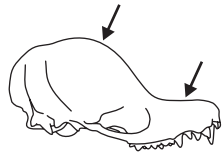

Fig. 46

2(1)e Total number of teeth less than or equal to 22. Canines and incisors sharpened..... .....**Family Phyllostomidae, Subfamily Desmodontinae (2 species)**

Total number of teeth 26 or greater.....**2(1)f**

2(1)f One pair of upper incisors. Total number of teeth 26 to 30..... ..... **Family Molossidae (17 species)**

Two pairs of upper incisors. Total number of teeth 28 to 34..... ..... **Family Phyllostomidae excluding Desmodontinae (18 species)**

2(2) Bones of skull relatively heavy and many sutures visible; skull in many species longer than 54 mm.....**3**

3(1) Ten upper incisors and eight lower incisors ....**Order Didelphimorphia, Family Didelphidae (18 species)**

3(2) Fewer incisors above and below.....**4**

4(1) Enamel present, incisors present or absent.....**5**

4(2) Teeth absent or simple, subcylindrical, and without enamel, no incisors present (**Fig. 47**).....**6**

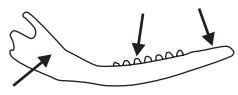

Fig. 47

5(1) Large gap between grinding teeth and incisors at front of lower jaw, and length of jaw from articular process more than 85 mm (**Fig. 48**) **7**

5(2) No large diastema in lower tooth row, or, if so, then jaw shorter than 85 mm **8**

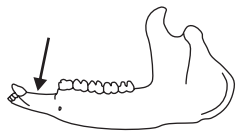

Fig. 48

6(1) Teeth either completely absent, or anterior upper tooth smaller than next tooth and space between them less than length of crown of second tooth. Alveolar length of upper tooth row less than 30 mm..... .....**Order Pilosa, Family Myrmecophagidae (2 species)**

6(2) Teeth simple, subcylindrical, and without enamel. No incisors present (**Fig.** 47)..... ..... **Order Cingulata (2 families)**

6(2)a When viewed dorsally the skull is elongated, widening gradually at zygomatic processes, but overall with conical appearance (**Fig. 49**). Mandible gracile with ramus slender, barely wider than mandibular body and gradually sloping upwards (**Fig.** 47)..... **Family Dasypodidae (2 species)**

When viewed dorsally the snout is short, with skull, widening suddenly at the zygomatic processes, giving a more "squared" appearance (**Fig. 50**). Mandible robust with ramus broad, clearly widening from mandibular body and almost at a right angle to it (**Fig. 51**) ..... **Family Chlamyphoridae (9 species)**

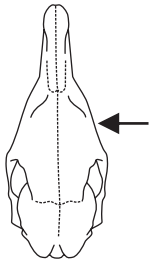

Fig. 49

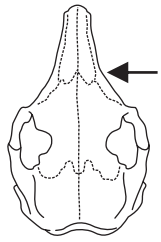

Fig. 50

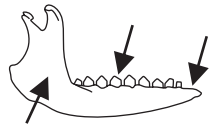

Fig. 51

7(1) Upper incisor teeth present; skull as shown in **Figs. 52, 53**..... ..... **Order Perissodactyla (2 families)**

7(1)a Nasal bones relatively long anteriorly; nasal opening on skull not unusually displaced posteriorly (**Fig. 52**) .....**Family Equidae (2 species, commensal)**

Nasal opening of skull displaced posteriorly (**Fig. 53**)..... .....**Family Tapiridae (1 species: *Tapirus terrestris*)**

Fig. 52

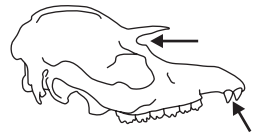

Fig. 53

7(2) Some species have no upper incisors (**Fig. 55**). Skull as shown in **Figs. 53–58**..... ..... **Order Artiodactyla (5 families)**

7(2)a Canine teeth large. Upper incisors present and not reduced to a single lateral pair in adults (**Fig. 54**) .....**7(2)b**

Canine teeth absent or relatively small. Upper incisors absent or reduced in adults to a single lateral pair .....**7(2)c**

7(2)b Upper canines curving outward. Three pairs of upper incisors (**Fig. 54, left**). Lower third molar longer than 35 mm. First lower premolar sometimes present. Domestic, may be feral ..... **Family Suidae (1 species, domesticated or feral: *Sus scrofa*)**

Upper canines directed downward (**Fig. 54, right**). Two pairs of upper incisors. m3 considerably shorter than 35 mm. p1 never present .... **Family Tayassuidae (3 species)**

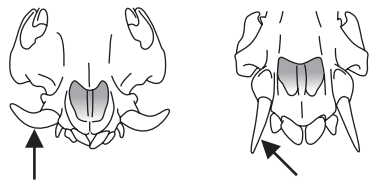

Fig. 54

7(2)c No horns or antlers at any time. Two pairs of caniniform teeth in upper jaw (one a pair of incisors, the other a pair of canines), and usually a pair of canines below (**Fig. 55**). Canines larger and more hooked in males. Three pairs of lower incisiform teeth. Deep medial posterior notch of palate extends considerably farther forward than lateral notches do (**Fig. 56, left**) ....**Family Camelidae (1 species: *Lama guanicoe*)**

Horns or antlers may be present in one or both sexes, continuously or at certain times of the year. Caniniform teeth absent. Four pairs of lower incisiform teeth (lateral pair actually canines). Anterior end of medial posterior notch of palate even with or posterior to lateral notches (**Fig. 56, right**).....**7(2)d**

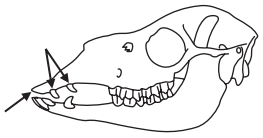

Fig. 55

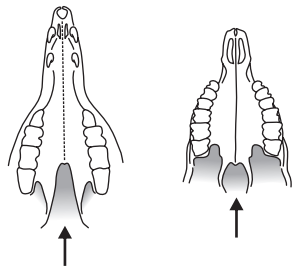

Fig. 56

7(2)d Vacuity conspicuous between lacrimal and nasal bones (**Fig.** 57). Molariform teeth brachydont (relatively low crowned). Antlers of bony material and with no permanent covering, present in males at least part of year, and sometimes branched .... **Family Cervidae (5 species)**

Vacuity inconspicuous or not present (**Fig. 58**). Molariform teeth more hypsodont (high-crowned). Horns (with bony core and covering of horn), if present, never shed, never branched, and in some species present in both sexes. Domestic, may be feral..... **Family Bovidae (several species, all domestic or feral)**

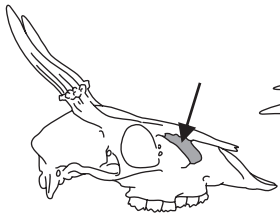

Fig. 57

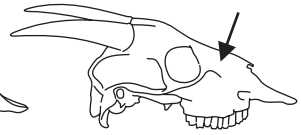

Fig. 58

8(1) Canine teeth absent, major gap (diastema) between incisors and grinding teeth at back of jaws (**Fig. 59**)..... ..... **Order Lagomorpha, Family Leporidae (2 species, 1 introduced)**

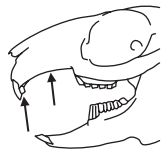

Fig. 59

8(2) Canine teeth present and often noticeably larger than adjacent incisors and premolars. No large diastemal gap.....**9**

9(1) Total number of upper and lower incisors = 12 (3 pairs above, 3 pairs below). Outer upper incisors (I3) larger than other pairs (I1 or I2) .... **Order Carnivora (5 families)**

9(1)a Muzzle short, orbit much closer to canines than to rear of skull. (**Fig. 60**) Three or four upper teeth behind canines.....**9(1)b**

Muzzle extended and may be somewhat narrowed (**Fig. 61**). Orbit approximately equidistant between canines and rear of skull, or slightly closer to the canines than to the rear of the skull. Number of upper teeth behind canines variable and may be greater than four .....**9(1)d**

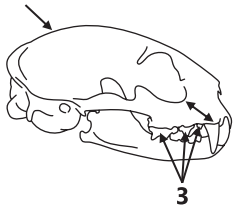

Fig. 60

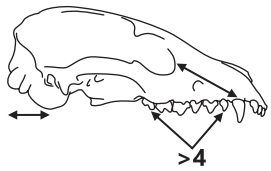

Fig. 61

9(1)b Skull basically rounded in lateral view (**Fig. 60**). Almost no muzzle. Brain case rounded. The posteriormost of the upper teeth (the true molar) is strongly reduced, far smaller than the preceding tooth (= carnassial or last premolar)..... .....**Family Felidae (8 species, plus 1 commensal)**

Skull with extremely elongated braincase, much longer than facial region (**Figs. 62, 63**). When viewed laterally the top of the braincase is basically straight. Distance between orbit and anterior nares less than interorbital breadth..... **9(1)c**

9(1)c Four upper teeth behind canine (**Fig. 62**). The posteriormost of the upper teeth about twice as wide mediolaterally as from front to back and with a medial constriction. Post-orbital processes present. Bony palate extending well behind teeth, usually more than the distance between teeth.....**Family Mustelidae (5 species)**

Only three upper teeth behind canine (**Fig. 63**). The posteriormost upper tooth (M1) large, its length about the same as its width. No post-orbital processes. Little extension of bony palate behind level of teeth, extension less than distance between teeth..... **Family Mephitidae (1 species: *Conepatus chinga*)**

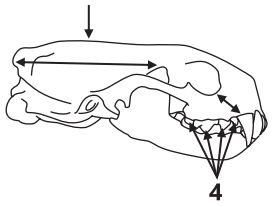

Fig. 62

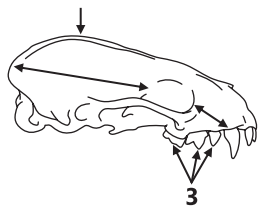

Fig. 63

9(1)d Molariform teeth relatively low and rounded, none of them with sharp bladelike edge ..... **Family Procyonidae (2 species)**

Some molariform teeth carnassial (bladelike), especially in adults (the last upper premolar [P4] and first lower molar [m1]). In young the carnassial teeth are P3 and p4. The number of teeth in the upper jaw behind each canine is more than four (**Fig. 61**). Distance between orbit and anterior nares more than interorbital breadth. Braincase not extending noticeably behind ears. One species domestic, may be feral ..... **Family Canidae (4 species, plus 1 commensal)**

9(2) Total number of upper and lower incisors = 8 (2 pairs above, 2 pairs below) and I2 smaller than I1 ..... **Order Primates (5 families)**

9(2)a Total number of teeth 32 ..... **9(2)b**

Total number of teeth 36. Dental formula i2/2 c1/1 p3/3 m2/2 = 36 ..... **9(2)c**

9(2)b Two premolars and two or three molars. Skull large with steep frontal bone. Width of braincase not less than 100 mm .... **Family Hominidae (1 species: *Homo sapiens*)**

Three premolars and two molars. Skull small with receding frontal bone. Width of braincase does not exceed 50 mm..... ..... **Family Callitrichidae (1 species and 1 introduced)**

9(2)c Face showing airorhynchy (strongly sloping). Braincase small and elongated. Mandible extremely robust (**Fig. 64**) ..... **Family Atelidae (1 species: *Alouatta caraya*)**

Face does not show airorhynchy, and is situated on a near vertical plane. Braincase large or fairly large ..... **9(2)d**

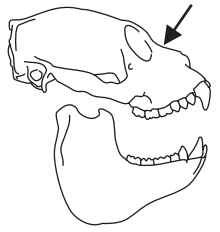

Fig. 64

9(2)d Eye sockets extremely large (**Fig. 65**), occupying the vast majority of the facial region ..... **Family Aotidae (1 species: *Aotus azarae*)**

Eye sockets not of exaggerated size ..... **9(2)e**

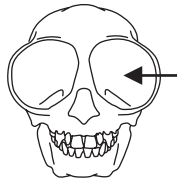

Fig. 65

9(2)e Pronounced sagittal crest in males. Canines enlarged. Zygomatic arch robust and arched. Mandibular base with relatively straight lower margin, running vaguely parallel to the tooth row. Ramus appears vaguely right-angled. (**Fig. 66**) .... **Family Cebidae (1 species: *Sapajus cay*)**

Sagittal crest absent or low in males. Canines not enlarged. Zygomatic arch gracile and low. Mandibular base extending diagonally to the angle, diverging from and not parallel with tooth row. Ramus extremely large and deep, does not appear right-angled. (**Fig. 67**).....**Family Pitheciidae (1 species: *Plecturocebus pallescens*)**

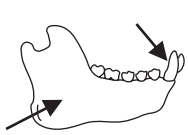

Fig. 66

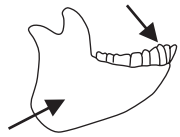

Fig. 67

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SUPPLEMENTAL INFORMATION TABLES

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Table S1. Collections by department.

Collection	Alto Paraguay	Boquerón	Chaco*	Nueva Asunción**	Presidente Hayes	Western Paraguay	Alto Paraná	Amambay	Caaguazú	Caazapá	Canindeyú	Distrito Capital	Central	Concepción	Cordillera	Guairá	Itapúa	Misiones	Ñeembucú	Paraguarí	San Pedro	Eastern Paraguay	Unknown	Total
AMNH	188	181			55	424		24	4		174	315	11	8		82	12	39	7	58	7	741	34	**1199**
ASNHC						0																0	1	**1**
BMNH						0										2						2	348	**350**
BW						0																0	78	**78**
CCCI						0																0		**0**
CMBI–M					1	1	117				20	1			1							139	61	**201**
CML		1				1					16		1		5					19	1	42	3	**46**
CZPLT						0											1		3		465	469	57	**526**
DMNS						0										4						4		**4**
EBD	20	111	7	131	1	270							7				12	20				39	6	**315**
FACEN						0																0		**0**
FMNH	90	843	4	2	357	1296	3						40					5		55	10	113	18	**1427**
IBIS		6			1	7	1				2		1				1	2	35	7		49	5	**61**
IIBP–M						0	1	20	26	17				11								75		**75**
IRSCNB				12		12														3		3	26	**41**
KU	1	8			13	22											85	1				86		**108**
LACM						0																0	1	**1**
LSUMZ					2	2	4		6	2	9	4	2	2			7			2		38	2	**42**
MACN	75				4	79			1				4		2		171				1	179	8	**266**
MCNB						0																0	3	**3**
MCZ						0										13			6	4	3	26	143	**169**

*Chaco Department became part of Alto Paraguay Department in 1992.
**Nueva Asunción Department became part of Boquerón Department in 1992.

Table S1. Collections by department (cont.)

Collection	Alto Paraguay	Boquerón	Chaco*	Nueva Asunción**	Presidente Hayes	Western Paraguay	Alto Paraná	Amambay	Caaguazú	Caazapá	Canindeyú	Distrito Capital	Central	Concepción	Cordillera	Guairá	Itapúa	Misiones	Ñeembucú	Paraguarí	San Pedro	Eastern Paraguay	Unknown	Total
MHNG						0	3						3									6	1639	**1645**
MNHNP	436	291	240	150	286	1403	65	333	12	41	370		81	201	95		296	44	45	241	65	1889	23	**3315**
MNHNU		1				1							3			3						6	2	**9**
MNRJ						0			5				7								5	17		**17**
MSB	16	79	6	7	9	117		51	42		13			20	1		1	13		1		142		**259**
MTD	9	22			12	43																0	4	**47**
MVZ		110			614	724	1		10		20		195	55	92		59	1	1	4	2	440	3	**1167**
MZUSP						0	1						1				3			6		11	4	**15**
NHMG						0																0	1	**1**
O						0																0	5	**5**
OKMNH		4				4														6		6		**10**
RDO	604	965			680	2249		41		77	2780	4	17	357	52		479	34	134	76	216	4267	8	**6524**
ROM				1	1	2																0	5	**7**
TCWS						0																0	2	**2**
TTU	644	371			528	1543	1	85	1	85	2178		5	259	83	1	381	37	139	109	1370	4734		**6277**
UAM						0					97											97		**97**
UCS	22	1005			502	1529		2				3	13		1		85					104	236	**1869**
UF	13	11	4	4	3	35																0	136	**171**
UMMZ	82	87			437	606		127	64	15	562		275	30	151		300	147	28	487	167	2353	264	**3223**
USNM	3	103				106	3	28	14				11	1	4		9	63		115		248	577	**931**
Totals	**2203**	**4199**	**261**	**307**	**3506**	**10476**	**200**	**711**	**185**	**237**	**6241**	**327**	**677**	**944**	**487**	**105**	**1902**	**406**	**398**	**1193**	**2312**	**16325**	**3703**	**30504**
						34%																**54%**	**12%**	**100%**

Table S2. Collections by order and family.

	Didelphimorphia	Cingulata	Pilosa	Primates				Rodentia										Lagomorpha	Chiroptera						Carnivora					Perissodactyla	Artiodactyla			Undetermined or other	
Collection	Didelphidae	Dasypodidae	Myrmecophagidae	Cebidae***	Atelidae	Aotidae	Pitheciidae	Sciuridae	Cricetidae	Muridae	Ctenomyidae	Echimyidae	Erethizontidae	Chinchillidae	Caviidae	Dasyproctidae	Cuniculidae	Myocastoridae	Leporidae	Phyllostomidae	Emballonuridae	Molossidae	Vespertilionidae	Noctilionidae	Natalidae	Felidae	Canidae	Mustelidae	Mephitidae	Procyonidae	Tapiridae	Tayassuidae	Camelidae	Cervidae		**Totals**
AMNH	15	2	1	3	2	4	6		135	17	1	3			8			2	4	161	15	483	247	49		4	17	3	4	1		5		4	3	**1199**
ASNHC		1																																		**1**
BMNH		3	1	6	2	2	3		127		1	2	1			1	1		1	86		74	35			2						1		1		**350**
BW	2	14	8	1		7									1							15				9	3	4	1	4		3		5	1	**78**
CCCI																																				**0**
CMBI–M	12	9	5	4	6				7	11			3		5	9	4	5	2	6		1	1			29	23	11		10	3	13		18	4	**201**
CML									1											40			4											1		**46**
CZPLT	54	9	2		3				112	10		4			6	2				194		17	11			2						1		2	97	**526**
DMNS																																		4		**4**
EBD	5	16	2	1		5	4		127						1				5	14		74	2			11	7		5		2	19		14	1	**315**
FACEN																																				**0**
FMNH	27	11		2	2	4	1		1156	11	19	3		3	18	1			5	39	1	80	16	3		2	6	1	2	1		13				**1427**
IBIS	5	1							13		33									1	2														6	**61**
IIBP–M																																			75	**75**
IRSCNB	1								32						8																					**41**
KU	3	1						1	31										2	59		4	3			1	2					1				**108**
LACM																																1				**1**
LSUMZ	2																			28		8		2											2	**42**
MACN	20	10	1	7	3	4	4		11	6	3	1			4	2	2		4	32		4	18	1		5	5	5		4	2	5		10	93	**266**
MCNB		2	1																																	**3**
MCZ	4	2	3	2	6				22	1	1	1			8	3				21		8	21			29	8	12		2	4	5		6		**169**
MHNG	23	8	2	3		1	1	1	69	72		1		5	14				2	661		412	313	26		7	4		1	5	2	7		5		**1645**

Table S2. Collections by order and family (cont.)

Collection	Didelphimorphia	Cingulata	Pilosa	Primates				Rodentia										Lagomorpha	Chiroptera					Carnivora					Perissodactyla	Artiodactyla			Undetermined or other	Totals
	Didelphidae	Dasypodidae	Myrmecophagidae	Cebidae***	Atelidae	Aotidae	Pitheciidae	Sciuridae	Cricetidae	Muridae	Ctenomyidae	Echimyidae	Erethizontidae	Chinchillidae	Caviidae	Dasyproctidae	Cuniculidae	Myocastoridae	Leporidae	Phyllostomidae	Emballonuridae	Molossidae	Vespertilionidae	Noctilionidae	Natalidae	Felidae	Canidae	Mustelidae	Mephitidae	Procyonidae	Tapiridae	Tayassuidae	Cameliidae	Cervidae		
MNHNP	61	70	22	19	12	10	8		564	25	7	5	2	6	45	3	5	3	10	1111	38	638	240	80	1	30	37	14	3	21	15	95	1	66	48	**3315**
MNHNU																						4	3			1						1			**9**
MNRJ	2								4	6		3			1	1																			**17**
MSB	15	10							141	25	12	3	1		3			1	1	29		2	6				1		1	1		3		3	1	**259**
MTD	5	4	1						14	3		4			3							2	1			4	1		1				4		**47**
MVZ	18	10	2						189	9	1	10			8				3	185		122	547	34		3	12			3	1	7		3		**1167**
MZUSP	1				1				4			1								1		4	1			1	1								**15**
NHMG	1																																		**1**
O																						1				2		1			1				**5**
OKMNH																				6		4														**10**
RDO	210	23	2		1			1	4650	38	14	60		1	74				2	785	1	440	128	21			5				1		2	65	**6524**
ROM		1																				4				1						1			**7**
TCWS																																2			**2**
TTU	63	29	1						1274	19	30	16			31		2	2	8	3582		894	259	54			3			3		1	5	1	**6277**
UAM		8		8					23	4							2			52															**97**
UCS	43	94	9			1			519	3	3			5	20					34		208	46	51		129	191	9	5	21	33	334	2	105	4	**1869**
UF		5				1	3		12		1									2		5	1	6		109		24		1		1				**171**
UMMZ	148	12	5	8	4	3	2		1754	5	1	46	3		21	3		4	13	694	11	218	146	42		14	9	2	2	9	6	17		21		**3223**
USNM	54	3		50	5	1	1		198	61	1	8	2	1	7	2	1	1	7	203		177	133	1		2	1	1		1		4		5		**931**
Totals	**794**	**358**	**68**	**114**	**47**	**43**	**33**	**3**	**11189**	**326**	**128**	**171**	**12**	**21**	**286**	**27**	**17**	**18**	**69**	**8026**	**68**	**3903**	**2182**	**370**	**1**	**393**	**339**	**88**	**24**	**88**	**70**	**540**	**3**	**284**	**391**	**30504**
Order totals	**1573**	**713**	**135**	**237**				**12198**											**134**	**14550**						**932**					**70**	**827**				

***Formerly included Callitrichidae, which is now considered to be a separate family.

Table S3. Collections by decade. See **Table 1** for names and locations of collections.

Collection	1850s	1860s	1870s	1880s	1890s	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	Unknown	Total	
AMNH					2	21	30	12	55	19	16	681	282	46				35	**1199**	NA
ASNHC																1			**1**	NA
BMNH					14	109		23					1					203	**350**	EU
BW						2					42			1				33	**78**	EU
CCCI																			**0**	PY
CMBI–M													41	81	17	21	3	38	**201**	PY
CML												1	3	40				2	**46**	SA
CZPLT																1	462	63	**526**	PY
DMNS								4											**4**	NA
EBD														312				3	**315**	EU
FACEN																			**0**	PY
FMNH						64	2	28		130	3		2		1183			15	**1427**	NA
IBIS														19	29	2		11	**61**	PY
IIBP–M																72		3	**75**	PY
IRSCNB						3			2				36						**41**	EU
KU								1				20	1		1	85			**108**	NA
LACM													1						**1**	NA
LSUMZ													15	1		13		13	**42**	NA
MACN						1		1	88	76	8				5			87	**266**	SA
MCNB																		3	**3**	EU
MCZ						48		11	63	27			1					19	**169**	NA
MHNG									6			1	117	1245	142			134	**1645**	EU
MNHNP													1	1571	1621	105		17	**3315**	PY
MNHNU					1					1	7								**9**	SA
MNRJ										7	10								**17**	SA
MSB														49	210				**259**	NA
MTD																		47	**47**	EU
MVZ						2					5		1157					3	**1167**	NA
MZUSP						10	1						1					3	**15**	SA
NHMG								1											**1**	EU
O						1	1											3	**5**	EU
OKMNH														10					**10**	NA
RDO															2554	2149	1813	8	**6524**	PY
ROM											4		1					2	**7**	NA
TCWS													2						**2**	NA
TTU									2			1	2		5990	281		1	**6277**	NA
UAM															97				**97**	NA
UCS												3	1846	8	2		1	9	**1869**	NA
UF									2				134	35					**171**	NA
UMMZ						2			7				2448	300	323	117		26	**3223**	NA
USNM	2					430		18	1		34	148	16	165				117	**931**	NA
Totals	**2**	**0**	**0**	**0**	**17**	**693**	**34**	**99**	**226**	**260**	**129**	**855**	**6108**	**3883**	**12174**	**2847**	**2279**	**898**	**30504**	
Paraguayan																			**10702**	**35.1%**
Foreign																			**19802**	**64.9%**
European																			**2485**	**8.1%**
North American																			**16964**	**55.6%**
South American																			**353**	**1.2%**

Table S4. Collections within each family, by decade.

Family	1850s	1860s	1870s	1880s	1890s	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	Unknown	Total
Didelphidae					1	19	4	2	6	16	11	11	213	78	150	104	128	51	**794**
Dasypodidae								3	3	13	11	1	117	88	76	12	10	24	**358**
Myrmecophagidae						1			2	1	5		17	21	7	3	1	10	**68**
Cebidae*						1		2	1	5	3		18	14	17	1		52	**114**
Atelidae	1					1		2	1	1		2	4	5	10	1	2	17	**47**
Aotidae					2		3	1		7	2		5	17				6	**43**
Pitheciidae					3		6	1		5			2	13	1	1		1	**33**
Sciuridae														1	1	1			**3**
Cricetidae					9	132	2	53	16	57	19	85	1917	835	4331	1915	1718	100	**11189**
Muridae						11	2	3	3	14		59	21	61	86	14	23	29	**326**
Ctenomyidae						1			2	20			6	24	66			9	**128**
Echimyidae					1	10		1			6		51	4	52	35	4	7	**171**
Erethizontidae						2			1				2	4		1		2	**12**
Chincilllidae										3			5	6	1	1		5	**21**
Caviidae						5	4	4	6	11	2	3	54	30	107	29	3	28	**286**
Dasyproctidae						1			3	1	2		6	4	3	2		5	**27**
Cuniculidae									2				2	3	6			4	**17**
Myocastoridae												1	2	3	5	2		5	**18**
Leporidae						8	2	2	5	5			14	13	11	6		3	**69**
Phyllostomidae						156		2	56	12	15	71	1006	1201	4690	420	210	187	**8026**
Emballonuridae												7	56		2		1		**66**
Molossidae	1					198		6	13	12	16	369	677	586	1752	144	19	112	**3905**
Vespertilionidae						120		3	31	13	5	184	742	406	536	48	26	68	**2182**
Noctilionidae											6	49	124	74	116			1	**370**
Natalidae															1				**1**
Felidae					1	11	1	1	14	5	8	1	258	41	14	4		34	**393**
Canidae						4	6	1	5	7	3	10	211	43	19	7	1	22	**339**
Mustelidae						5	2		7	3	5		33	14	7	3	1	8	**88**
Mephitidae										2			11	10				1	**24**
Procyonidae						2			3	2	4		36	28	6	2		5	**88**
Tapiridae						1			3				42	9	10	1		4	**70**
Tayassuidae						1		6	3	4	3		376	95	34	3		15	**540**
Camelidae													2		1				**3**
Cervidae						3	2	5	7	3	3	1	128	72	29	4		27	**284**
Undetermined								1	33	38		1	6	24	27	84	131	56	**401**
Totals	**2**	**0**	**0**	**0**	**17**	**693**	**34**	**99**	**226**	**260**	**129**	**855**	**6164**	**3827**	**12174**	**2848**	**2278**	**898**	**30504**

* Formerly included Callitrichidae, which is now considered to be a separate family.

Table S5. Departments by decade.

Department	1850s	1860s	1870s	1880s	1890s	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	Unknown	Total
Alto Paraguay								1		76	8	132	49	253	1602	66	3	13	**2203**
Alto Paraná							1	3					27	114	35	14	3	3	**200**
Amambay													151	303	236	21			**711**
Boquerón					1					80	7	87	1366	281	1751	594	4	28	**4199**
Caaguazú									1	3	18	1	74	5	49	28		6	**185**
Caazapá														30	174	29		4	**237**
Canindeyú										1		173	528	105	2607	1212	1608	7	**6241**
Distrito Capital						1					1	273	47	1		3	1		**327**
Central						4		9		40	4	16	485	25	20	70		4	**677**
Chaco*								3		1			1	252	2			2	**261**
Concepción									8				67	84	650	134		1	**944**
Cordillera													225	52	174	35		1	**487**
Guairá								16	50	12	17							10	**105**
Itapúa						2	11		88	4			404	138	806	360	3	86	**1902**
Misiones						5		1				82	123	40	150	5			**406**
Ñeembucú						5			5				10	1	364		3	10	**398**
Nueva Asunción**													15	283	7			2	**307**
Paraguarí						103						47	438	290	297	14		4	**1193**
Presidente Hayes							19		2	24	1	40	1317	261	1592	216	7	27	**3506**
San Pedro								10		4	5		17	95	1492	32	633	24	**2312**
Unknown	2				16	573	3	56	72	15	68	4	764	1270	166	14	14	666	**3703**
Total	**2**	**0**	**0**	**0**	**17**	**693**	**34**	**99**	**226**	**260**	**129**	**855**	**6108**	**3883**	**12174**	**2847**	**2279**	**898**	**30504**

*Chaco Department became part of Alto Paraguay Department in 1992.
**Nueva Asunción Department became part of Boquerón Department in 1992.

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Despite having one of the longest histories of mammalian research on the South American continent, Paraguayan mammalogy remains underdeveloped due to a lack of trained researchers and opportunities for study, and cultural under-valuation of biological sciences. While this situation is improving with government investment in scientific endeavor, capacitation of educators and greater societal awareness of environmental issues, Paraguay still lags behind its neighbors in the production of zoological literature, and mammalogy is no exception. This review aims to provide a succinct overview of the current state of knowledge about Paraguayan mammals and mammalogy. We hope this monograph will provide a detailed and solid framework for ongoing work and serve as a stimulus for future research.

Pablo V. Teta, Guest Editor

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