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## HISTORY OF MAMMALOGY IN THE GUIANAS

Burton K. Lim<sup>1</sup>, and Francois M. Catzeflis<sup>2</sup>

<sup>1</sup>Department of Natural History, Royal Ontario Museum, 100 Queen’s Park, Toronto, Ontario, Canada, M5S 2C6; Email: [burtonl@rom.on.ca](mailto:burtonl@rom.on.ca)

<sup>2</sup>Laboratoire de Paléontologie, UMR-5554 CNRS, Université Montpellier-2, Institut des Sciences de l’Evolution, Case Courrier 064, Place Eugène Bataillon, 34095 Montpellier cedex 05, France ; E-mail: [francois.catzeflis@univ-montp2.fr](mailto:francois.catzeflis@univ-montp2.fr)

## ABSTRACT

The Guianas consists of Guyana, Suriname, and French Guiana on the northeastern coast of South America between the Orinoco and Amazon Rivers. Since colonial times, this area has received varying levels of scientific exploration and research. The study of mammalogy has been no different with many new species described by Linnaeus after the adoption of his binomial nomenclature system for animals in 1758, in particular specimens with type localities from Suriname. There was a relative draught of biological discovery in the Guianas until the floral and faunal collections made during the geographic boundary survey of Guyana by the Schomburgk brothers in the 1840's. Taxonomic studies became common by the start of the next century with the prodigious work of Oldfield Thomas at the British Museum of Natural History. The only mammalogical study across international borders was by George Tate at the American Museum of Natural History but this was based primarily on collections from the neighboring highland regions of Venezuela with secondary reference to the Guianas, and it did not include bats. French Guiana experienced an extended period of scientific inactivity from the beginning of the 19<sup>th</sup> to the middle of the 20<sup>th</sup> century when ecological research became prominent in that colony. Since this time, the knowledge of mammalian diversity in all three states of the Guianas has increased substantially and research has progressed beyond checklists to synthetic studies of plant-animal interactions, evolutionary relationships, and biogeography.

## RESUMEN

Key words: bats, French Guiana, Guiana Shield, Guyana, mammals, Suriname.

Palabras clave:

## INTRODUCTION

Since the European discovery of the New World by Christopher Columbus in the late 15th century, the northeastern coast of South America between the Orinoco River and the Amazon River has been referred to as the Guianas. This stretch of land along the Atlantic Ocean was largely ignored as Spain concentrated their South American colonial activity in this region to Venezuela and Portugal to Brazil. It was not until the late 16th century that attention from other European countries was drawn to the Guianas by the chronicles of the English explorer Sir Walter Raleigh (1596). Dutch settlements began to appear in this area during the 17th century, but notwithstanding anecdotal accounts, the scientific study of mammals in the Guianas has its origin in the early 18th century with Albertus Seba, a German-born apothecary in Amsterdam who collected exotic plants and animals for pharmaceutical purposes from sailors returning from voyages overseas (Müsch et al., 2011). At that time, public museums did not exist as we know them today but private cabinets of curios were fashionable (Stein, 2003). After selling his original collections to Czar Peter of Russia, Seba began to accumulate new specimens and documented them in a four-volume publication of plates and text over a four-decade period (Seba, 1734-1765). The plates from the first volume were used extensively by the Swedish biologist Carl Linnaeus (Holthuis, 1969), whose tenth edition of *Systema Naturae* marked the beginning of modern scientific classification of animals based on binomial nomenclature. The type localities of mammals from South America in Linnaeus

(1758) that cited Seba's plates were restricted by Thomas (1911a) to the then Dutch colony of Suriname, unless otherwise noted. Some of these type specimens were subsequently acquired by and deposited in the British Museum of Natural History (BMNH) in London (Thomas, 1892).

Geographically, the Guianas is comprised of the three non-Latin American states in South America: Guyana, Suriname, and French Guiana (Fig. 1). It is located east of Venezuela and north of Brazil with the Atlantic Ocean forming its northeastern boundary. The total area of the Guianas is 460,000 km<sup>2</sup>, which is slightly larger than Paraguay, and the combined population is almost 1.5 million, which is less than half of Uruguay. Most people live along the coast and the economies of these states are the smallest on the continent with minimal transportation infrastructure into the southern interior, which has contributed to the persistence of pristine habitats. Rainforest is the primary vegetative land cover, but there are several areas where grasslands are present: coastal savanna of the Berbice in northeastern Guyana across Suriname to French Guiana and Brazil; interior savanna of the Rupununi in southwestern Guyana, which is contiguous with the Rio Branco savanna of Brazil; interior savanna of the Sipaliwini in southern Suriname, which is contiguous with the Paru savanna of Brazil; and the upland savanna of the Pakaraima Mountains in western Guyana, which is contiguous with the Gran Sabana of Venezuela. Although the original habitat on the coast was mangrove swamp and marsh forest much of the central coastal area is inhabited and converted to agricultural land. However, there are still natural wetlands or marshes in eastern French Guiana, which are contiguous with Amapa in Brazil, and in western Guyana, which are contiguous with the Orinoco in Venezuela.

The main topographic feature of the Guiana Shield is the Pakaraima Mountains of western Guyana that extends into southern Venezuela. This upland plateau begins at an elevation of over 400 m with flat-topped mountains including Mount Roraima at approximately 2,800 m, which forms the tri-nation border of Guyana, Venezuela, and Brazil. An eastern outlier of this sandstone formation is Tafelberg in central Suriname at about 1,000 m. The southern boundary of the Guianas is formed by the Acarai and Tumucumac mountain chain that reaches 1,000 m and separates the southern drainage to the Amazon River in Brazil from the northern drainage to the Atlantic Ocean. The main rivers of the Guianas are the Essequibo that bisects Guyana, the Courentyne that separates Guyana and Suriname, the Maroni that separates Suriname and French Guiana, and the Oyapock that separates French Guiana and Brazil.

Guyana is the former colony of British Guiana and became an independent country in 1966. It was originally settled by the Dutch in the 17th century and was composed of the colonies of Essequibo, Demerara, and Berbice that were centred around the major rivers of the same name. They were eventually ceded to the British in 1814 and combined into a single colony in 1831. Suriname is the former colony of Dutch Guiana and became independent in 1975. French Guiana is an overseas department of France and the only part of South America that is not sovereign. The political history of the Guianas has been quite different from the Latin American countries of South America, which gained independence from Spain or Portugal in the 1800's. This extended period of colonialism in the Guianas is reflected in the delayed development of universities, which did not begin until the 1960's, and of research by local scholars. This essential absence of resident academics was pervasive throughout

most fields of study, and much of the history of mammalogy in the Guianas is dominated by foreign or overseas researchers.

In this summary of the history of mammalogy in the Guianas, we endeavoured to cite the major publications such as the descriptions of new species, significant collections, checklists, and primary research from an historical perspective. However, it is not a complete list of specimens collected from the Guianas, nor a comprehensive bibliography but a first attempt at establishing a foundation for more detailed study in the region. Taxonomy follows Wilson and Reeder (2005) unless otherwise noted, however, species listed in cited publications have not been verified to confirm identification of specimens and taxonomic authorities on synonymies are not exhaustive.

## HISTORY OF MAMMALOGY

### Suriname

Linnaeus (1758; 1766) described 16 species of mammals from Suriname, most of which were based on the plates of Seba (1734-1765), that are currently still recognized as valid (Wilson and Reeder, 2005). This earlier trend of European-based classifiers of the general mammalian fauna continued until the end of the 18<sup>th</sup> century with 7 more new species from the Dutch colony by noted taxonomists such as Pallas, Schreber, Erxleben, and Zimmerman (Table 1). Although some of these earlier descriptions were based on specimens, holotypes were not routinely designated and some species were described using natural history observations and illustrations (Baker, 1991). Popular accounts of mammals from Suriname included those by the

American physician Edward Bancroft (1769) who lived in Demerara from 1763-1766, which at that time was also a Dutch colony, and the British-Dutch soldier John Stedman (1796) who was stationed in Suriname from 1772-1777.

The next century saw a change to a more rigorous approach to taxonomy by museum zoologists, including Coenraad Temminck at the Rijksmuseum van Natuurlijke Historie (RMNH) in Leiden and Wilhelm Peters at the Museum für Naturkunde in Berlin, who described several new species from Suriname during broader taxonomic studies (Table 1). Over 100 years passed before the next new and currently valid species had a type locality from the country (Genoways and Williams, 1980). However, in the two decades prior to this, Antonius Husson (1962; 1978) of the RMNH published monographs on bats and mammals of Suriname that represented the first modern taxonomic treatments for a South American country (Gardner, 2008). Unless otherwise noted, Husson's interpretation and reference to the first occurrence of a species in Suriname is used for a more detailed chronology that follows below.

In the 19<sup>th</sup> century, an agouti (*Dasyprocta cristata*) was described by E. Geoffroy (1803) from Suriname but its provenance was questionable (Voss et al., 2001) and may represent a slight variant of *D. leporina* (Husson, 1978). H. H. Dieperink, a military apothecary stationed in Paramaribo, amassed natural history specimens for the RMNH from 1824-1836 (Husson, 1978). He collected a specimen of porcupine that was selected by Husson (1978) as the lectotype for the species described by Jentink (1879) as *Hystrix brandtii*, which is now a junior synonym of *Coendou prehensilis*. In addition, Dieperink collected the type specimen of *Saccopteryx bilineata* that was described by Temminck (1838). Temminck (1840) also described a new species of bat as *Vespertilio arsinoe*, which Husson (1978) considered to be a junior synonym of *Myotis albescens*. Another new species of bat



was described by Temminck (1841) from Suriname as *Emballonura lineata*, which is now a synonym of *Rhynchonycteris naso*.

August Kappler was a German soldier originally stationed in Suriname who eventually settled in the colony from 1842-1879 as a trader in Albina, which was a community that he had founded (Holthuis, 1959). He wrote several popular natural history accounts primarily after his return to Germany (Husson, 1978), including a list of mammals from Suriname with specimens deposited in the Stuttgart Museum (Kappler, 1881). In addition, he was honoured by Krauss (1862) who named a new species of armadillo as *Dasypus kappleri* and by Peters (1867) who named a new species of bat as *Peropteryx kappleri*. The type specimen of *Choeroniscus minor* that was described by Peters (1868) was collected by Kappler in 1851. A new genus and species of bat (*Myopterus pullus*) was proposed by Miller (1906) based on four specimens collected by Kappler that were originally identified by Peters as *Cormura brevirostris*. However, Thomas (1913) synonymized this taxon with *C. brevirostris* after concluding that there were insufficient differences in the characters used by Miller to warrant separation as a distinct genus or species. Another specimen collected by Kappler was the holotype of *Lutra mitis*, which was described by Thomas (1908) and is now synonymized with *Lontra longicaudis*.

Other notable taxonomic work based on specimens from Suriname include a new species of bat *Thyroptera bicolor* that was described by Cantraine (1845), which was subsequently synonymized under *T. tricolor*. *Stenoderma (Pygoderma) microdon* was described by Peters (1863) based on 2 specimens from Suriname but this occurrence was considered an erroneous record because it has not been reported from any country in the Guianas since then (Voss and Emmons, 1996). Peters (1865) described a bat deposited at the RMNH as *Artibeus (Dermanura) quadrivittatus*,

which was synonymized under *A. cinereus cinereus* by Hershkovitz (1949). Another bat species was described by Peters (1865) as *Artibeus fallax*, and restricted to Suriname by Husson (1962), that was considered as conspecific with *A. planirostris* by Lim et al. (2004). A new genus and species (*Alectops ater*) was described from Suriname by Gray (1866) that was synonymized by Dobson (1878) under *Phyllostomus elongatus*. Dobson (1876) also described the species *Nyctinomus megalotis* based on an adult male specimen in the BMNH that was eventually synonymized with *Tadarida macrotis*. A bat acquired by the Museum of the Boston Society of Natural History in 1839 from Dr. Craigin when he was U.S. consul in Paramaribo (Allen, 1902) was described as a new species *Ametrida minor* by Allen (1894). It was subsequently synonymized under *A. centurio* by Peterson (1965b). E. Barlett collected the holotype that was used in the description of *Oryzomys microtinus* by Thomas (1894), which is now a synonym of *Zygodontomys brevicauda*. A new species of manatee *Manatus köllikeri* was described by Kükenthal (1897) but is currently considered synonymous with *Trichechus manatus*. During the description of *Saccopteryx canescens*, specimens from Suriname were designated as paratypes (Thomas, 1901a). A bat specimen was collected by M. Greshoff in 1903 from Parimaribo that was used by Jentink (1904) as the holotype for *Eptesicus melanopterus*. This species is now considered a synonym of *E. furinalis* by Lim et al. (2005a). Based on specimens collected by W. J. Bresser in 1862, Husson (1962) described *Eumops geijskesi* that was later synonymized under *E. maurus* by Eger (1977).

Non-taxonomic work began in the second half of the 20<sup>th</sup> century. An animal rescue project during the flooding of Brokopondo Lake after the completion of Afobakka Dam in 1965 documented 31 species of large mammals and relocated over

8,000 individuals (Walsh and Gannon, 1967). Primatological research became prominent in Suriname beginning in the 1970's (e.g., Fleagle and Mittermeier, 1980). From 1977-1981, Hugh Genoways and Stephen Williams at the Carnegie Museum of Natural History (CM) in Pittsburgh established a cooperative research programme with the Foundation for Nature Preservation in Suriname (Stichting voor Natuurbehoud Suriname; STINASU) to survey small mammals (Genoways et al., 1982). Representative collections were deposited at the University of Suriname in the National Zoological Collection of Suriname (NZCS). Three new species of bats were described including *Tonatia schulzi* (Genoways and Williams, 1980), now referred to as *Lophostoma schulzi*, *Molossops neglectus* (Williams and Genoways, 1980), and *Rhogeessa hussoni* (Genoways and Baker, 1996). This programme also represented the only concerted effort to compile karyotypic information (Honeycutt et al., 1980; Baker et al., 1981) and cellular structure of gastric mucosa (Phillips et al., 1984; Studholme et al., 1986) for bats in the Guianas. Collecting localities were summarized in McLaren and Genoways (2003). In 2002, Lim and Engstrom at the Royal Ontario Museum (ROM) in Toronto also began a research and collection programme in Suriname with representative specimens deposited at the NZCS. Previously unreported specimens from the CM were incorporated in a taxonomic review of the fruit-eating bat *Artibeus amplus* (Lim et al., 2003). In addition, an inventory of mammals at Brownsberg Nature Park (Lim et al., 2005) made this area the best known in the country. Other small mammal surveys were conducted in the country, including participation in an environmental assessment in the Bakhuis Mountains of western Suriname for a proposed bauxite mine (Borisenko et al., 2008; Lim, 2009), which eventually did not become operational. There have also been Conservation International Rapid Assessment Program (CI RAP) surveys in Suriname

including the mammals of Nassau and Lely Mountains in the east (Solari and Pinto, 2007) and Kwamalasamutu in the south (Gajapersad et al., 2011; Lim and Joemratie, 2011).

### French Guiana

Although Linnaeus (1758; 1766; 1771) described 5 species of mammals from French Guiana that are still currently recognized as valid (Table 1), George Buffon at the Royal Gardens in Paris was the most influential in the colony with his publication of the multi-volume encyclopedic *Histoire Naturelle* (Buffon, 1750-1789). However, he preferred vernacular names over the binomial nomenclature system of Linnaeus, so Buffon does not appear as an authority in the taxonomic literature. For example, the name *Viverra touan* was described by Shaw (1800) based on “Le Touan” of Buffon (1789), of which a specimen collected by S. Klage from Cayenne on 26 February 1917 was designated as the neotype by Voss et al. (2001) that represents the tricolour form of *Monodelphis brevicaudata*. Similarly, *Coendou longicaudatus* was described by Daudin (1802) based on “Coendou à longue queue” of Buffon (1789). Buffon relied heavily on the notes and specimens sent by M. de la Borde, the royal physician in Cayenne, as well as specimens from Brazilian Amazonia. For some groups, such as Primates, he described and/or recognized more species than are known today. For example, with the explicit mention of a geographic origin of “Guyane”, “Guyane française”, or “Cayenne”, he mentioned two species of *Ateles* (Atèle chameck, *Ateles subpentadactylus*, Geoffr; Atèle coaïta, *Ateles paniscus*, Geoffr), three species of *Cebus* (Sapajou sajou, *Cebus apella*, Geoffr; Sapajou gris, *Cebus griseus*, Geoffr; Sapajou cornu, *Cebus fatuellus*, Geoffr.), two species of *Pithecia* (Saki à ventre roux,

*Pithecia rufiventer*, Geoffr; Saki yaruqué, *Pithecia leucocephala*, Geoffr.), and three species of *Saguinus* (Ouistiti Tamarin, *Jacchus rufimanus*, Geoffr.; Ouistiti marikina, *Jacchus rosalia*, Desm; Ouistiti pinche, *Jacchus oedipus*, Geoffr., Desm.). Because Buffon wrote about South American mammals in several different sections of his many books, one has to compare the names and descriptions throughout to realize that Buffon had cited all French Guianan Primates, namely: *Alouatta macconnelli*, Alouate roux; *Ateles paniscus*, Atèle coaïta; *Cebus apella*, Sajou brun or sapajou or singe-capucin; *Cebus olivaceus*, Sajou gris or singe-capucin gris; *Chiropotes chiropotes*, Capucin (Brachyurus chiropotes); *Pithecia pithecia*, Saki yaruqué; *Saguinus midas*, Ouistiti Tamarin; and *Saimiri sciureus*, Saïmiri or sapajou aurore or sagouin saïmiri or Sapajou de Cayenne.

At a similar time as Buffon, a two-volume natural history account was published by Bertrand Bajon (1777-1778), a physician who lived in French Guiana for 12 years (Hershkovitz, 1987). After the French Revolution, the Royal Gardens became part of the Muséum National d'Histoire Naturelle (MNHN) and the chair of zoology Étienne Geoffroy (1803) described 5 species of mammals from French Guiana in his “Catalogue des mammifères du Muséum National d'Histoire Naturelle”. However, the next one and a half centuries were relatively quiet in terms of biological discovery in French Guiana. Notable exceptions include Frédéric Cuvier (1823; 1828) at the MNHN who described a new species of otter *Lutra enudris*, which is now considered a subspecies of *Lontra longicaudis*, and a new species of bat *Furipterus horrens*. The type specimen of *Dasyprocta lucifer cayennae* was collected by G.K. Cherrie and B.T. Gault from Approuague, Cayenne and described as a new subspecies by Thomas (1903) but is now synonymized under *D. leporina*.

Konstanty Roman Jelski (1837-1896) was a Polish naturalist who spent four years (1865-1869) in French Guiana collecting and preserving animals and plants for W. Taczanowski at the Museum of Natural History of Varsovia in Poland. In his memories, originally published in Polish in 1898 and more recently translated into French by Daskiewicz et al. (2007), Jelski described his long sojourn to various parts of coastal French Guiana, and cites numerous species of mammals which were collected, prepared by him, and sent for scientific examination to Taczanowski. Several interesting observations pertaining to mammalian ecology were reported by Jelski, such as a colony-roost of *Noctilio leporinus* in a hollow tree (“courbaril” = *Hymenea courbaril*) near Cayenne with several of these bats having Strebliidae (Diptera) ectoparasites. He described a leaf tent in which several bats “with a medio-dorsal white line” were roosting near Saint Laurent du Maroni. Four armadillos (*Dasybus novemcinctus*, *D. kappleri*, *Cabassous unicinctus*, and *Priodontes maximus*) were known to him, and he discriminated all six felids including two smaller ones (*Leopardus tigrinus*; *Leopardus wiedii* – known as *Felis macroura* at that time) caught near Saint Laurent du Maroni and prepared by him as specimens. During his stay at Saint Laurent du Maroni, Jelski met August Kappler (1815-1887), who was living at Albina on the Surinamese bank of the Maroni River, and immediately appreciated his skills in preparing collected specimens of birds and mammals. The nephew of Kappler showed Jelski several roosting *Thyroptera* spp. in the rolled young leaves of balourou (*Heliconia* spp.) near Saint Laurent du Maroni. Jelski obtained two white bats (*Diclidurus*) caught in a house, and told his good fortune to Kappler who was actively looking for such specimens upon the request of Wilhelm Peters at the Museum für Naturkunde in Berlin. Jelski sent these two specimens to Taczanowski, who then loaned them to Peters. However, Peters (1869) described

*Diclidurus scutatus* without specifying the type locality. According to Jelski (Daszkiewicz et al., 2007:154-155), these two white bats came from the house in Saint-Laurent-du-Maroni, and not from “Belem, Para, Brazil”, as restricted by Husson (1962:59).

Menegaux (1902) published the catalogue of mammals presented to the Paris Museum of Natural History by Francis Geay, an explorer who visited the eastern part of French Guiana on several occasions between 1897 and 1901 (Geay, 1901). The species collected by Geay include two squirrels (*Sciurus aestuans* and *Sciurillus pusillus*), a spiny rat (*Mesomys hispidus*), four large opossums (*Didelphis marsupialis*, *D. imperfecta*, *Caluromys philander*, and *Philander opossum*), and various large non-volant mammals (*Odocoileus cariacou*, *Myoprocta acouchy*, *Choloepus didactylus*, *Bradypus tridactylus*, and *Tamandua tetradactyla*). Of further interest is a specimen attributed by Menegaux (1902: 491) to *Reithrodon alstoni* Thomas 1881 (synonym of *Sigmodon alstoni* Thomas 1881) which has then been re-examined independently by R.S. Voss (pers. comm.) and F.M. Catzeflis (pers. comm.) as *Hylaemys megacephalus* (Fisher, 1814).

For bats, it was not until the mid-1960's that the first comprehensive study was made by Andre Brosset and Gerard Dubost at the MNHN that added over 20 species to the faunal list of French Guiana (Brosset and Dubost, 1967). Taxonomic research continued on other small mammals including a new species of cane mouse (*Zygodontomys reigi*) that was described from Cayenne based primarily on a new karyotype (Tranier, 1976) and subsequently considered a junior synonym of *Z. brevicauda* by Voss (1991). A new subspecies of climbing rat (*Rhipidomys leucodactylus aratayae*) was described by Guillotin and Petter (1984). However, the next major addition to the mammalian fauna of French Guiana was the study on seed

dispersal initiated in 1979 that increased the checklist by about 30 species of bats by Andre Brosset and Pierre Charles-Dominique (1990) at the MNHN. This culminated in a monograph on the bats of French Guiana (Charles-Dominique et al., 2001).

Other ecological studies of plant-animal interactions in French Guiana were becoming prevalent including research on rodents and marsupials by Pierre Charles-Dominique, Martine Atramentowicz and colleagues (Charles-Dominique et al., 1981), on rodents by Pierre-Michel Forget also at the MNHN (Forget, 1990; 1996; Forget et al., 2000) and bats by Tatyana Lobova, Cullen Geiselman, and Scott Mori associated with the New York Botanical Gardens (Lobova et al., 2009).

Two localities in French Guiana have been thoroughly surveyed for mammalian diversity: Arataye/Nouragues and Paracou. Voss and Emmons (1996) reported a total of 122 species of mammals at Arataye in east-central French Guiana after compiling data gathered over 17 years from various scientists sojourning at Nouragues and Saut-Pararé; of which 61 species were bats and 21 were rodents. Voss and Emmons (1996) predicted, based on known geographic distributions, 9 additional species of non-volant mammals and 34 species of bats. Since their publication, 4 non-volant species (*Didelphis imperfecta*, *Neusticomys oyapocki*, *Oecomys bicolor*, and *O. rutilus*,) and 17 species of bats have been documented at or near the Arataye locality (Catzefflis, unpublished data; Delaval and Charles-Dominique, 2006; Feer and Charles-Dominique, 2001). Arataye/Nouragues is now characterized by 143 species of mammals, a high value similar to the locality of Paracou near Sinnamary, in northern French Guiana. In-depth surveys of mammals at Paracou were undertaken by Nancy Simmons and Rob Voss at the American Museum of Natural History (AMNH) in New York from 1991-1994. The taxonomy, ecology, and natural history was summarized in two monographs on bats (Simmons and Voss, 1998) and non-volant



mammals (Voss et al., 2001), which included the description of 3 new species (*Micronycteris brosetti*, *Neacomys dubosti*, and *N. paracou*). Voss et al. (2001) listed 142 species at Paracou, to which are added *Didelphis imperfecta* (Adler et al., 2006) and *Marmosa lepida* (Catzeflis, 2010).

A fair amount of new knowledge on medium- and large-sized non-volant mammals was gained by the rescue operations of various vertebrates during the flooding of Petit-Saut hydroelectric dam near Sinnamary from 1993 to 1995 (Vié, 1999). A new species of rodent, *Isothrix sinnamariensis*, was described by Vié et al. (1996) based on two animals salvaged from the canopy of trees which were flooded by 9 to 14 m of water. Later, this species was caught at ground level in Nouragues (two specimens: Catzeflis, 2010), in Guyana (Lim et al., 2006), and in Suriname (Lim and Joemratie, 2011). External measurements for 40 species of non-volant mammals rescued from Petit-Saut were published by Richard-Hansen et al. (1999), with large samples characterizing some species such as 474 *Bradypus tridactylus*, 175 *Choloepus didactylus*, 87 *Saguinus midas*, and 51 *Dasypus kappleri*. The molecular typing of 160 *Didelphis* spp. caught in an area of approximately 60 km<sup>2</sup> within the artificial lake of Petit-Saut assisted in the identification of 31 *D. imperfecta* (known at that time as *D. albiventris*) and 129 *D. marsupialis* (Catzeflis et al., 1997), and documented their sympatry and relative abundance at this regional scale. Further molecular phylogenetic studies based primarily on small non-volant mammals collected from French Guiana were initiated by Francois Catzeflis at the Université de Montpellier (Lavergne et al., 1997; Steiner et al., 2000; Steiner and Catzeflis, 2003; 2004; Catzeflis and Tilak, 2009).

## Guyana

Linnaeus (1758; 1766) described two species with type localities in Guyana (Table 1), the squirrel monkey (*Sciureus saimiri*) and howler monkey (*Alouatta macconnelli*). However, it took over 120 years for the next new currently valid species to be discovered in the country, the vampire bat *Diaemus youngi* by Fredericus Jentink (1893) at the RMNH. In the intervening years, there were anecdotal accounts of mammals by naturalists such as Charles Waterton (1825), who collected primarily birds during travels in British Guiana from 1812-1824. He met Charles Edmonstone from Scotland who from 1781-1817 lived at Warrow's Place, a timber business on Mibirri Creek in Demerara. Edmonstone collected the holotypes of *Simia sagulata* (Traill, 1819a) that is now synonymous with *Pithecia pithecia*, *Felis unicolor* (Traill, 1819b) that is synonymous with *Puma yagouaroundi*, and *Vivera poliocephalus* (Traill, 1819c) that is currently considered a subspecies of *Eira barbara*. Gray (1837) described a new species of giant otter *Pteronura sambachii* from Demerara that is now synonymized under *P. brasiliensis*. Ball (1844) described *Felis melanura*, which is a synonym of *Leopardus pardalis*, from a specimen that Husson (1978) restricted the type locality to Guyana.

The first comprehensive scientific survey made in the Guianas was by Richard Schomburgk, a German botanist who was collecting plants and animals under the commission of the King of Prussia, Fredrick William IV (Hershkovitz, 1987). This biotic inventory was conducted in 1840-1844 during a boundary survey of Guyana for the British government that was led by his older brother Robert Schomburgk. The mammal specimens were identified by Jean Cabanis at the Museum für Naturkunde in Berlin where the collections were deposited. Additional observations of mammals

were reported in a three-volume publication in German by Richard Schomburgk (1847-1848), of which the first two volumes were translated into English by the anthropologist Walter Roth (1922-1923) who was stationed in Guyana as a British magistrate (Herskovits, 1936). Three new species were described from this collection including *Cebus olivaceus*, *Didelphys musculus* that is now synonymized under *Marmosa murina*, and *Cervus savannarum* that is synonymized under *Odocoileus cariacou*. Other natural history notes on mammals were documented by Robert Schomburgk (1840) during his earlier exploration of Guyana in 1835-1839 for the Royal Geographic Society in London. We consider the list of 57 species compiled in Herskovitz (1987) of mammals observed by the Schomburgks as the beginning of the scientific study of mammals in the region. This includes the fruit-eating bat *Artibeus planirostris* and the free-tailed bat *Cynomops abrasus* that were not noted by Herskovitz (1987) but were documented by Dobson (1878) from specimens presented to the BMNH by Robert Schomburgk. In contrast, two species were listed but have not been confirmed in Guyana including the brown-throated sloth (*Bradypus variegatus*) and the night monkey (*Aotus*), which was reported as a house pet. Both species are found further west in Amazonas and Bolivar states of southern Venezuela (Voss et al., 2001; Lim et al., 2005b). The Schomburgks' checklist represents one-quarter of the currently known mammal species from Guyana. However, for the mammals larger than a rat (> 0.5 kg), remarkably 80% of the diversity (43 of 53 species) was documented by them.

The first comprehensive monograph on bats was published by George Dobson (1878) and listed 12 species from Guyana. He was an Irish-born medical officer in the British Army who visited the colony in 1873 and exchanged specimens including *Artibeus planirostris* and *Rhynchonycteris naso* with the BMNH. Dobson examined

specimens of bats at most of the major European museums during the compilation of his treatise. Reverend W. Y. Turner of the Wesleyan Missionary Society was the church pastor in Better Hope, Demerara who was also a correspondent with the BMNH. He collected specimens of opossums including two *Didelphis marsupialis*, one *Philander opossum*, and two lutrine opossums (Thomas, 1888), one of which was used to describe a new species in his honour (*Lutreolina turneri*) by Günther (1879a). This species was subsequently recognized as a smaller subspecies of *L. crassicaudata* by Marshall (1978). Turner also collected a specimen of crab-eating fox in 1879 that was described as a new species *Cerdocyon rudis* by Günther (1879b), which Berta (1982) synonymized under *C. thous*. In 1886, the English zoologist William Sclater collected 13 specimens of 8 species for the BMNH during a visit to Demerara, including a new species of climbing rat that was described by Thomas (1887) as *Rhipidomys sclateri*. This species is now synonymized with *R. leucodactylus*.

A spiny rat (*Loncheres guianae*) collected by John Quelch in Demerara was described as a new species (Thomas, 1888) that was subsequently synonymized under *Makalata didelphoides*. Quelch was formerly a zoologist at the BMNH but was then the curator of the British Guiana Museum and editor of *Timehri*, the journal of the Royal Agricultural and Commercial Society of British Guiana that was formed in 1844 as the literary and scientific society of the colony. After a fire burnt down their offices, they built a new structure, which included an addition that became the British Guiana Museum in 1870. The society fulfilled one of their founding objectives in 1882 with the publication of the biannual periodical *Timehri*. Quelch (1892) also reported 15 species of bats from the colony based primarily on observational records but some species were represented by museum specimens.

A collection of 80 specimens representing 17 species of bats, including the description of *Diaemus youngii* as a new species of vampire bat was reported on by Jentink (1893). These specimens were presented to the Leyden Museum by Charles Young, an Irish-born doctor in the British Medical Service who lived in New Amsterdam and collected bats in the vicinity of Berbice. In a later update, five additional species of bats were reported by Young (1896). In 1894, a carnivore was captured alive by A. Murray in a wooded area near Bastrica on the Essequibo River and presented to the Zoological Society Menagerie in London (Flower, 1895). After its death, a thorough review of the anatomy was done by Beddard (1900). The specimen was subsequently described as a new species *Bassaricyon beddardi* by Pocock (1921) at the BMNH.

Frederick McConnell was an English trader who with his brother ran the family business of Booker Brothers, McConnell & Co. Ltd., which was the largest owner of sugar cane plantations in Guyana. He financed two biological expeditions in 1894 and 1898 to Mount Roraima in conjunction with John Quelch and the British Guiana Museum. Although the primary focus was plants and birds, two specimens of mammals deposited in the BMNH were described as new species from the second expedition. The climbing rat *Rhipidomys macconnelli* was collected at the summit of Roraima (de Winton, 1900) and the squirrel *Sciurus macconnelli* was collected at the base of Roraima (Thomas, 1901b). The latter species is now considered a subspecies of *S. aestuans*. McConnell also financed a trip in 1900 by Quelch to the Kanuku Mountains and surrounding Rupununi savannas in southwestern Guyana. The collection of 29 species was deposited in the BMNH and included two new genera, seven new species, and three new subspecies (Thomas, 1901b). The new genera included the bat *Mesophylla* and the rat *Sigmomys*, which is now considered a

subgenus of *Sigmodon*. The new species included *Molossus maurus* that is now a species of *Eumops*, *Phyllostoma latifolium* that is now referred to as *Phyllostomus latifolius*, *Mesophylla macconnelli*, *Sciurus quelchii* that is a subspecies of *S. aestuans*, *Rhipidomys nitela*, *Holochilus guianae* that is synonymized under *H. sciureus*, and *Sigmomys savannarum* that is synonymized under *Sigmodon alstoni*. The new subspecies included *Canis cancrivorus savannarum* that is now synonymized under *Cerdocyon thous thous*, *Oryzomys navus messorius* that is now synonymized under *O. fulvescens*, and *Cavia porcellus guianae* that is now a subspecies of *C. apera*. In addition, a series of six specimens of spiny rats identified as *Proechimys cayennensis* was subsequently described as a new species *P. vacillator* by Thomas (1903) but is now considered a subspecies of *P. guyannensis*. Quelch (1901) also reported 67 currently recognized species of mammals from the colony based on his personal experience and knowledge. However, there was no attempt at consulting the accumulating scientific literature and 5 species listed in his earlier paper on bats (Quelch, 1892) were not included in this latest compilation.

Three specimens collected by S. B. Warren along the Demerara River in 1905 were identified as new taxa by Thomas (1905) including *Neacomys guianae*, *Proechimys warreni* that is now synonymized under *P. guyannensis*, and *Marmosa cinerea demerarae* that is currently recognized as *Micoureus demerarae*. In the following year, Warren collected a mouse opossum approximately 50 km upstream of Georgetown along the Demerara River. It was described as a new species (*Marmosa chloe*) by Thomas (1907), which was subsequently synonymized under *M. murina*. In addition, he collected an arboreal rice rat *Oecomys nitedulus* about 20 km upstream along the Demerara River that was described as a new species by Thomas (1910b) but is now considered synonymous with *O. bicolor*. Another new species of mouse

opossum (*Marmosa parvidens*) was described by Tate (1931) from a specimen collected by Warren in 1906 at approximately 50 km upstream along the Demerara River.

In 1908, McConnell's local collector in the colony (Mr. Crozier) obtained from the vicinity of the Mazaruni River an incomplete specimen of a bat with only part of the jaw intact (Thomas, 1913). It was the first specimen of *Cyttarops alecto* collected but was not designated the holotype because of the poor condition of preservation. McConnell was also honoured by Elliot (1910) with the naming of a new species of howler monkey *Alouatta macconnelli* from the coast of Demerara. In that same year, McConnell presented to the BMNH a collection of 25 species from the vicinity of the Supinaam River of Demerara (Thomas, 1910a). There were four new taxa described including *Tonatia laephotis* that is now a subspecies of *Lophostoma silvicolium*, *Nectomys squamipes melanius* that is recognized as a distinct species, *Oryzomys macconnelli* that is referred to as *Euryoryzomys macconnelli*, and *Oecomys guianae* that is synonymized under *O. roberti*. In addition, another specimen of arboreal rice rat *O. rex* was described as a new species by Thomas (1910b) and a new species of free-tailed bat *Molossus mastivus* was described by Thomas (1911b) that is now considered a subspecies of *Cynomops abrasus*. After McConnell's death in 1914, his wife presented a specimen of pygmy squirrel acquired by Crozier in the previous year from Great Falls on the Demerara River and which represented the first documentation of this species from the colony. It was described by Thomas (1914a) as a new genus *Sciurillus* and by Thomas (1914b) as a new subspecies *S. pusillus glaucinus*. A series of agoutis were collected from the "Moon Mountains, Southern British Guiana, about 1° N, 59° W" (Thomas, 1917), which is now located within Brazil. These specimens were presented posthumously to the

BMNH by McConnell and used to describe the new subspecies *Dasyprocta aguti lunaris*, which is now referred to as *D. leporina lunaris*. Another specimen collected from Bonasica on the Essequibo and presented to the BMNH by McConnell was exchanged with the AMNH and described as a new subspecies of acouchy *Myoprocta exilis demararae* by Tate (1939). This taxon is now synonymized under *M. acouchy*.

Leo Miller of the AMNH collected birds and mammals in Guyana in 1913. Noteworthy discoveries from this expedition included a new species of climbing rat *Rhipidomys milleri* described by Allen (1913) that is now synonymized under *R. nitela*, a new subspecies of red brocket deer *Mazama americana tumatumari* described by Allen (1915a) that is synonymized under the nominate subspecies (Tate, 1939), a new subspecies of ocelot *Leopardus pardalis tumatumari* described by Allen (1915b) that is synonymized under *L. p. melanurus*, and a new subspecies of tapir *Tapirus terrestris guianae* described by Allen (1916), which is synonymized under the nominate subspecies.

The New York Zoological Society established the Tropical Research Station near the town of Bartica in Guyana at Kalacoon and then Kartabo under the directorship of the ornithologist William Beebe from 1916 to 1926. In addition to an intensive survey of the fauna in a single area near the confluences of the Potaro, Mazaruni, and Essequibo Rivers, the station represented the first long term ecological study in the Guianas (Osborn, 1921). A preliminary checklist of mammals by Beebe (1919) based on the literature record enumerated 119 species in Guyana. This was the most comprehensive scientific attempt at documenting the mammalian fauna in the colony since Schomburgk (1848-1849) and Quelch (1901), and corresponds to 99 species based on current taxonomy but excluding three introduced species (*Herpestes javanicus*, *Mus musculus*, and *Rattus rattus*), two marine species (*Delphinus delphis*



and *Eubalaena australis*), and two species not considered to occur in Guyana (*Aotus trivirgatus* and *Blastocercus dichotomus*).

Four new taxa were reported from Kartabo by Anthony (1921a) including *Tayassu pecari beebei* that is now synonymized with the nominate subspecies, *Pecari tajacu macrocephalus* that is synonymized under the nominate subspecies, *Oecomys rutilus*, and *Echimys longirostris* that is synonymized with *Makalata didelphoides*. There were 56 species documented by specimens deposited at the AMNH from Kartabo, Kalacoon, the Penal Settlement on the opposite side of the Mazaruni River from the research stations, and Samiri Island in the Mazaruni River. Excluding two introduced species of murid rodents, but including an additional 14 species that were documented by sightings (Anthony, 1921b), these 68 native species represented the most thorough survey of mammals from one area in the Guianas. However, bats was a major group of mammals that were not extensively sampled around the Tropical Research Station. Subsequently, specimens of dolphin (*Sotalia fluviatilis*) were collected in the Kartabo area and deposited at the U.S. National Museum of Natural History (USNM) and Carnegie Museum of Natural History that represented the first report from Guyana (Williams, 1928; McLaren et al., 1986). In addition, another species of rice rat was identified as *Oecomys trinitatis* by Tate (1939) from the original collections.

During a study of the bats of Trinidad and Tobago by Goodwin and Greenhall (1961), examination of comparative material from later collections at Kartabo by Beebe added three more species to the checklist. They also documented the first report of the nectar-feeding bat *Choeroniscus minor* in Guyana based on a specimen collected by the AMNH mammalogist Herbert Lang during a 1922-1923 expedition to Kamakusa further up the Mazaruni River from Kartabo. Similarly, Voss (1988)

identified from Beebe's material the first report of *Neusticomys venezuelae* and Koopman (1993) the first report of *Molossus pretiosus* in the country. The indigenous non-volant terrestrial mammals from the Kartabo area were most recently summarized by Voss and Emmons (1996).

George Tate of the AMNH participated on three expeditions to tepuis in Venezuela to collect birds and mammals: Mount Roraima in 1927-1928, Mount Duida in 1928-1929, and Mount Auyantepui in 1937-1938. The route to Mount Roraima was through Brazil and returned via Guyana. Although the collections were made primarily in Venezuela, the holotype of an endemic new genus and species of mouse *Podoxymys roraimae* was listed as the summit of Mount Roraima in British Guiana (Anthony, 1929). Tate (1939) summarized and discussed the biogeography of the mammals not only of the highland area but of the greater Guiana region, which represents the first and most comprehensive synthetic review of the mammalian fauna in this region.

Arthur Greenhall was an American zoologist working at the Department of Agriculture in Trinidad who traveled to Guyana for research on rabies after the first reported outbreak in the colony (Nehaul, 1955). Specimens collected were deposited at the USNM. He compiled a list of 109 species of bats that may occur in the Guianas based on distributional range (Greenhall, 1959), of which 86 are currently recognized species that have been documented in the area (Lim et al., 2005b). However, less than half of these species had been confirmed at that time. Greenhall returned to the United States as Chief of the Mammal Section at the U.S. Fish and Wildlife Service where he collaborated on the University College Bangor Expedition to Guyana in 1963. A collection of bats was obtained by J. N. Davies at primarily a forest reserve 24 miles along the Potaro Road from Bartica (Hill, 1964). A total of 76 specimens

representing 31 species were collected and deposited at the BMNH and USNM, including a new genus and species, *Barticonycteris daviesi*, which is now classified as *Glyphonycteris daviesi*.

In 1961, Randolph Peterson from the ROM conducted a fieldtrip to Guyana with an emphasis on the southern Rupununi region. He made contact with Stan Brock at Dadanawa, a 5,000 km<sup>2</sup> cattle ranch in the savannas bordering Brazil, and established a long-term collecting programme in the surrounding grassland and forested areas. Noteworthy specimens included a series of flat-headed bats that were used to describe a new genus by Peterson (1965a) for the species *Neoplatymops mattogrossensis*. Although some consider it a subgenus of *Molossops* (Simmons, 2005), others still consider it a valid genus (Eger, 2008). Some specimens were used to document a case of sexual dimorphism that contributed to the erroneous separation of *Ametrida centurio* into two putative species (Peterson, 1965b). In addition, a new species, *Vampyressa brocki*, was described by Peterson (1968) based on one specimen collected by his field collaborator. Four mouse opossums collected in 1964-1965 were eventually identified by Voss et al. (2001) as the first country records for the uncommon species *Gracilinanus emiliae* and *Hyladelphys kalinowskii*. Similarly, two specimens of disk-winged bats were designated paratypes for the description of a new species *Thyroptera devivoi* by Gregorin et al. (2006). Brock also collected specimens for the USNM from 1963-1967. He continued depositing material at the ROM until 1969 and then passed on the field collaboration to Jerome Marques at Dadanawa who continued until 1974. A similar collecting programme was arranged during a ROM field expedition by Brock Fenton and Geoff Turner with other local contacts in the bauxite mining area of Ituni in northeastern Guyana. Baldwin Persaud and David Courtman independently collected bats from 1970-1975. Notable collections by

Persaud included the second specimen of *V. brocki* (Peterson, 1972) and the first report of *Lophostoma schulzi* in Guyana (McCarthy and Handley, 1987), which was not collected by Stan Brock as originally reported. These collections from Guyana deposited at the ROM also contributed to systematic studies of bonneted bats, *Eumops* (Eger, 1974; 1977).

In addition to collections made by Brock, the USNM also has specimens from B. K. Mortensen who collected mammals in 1975 from Guyana. Some of this material was used in the description of a new species of bat *Artibeus gnomus* by Handley (1987). The first trip by Don Wilson of the USNM to Guyana was in 1989 and, combined with collections at the ROM, contributed to the first documentation in the country of two species of fruit-eating bats, *Artibeus amplus* and *A. obscurus* (Lim and Wilson, 1993). A few years later, Louise Emmons of the USNM participated in a CI RAP survey of the western Kanuku Mountains. She collected the first record of the arboreal spiny rat *Mesomys hispidus* in Guyana and summarized the collections deposited at the BMNH, USNM, and ROM from the Rupununi region, which added 23 species (mostly bats) to the faunal list (Emmons, 1993). Representative collections were also deposited at the newly established Centre for the Study of Biological Diversity, University of Guyana (UG). The CSBD building was constructed in 1992 with financial support from the Royal Bank of Canada that was arranged with the assistance of the Biological Diversity of the Guiana Shield programme at the USNM, which has been conducting primarily botanical studies in Guyana since 1983 but has more recently expanded its coverage to other organismal groups.

A preliminary survey of bats was conducted in 1992 at the recently designated Iwokrama Forest in central Guyana as part of a biodiversity study by the Open University in England (Smith and Kerry, 1996). Specimens were prepared only for

species deemed difficult to identify or considered rare for the country and deposited in the BMNH. A list of 96 species of bats was documented from Guyana including 4 new records for the country based on their survey, literature records, and specimens at the BMNH, USNM, and ROM.

After Peterson, Burton Lim and Mark Engstrom at the ROM continued research on mammals in Guyana from 1990 to the present with representative collections also deposited at the CSBD. The earlier material amassed by Peterson contributed to a morphological reappraisal of stenodermatine bat phylogeny (Lim, 1993). The summary of bats by Smith and Kerry (1996) utilized unpublished reports from the first four trips of the second phase of ROM fieldwork in Guyana by Lim and Engstrom. Included in some of this material collected in 1991 was the first report of *Oryzomys yunganus* from the country (Musser et al., 1998). Other fieldwork in 1996 documented the first occurrence of the brush-tailed rat *Isothrix sinnamariensis* in Guyana (Lim et al., 2006). The official faunal survey of Iwokrama Forest was undertaken in 1997 and coordinated by the Academy of Natural Sciences in Philadelphia. By the completion of the project, Iwokrama Forest was biologically the best known area in Guyana. The collaborative efforts of the ROM and University of Kansas added the first records of 10 bat species to Guyana (Lim et al., 1999). The second portion of the faunal survey of Iwokrama coupled with examination of museum collections resulted in a further addition of 11 species of bats (Lim and Engstrom, 2001), 2 species of mice, and 1 species of mouse opossum (Voss et al., 2001).

Other field research in Guyana during the 1990's included work on primates by Shawn Lehman (2000; 2004) as part of his doctoral study at the University of Washington. A second CI RAP expedition to the eastern Kanuku Mountains in 2001

resulted in the first unambiguous documentation of *Proechimys cuvieri* in Guyana (Lim and Norman, 2002), although earlier fieldtrips had identified this relatively common spiny rat including collections from Iwokrama (Lim and Engstrom, 2005). Fieldwork in the Pakaraima Highlands from 2002-2004 documented for the first time the Guiana Shield endemic spiny rat *Proechimys hoplomyoides* (Lim et al., 2005b). During the 2002 fieldtrip to Mount Ayanganna, the distribution of the recently described short-tailed opossum *Monodelphis reigi* by Lew and Pérez-Hernández (2004) was extended into Guyana (Lim et al., 2010). A third CI RAP survey that included large mammals was conducted in the Konashen area of southern Guyana (Sanderson et al., 2008). The first comprehensive analysis of DNA barcoding in mammals was done on bats from Guyana (Clare et al., 2007). The species checklist of 223 mammals from Guyana was more recently summarized by Engstrom and Lim (2002) and updated by Lim et al. (2005b).

## DISCUSSION

There are 232 species of mammals documented from the Guianas with 222 species from Guyana, 194 species from Suriname, and 186 species from French Guiana (Lim, 2012). This includes the removal of *Micronycteris microtis* as a valid species separate from *M. megalotis* (Porter et al., 2007) and the systematic revision of *Platyrrhinus helleri* that restricted the nominate species to Central America with the recognition of *P. incarum* and *P. fusciventris* in all three countries of the Guianas (Velazco et al., 2010). Additional updates for Suriname include the removal of *Eumops glaucinus* (Husson, 1962; Simmons and Voss, 1998) and *Oecomys rex* due to unconfirmed records (Lim et al., 2005b), and the addition of *Isothrix sinnamariensis*

and *Neusticomys oyapocki* (Lim and Joemratie, 2011). For French Guiana, further changes include the addition of *Lasiurus ega* and *Cerdocyon thous*, and the removal of *Myotis albescens* and *Sigmodon alstoni* (Catzefflis, 2010; and pers. comm.). The overall diversity in the Guianas includes 12 orders of mammals with bats comprising over half of the species and rodents accounting for almost 20%. Only two species are endemic to the Guianas: *Molossus barnesi* is known from northern French Guiana (Simmons and Voss, 1998), and *Isothrix sinnamariensis* is known from all three of the Guianas (Lim et al., 2006; Lim and Joemrotie, 2011; Vié et al., 1996).

The study of mammalogy in the Guianas has been heterogeneous among the three countries since colonial times. Suriname was the type locality of over one-third of the newly described species from South America in the first half century after the adoption of Linnaeus's (1758) binomial classification system (Fig. 2; Baker, 1991). Although there was a steady description of new species from European-based taxonomists into the next century, Kappler (1881; 1887) was the first field-based naturalist who made a significant contribution to the knowledge of mammals in Suriname. There was a dearth of taxonomic activity in the first half of the 20<sup>th</sup> century (Fig. 3) but Husson (1962; 1978) at the RMNH put Suriname at the forefront of mammalogical study in South America in the second half of the century (Gardner, 2008). This trend continued into the 1980's with several publications by Genoways and Williams based on faunal surveys by the CM. More recently, field expeditions by Lim at the ROM have added several new country records and summarized mammalian community ecology at several sites in Suriname.

French Guiana was also a relatively active area of early biological study in the late 18<sup>th</sup> century (Fig. 4), however, Buffon's use of vernacular names instead of adopting the binomial nomenclature system of Linnaeus resulted in his taxonomic

oblivion (Hershkovitz, 1987). Research did not return to prominence in the colony until the mid-1960's with work based primarily at the MNHN Laboratory of Ecology initiated by Brosset, Dubost, and Charles-Dominique with continuation by the next generation of ecologists such as Forget. Although some taxonomic work was done, the main emphasis was ecological studies such as plant-animal interactions. Over the past two decades molecular phylogenetic studies centred on French Guiana by Catzeflis and colleagues have contributed to our understanding of mammalian biogeography in South America.

Guyana was largely ignored biologically until the biotic surveys of the Schomburgks in the 1840's (Fig. 5), which made it at that time one of the better-known countries of South America (Hershkovitz, 1987). By the start of the 20<sup>th</sup> century, a combination of the collecting efforts of McConnell and the prodigious taxonomic descriptions of Thomas at the BMNH resulted in a productive period of mammalogical study in Guyana (Fig. 5). The establishment of the Kartabo Tropical Research Station by the New York Zoological Society under the leadership of Beebe from 1916-1926 marked the first long-term ecological study site in the Guianas. There was a relatively quiet period until the 1960's when Peterson at the ROM began a collection-based research programme that has been continued by Lim and Engstrom with research focused primarily on systematics and community ecology of mammals.

In terms of research resulting from field-oriented collecting, the first synthetic study was on squirrels by Thomas (1914a) who hypothesized a closer affinity of *Sciurillus* with Africa and Asia than with other squirrels from the Americas. Although the systematic relationships were interpreted slightly differently, a similar biogeographic connection to the Old World was corroborated by subsequent morphological study by Moore (1959). In addition, recent molecular analyses placed



*Sciurillus* in a basal lineage distinct from the more derived species of squirrels in *Sciurus* that are sympatrically distributed in the Neotropics (Mercer and Roth, 2003; Steppan et al., 2004). Although based primarily on fieldwork in Venezuela, Tate (1939) presented the first regional summary beyond political boundaries on the mammals of the Guianas. A half century later the first volume of mammals of South America by Eisenberg (1989) focused on the northern region. However, in comparison to Venezuela, Colombia, and Panama in the western portion of this area, the knowledge gap in the eastern portion (Guyana, Suriname, and French Guiana) was evident particularly with the lack of direct reference to research in the Guianas at that time. This was reflected in an earlier summary of the current state of knowledge of mammals in South America by Pine (1982) who categorized Suriname as one of the better known countries because of the recent work by Husson (1962; 1978) but research in French Guiana was just beginning and essentially was nonexistent in Guyana. It was not until the beginning of the current century that basic biological information such as a species checklist of mammals was compiled specifically for the Guianas (Lim et al., 2005b). Nonetheless, there has been a resurgence of mammalogical research in all three countries of the Guianas beginning in the 1960's that has resulted in a steady increase in publications that continue today not only in peer-reviewed scientific journals but also in monographic works (e.g., Lobova et al., 2009) that attests to the growing maturity of research in this previously neglected biogeographic region of South America.

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Table 1. Currently valid species with type localities in the Guianas based on Wilson and Reeder (2005).

| Species                          | Authority        | Type Country  |
|----------------------------------|------------------|---------------|
| <i>Ateles paniscus</i>           | Linnaeus, 1758   | French Guiana |
| <i>Cebus apella</i>              | Linnaeus, 1758   | French Guiana |
| <i>Saimiri sciureus</i>          | Linnaeus, 1758   | Guyana        |
| <i>Carollia perspicillata</i>    | Linnaeus, 1758   | Suriname      |
| <i>Vampyrum spectrum</i>         | Linnaeus, 1758   | Suriname      |
| <i>Saguinus midas</i>            | Linnaeus, 1758   | Suriname      |
| <i>Caluromys philander</i>       | Linnaeus, 1758   | Suriname      |
| <i>Cabassous unicinctus</i>      | Linnaeus, 1758   | Suriname      |
| <i>Cyclopes didactylus</i>       | Linnaeus, 1758   | Suriname      |
| <i>Didelphis marsupialis</i>     | Linnaeus, 1758   | Suriname      |
| <i>Bradypus tridactylus</i>      | Linnaeus, 1758   | Suriname      |
| <i>Marmosa murina</i>            | Linnaeus, 1758   | Suriname      |
| <i>Choloepus didactylus</i>      | Linnaeus, 1758   | Suriname      |
| <i>Noctilio leporinus</i>        | Linnaeus, 1758   | Suriname      |
| <i>Philander opossum</i>         | Linnaeus, 1758   | Suriname      |
| <i>Dasyprocta leporina</i>       | Linnaeus, 1758   | Suriname      |
| <i>Pithecia pithecia</i>         | Linnaeus, 1766   | French Guiana |
| <i>Cuniculus paca</i>            | Linnaeus, 1766   | French Guiana |
| <i>Alouatta macconnelli</i>      | Linnaeus, 1766   | Guyana        |
| <i>Cerdocyon thous</i>           | Linnaeus, 1766   | Suriname      |
| <i>Sciurus aestuans</i>          | Linnaeus, 1766   | Suriname      |
| <i>Hydrochoeris hydrochaeris</i> | Linnaeus, 1766   | Suriname      |
| <i>Glossophaga soricina</i>      | Pallas, 1766     | Suriname      |
| <i>Phyllostomus hastatus</i>     | Pallas, 1767     | Suriname      |
| <i>Puma concolor</i>             | Linnaeus, 1771   | French Guiana |
| <i>Saccopteryx leptura</i>       | Schreber, 1774   | Suriname      |
| <i>Potos flavus</i>              | Schreber, 1774   | Suriname      |
| <i>Leopardus tigrinus</i>        | Schreber, 1775   | French Guiana |
| <i>Galictis vittata</i>          | Schreber, 1776   | Suriname      |
| <i>Myoprocta acouchy</i>         | Erxleben, 1777   | French Guiana |
| <i>Mazama americana</i>          | Erxleben, 1777   | French Guiana |
| <i>Monodelphis breviceaudata</i> | Erxleben, 1777   | Suriname      |
| <i>Chironectes minimus</i>       | Zimmermann, 1780 | French Guiana |
| <i>Echimys chrysurus</i>         | Zimmermann, 1780 | Suriname      |
| <i>Priodontes maximus</i>        | Kerr, 1792       | French Guiana |
| <i>Tayassu pecari</i>            | Link, 1795       | French Guiana |
| <i>Procyon cancrivorus</i>       | G. Cuvier, 1798  | French Guiana |
| <i>Eumops auripendulus</i>       | Shaw, 1800       | French Guiana |



|                                  |                             |               |
|----------------------------------|-----------------------------|---------------|
| <i>Proechimys guyannensis</i>    | É. Geoffroy, 1803           | French Guiana |
| <i>Sciurillus pusillus</i>       | É. Geoffroy, 1803           | French Guiana |
| <i>Metachirus nudicaudatus</i>   | É. Geoffroy, 1803           | French Guiana |
| <i>Puma yagouaroundi</i>         | É. Geoffroy, 1803           | French Guiana |
| <i>Molossus rufus</i>            | É. Geoffroy, 1803           | French Guiana |
| <i>Furipterus horrens</i>        | F. Cuvier, 1828             | French Guiana |
| <i>Saccopteryx bilineata</i>     | Temminck, 1838              | Suriname      |
| <i>Dasypus kappleri</i>          | Krauss, 1862                | Suriname      |
| <i>Cynomops planirostris</i>     | Peters, 1865                | French Guiana |
| <i>Phylloderma stenops</i>       | Peters, 1865                | French Guiana |
| <i>Artibeus concolor</i>         | Peters, 1865                | Suriname      |
| <i>Peropteryx kappleri</i>       | Peters, 1867                | Suriname      |
| <i>Peropteryx leucoptera</i>     | Peters, 1867                | Suriname      |
| <i>Choeroniscus minor</i>        | Peters, 1868                | Suriname      |
| <i>Lamproncyteris brachyotis</i> | Dobson, 1878                | French Guiana |
| <i>Diaemus youngi</i>            | Jentink, 1893               | Guyana        |
| <i>Mesophylla macconnelli</i>    | Thomas, 1901                | Guyana        |
| <i>Phyllostomus latifolius</i>   | Thomas, 1901                | Guyana        |
| <i>Eumops maurus</i>             | Thomas, 1901                | Guyana        |
| <i>Rhipidomys nitela</i>         | Thomas, 1901                | Guyana        |
| <i>Molossus barnesi</i>          | Thomas, 1905                | French Guiana |
| <i>Micoureus demerarae</i>       | Thomas, 1905                | Guyana        |
| <i>Neacomys guianae</i>          | Thomas, 1905                | Guyana        |
| <i>Oryzomys macconnelli</i>      | Thomas, 1910                | Guyana        |
| <i>Oecomys rex</i>               | Thomas, 1910                | Guyana        |
| <i>Oecomys rutilus</i>           | Anthony, 1921               | Guyana        |
| <i>Bassaricyon beddardi</i>      | Pocock, 1921                | Guyana        |
| <i>Podoxymys roraimae</i>        | Anthony, 1929               | Guyana        |
| <i>Marmosops parvidens</i>       | Tate, 1931                  | Guyana        |
| <i>Glyphonycteris daviesi</i>    | Hill, 1964                  | Guyana        |
| <i>Vampyressa brocki</i>         | Peterson, 1968              | Guyana        |
| <i>Neusticomys oyapocki</i>      | Dubost and Petter, 1978     | French Guiana |
| <i>Proechimys cuvieri</i>        | Petter, 1978                | French Guiana |
| <i>Lophostoma schulzi</i>        | Genoways and Williams, 1980 | Suriname      |
| <i>Molossops neglectus</i>       | Williams and Genoways, 1980 | Suriname      |
| <i>Rhogeessa hussoni</i>         | Genoways and Baker, 1996    | Suriname      |
| <i>Lasiurus atratus</i>          | Handley, 1996               | Suriname      |
| <i>Isothrix sinnamariensis</i>   | Vié et al., 1996            | French Guiana |
| <i>Micronycteris brosetti</i>    | Simmons and Voss, 1998      | French Guiana |
| <i>Neacomys paracou</i>          | Voss et al., 2001           | French Guiana |
| <i>Neacomys dubosti</i>          | Voss et al., 2001           | French Guiana |

## FIGURE LEGENDS

Fig. 1. Map of the Guianas of northern South America, including Guyana, Suriname, and French Guiana.

Fig. 2. The discovery of new species of mammals from Guyana, Suriname, and French Guiana grouped into approximately half centuries.

Fig. 3. The rate of discovery of the 195 species of mammals known from Suriname. Arrows indicate 6 periods of increased discovery of species diversity.

Fig. 4. The rate of discovery of the 187 species of mammals known from French Guiana. Arrows indicate periods of increased discovery of species diversity.

Fig. 5. The rate of discovery of the 223 species of mammals known from Guyana. Arrows indicate 5 periods of increased discovery of species diversity.









