LESSER TAILLESS BAT

*Anoura caudifer* (E. Geoffroy, 1818)

*FIGURE 1* - Adult (©Marco Mello www.casadosmorcegos.org).

**TAXONOMY:** Class Mammalia; Subclass Theria; Infraclass Metatheria; Order Chiroptera; Suborder Microchiroptera; Superfamily Noctilionoidea; Family Phyllostomidae, Subfamily Glossophaginae, Tribe Glossophagini (López-Gonzalez 2005, Myers et al 2006, Oprea et al 2009). There are eight species in this genus, one of which occurs in Paraguay but the validity of some of these species has been called into question, some previously described species have later been synonymised (Nagorsen & Tamsitt 1981) and a review of the group is required (Jarrin & Kunz 2008). Carstens et al (2002) provided a phylogeny of the Glossophaginae based on morphological characteristics. They considered *Anoura* to belong to the "choeronycterine" group of the Glossophaginae along with *Choeronycteris, Choeroniscus, Hylonycteris, Lichonycteris, Musonycteris and Scleronycteris*.

The generic name *Anoura* is means “without a tail” (Palmer 1904). The species name *caudifer* is Latin meaning “tailed” in reference to the presence of a tail in this species in what has been misleadingly considered to be a diagnostic characteristic in a purportedly tailless group. Czaplewski & Cartelle (1998) describe Quaternary fossils of this species from Minas Gerais, Brazil.
The spelling of the species name in feminine form *caudifera* based on the assumption that the genus is female (Handley 1984) is incorrect. According to ICZN rules if the author fails to indicate whether a name is an adjective or substantive, the name should be treated as a noun in apposition and the original spelling stands, in this case being *caudifer*. (Oprea et al 2009).

The genus *Lonchoglossa* including this species was first proposed by Peters (1869) and Miller (1907) summarised the subtle differences between it and *Anoura*. He noted that *Lonchoglossa* was not well differentiated from *Anoura* but could be distinguished by the presence of a "rudimentary though evident tail, the nearly terete outer upper incisors and the position of the anterior upper premolars close to the base of canine". Additionally the "zygomatic arch though slender is apparently always present and completely ossified" as opposed to "incomplete or imperfectly ossified" in *Anoura*. Sanborn (1933) however found no evidence to support the dental differences between the two groups and commented on the extreme variability in both genera. Vieira (1942) later stated that zygomatic arches were weak but present in *Lonchoglossa*, in the process implying their absence in *Anoura*. In fact the zygomatic arches are present in recently dead *Anoura* but are often subject to degradation during the cleaning process and it is also worthy of note that the tail is small but visible in live specimens of this species, yet frequently is lost or difficult to see in preserved specimens. (Barquez & Olrog 1985).

The genus *Anoura* has an extremely complex taxonomic history and three new species have been described since 1994 (Molinari 1994, Muchhala et al 2005, Mantilla-Meluk & Baker 2006). Jarrin & Kunz (2008) summarised the taxonomic history of the genus and reassessed the validity of morphological characters used for species distinction. They argued that many are subjective, highly variable, possibly clinal and that small sample sizes used for the description of new species may lead to the exaggeration of proposed differences and hence the description of species that are invalid. Though they did not make any taxonomic assertions of their own they called into question the reliability of techniques used in the description of many of these new species in the genus and called for "rigorous tests" to be applied to avoid the risks of relying on "purely literary accounts influenced by personal perspectives of color, size and shape."

Tamsitt & Valdivieso (1966) declared that the subspecies *A.c.equatoris* Lönnberg was in fact indistinguishable from the nominate subspecies and that it should be considered monotypic. However they were working with a Colombian sample that showed high variability, possibly due to the inclusion of specimens from other taxa that were later described as distinct species. Their measurements listed are indicative of at least the presence of the hitherto unknown *Anoura hesimannui* Molinari (1994) in their sample. Mantilla-Meluk & Baker (2006) later reinstated *A.equatoris* as a valid taxon and described it as a distinct species, though this arrangement was not followed by Gardner (2007) on account of an error in the type location, stated as being on the east of the Andes by the authors, but in fact located on the western slope. Gardner (2007), whilst accepting that the separation was “probably correct” considered that this error added to the taxonomical confusion surrounding the species and that a thorough review of the entire complex currently known as *A.caudifer* was required.

Jarrin & Kunz (2008) however questioned the small sample sizes and the techniques used in the description of both of these species, and agreed with Tamsitt & Valdivieso (1966) and stated that a difference in forearm length of just 1mm is the only evidence supporting subspecific or specific differentiation of *A.(c.).equatoris*. They state "Hence, there is no definitive evidence for clinal variation between populations related to Amazonia, (affinis to *A. c. caudifer*) and the Andes (affinis to *A. c. equatoris*). Additional samples and multiple lines of evidence (e.g., morphological and molecular) along an eastern-western cline might clarify this issue."

We tentatively follow the conservative arrangement of considering *A.caudifer* monotypic. However as a result of the continuing confusion over species boundaries, the species account makes only limited reference to literature from Colombia, Venezuela and Ecuador where the existence of possibly sympatric cryptic species undescribed at the time of their publication may have resulted in an unwitting reference to composite samples. Comments on the validity of these cryptic species are beyond the scope of this work.

Synonyms adapted from Gardner (2007) and López-González (2005):

*Glossophaga caudifer* E.Geoffroy St.Hilaire 1818:418. Type locality "Rio de Janeiro", Brazil.

*Glossophaga ecaudata* E.Geoffroy St.Hilaire 1818:418. Type locality unknown.

*Glossophaga caudifera* JB Fischer 1829:139. Incorrect spelling.
Lonchoglossa caudifera W.Peters 1868:364. Name combination and incorrect spelling.
Lonchoglossa weidii Dobson 1878:507. Name combination.
Lonchoglossa weidii aequatoris Lönnberg 1921:65 Type locality “Illambo” (=Illambo), Pichincha, Ecuador.
Lonchoglossa caudifera aequatoris Sanborn 1933:27. Name combination.


SPANISH COMMON NAMES: Murciélaguito hocicudo (Barquez et al 1993), Murciélago longirostro con cola (Aguirre 2007), Murciélago de lengua larga (Emmons 1999), Murciélago hocicudo lenguilargo (Mares et al 1989).

GUARANÍ COMMON NAMES: No known names.

DESCRIPTION: A small, delicately-built bat with a long muzzle. Nose leaf small but conspicuous, higher than it is wide and continuous with upper lip. Upper lip smooth, lower lip with a deep medial groove bordered by thick callosities. Ears short, rounded and well-separated. Tragus normal, short and lacking crenulations, with blunt tip. Pelage dense and silky, extending to parts of the plagiotapatum, propatagium and first half of the forearm. Colouration dark brown above and slightly paler below. Dorsal hairs with greyish bases and ventral hairs unicoloured. Tamsitt & Valdivieso (1966) however noticed that pelage colour varied among individuals within a single population with some much darker than others. Anterior half of the back, area behind the ears and nape sometimes paler or, less often, reddish. Uropatagium much reduced, semicircular and bordered by a thin fringe of hairs. Tail extremely small and enveloped within the uropatagium, reaching to the border. Membranes dark brown or black. Calcar small and slightly shorter than the length of the foot. Thumb short and thin, with a short nail. (Barquez et al 1999).

CRANIAL CHARACTERISTICS: Skull elongate with rostrum less than length of the braincase and broader in the area of the canines. Postorbital constriction barely noticeable. Zygomatic arches complete and ossified in young individuals. No sagittal crest and only slight lambdoidal crest present. Auditory bullae small. Basiphenoidal pits present but shallow. Coronoid process of mandible approximately the same height as the mandibular condyle. (Barquez et al 1999).

Anderson (1997) gives the following measurements for 2 males and 2 females from Carnavi, Bolivia housed at AMNH: Skull Depth 7.2-7.67mm; Condylobasal Length 21-22.5mm; Zygomatic Width 9.4-11.4mm; Lambdaoidal Width 9.1-10mm; Width of Braincase 8.8-9.1mm; Width Across Upper Canines 3.0-4.2mm. Albuja-V (1999) gives the following mean and range measurements Greatest Length of Skull for 9 males and 12 females in Ecuador: male 21.8mm (20.8-23.8mm), female 21.6mm (20.8-22.1mm).

Barquez et al (1999) give the following measurements for individuals from Argentina (n=5 unless stated): Greatest Skull Length 22.9mm (+/- 0.52mm); Condylobasal Length 22.1mm (+/- 0.51mm); Zygomatic Width 9.9mm (+/- 0.42mm, n=2); Maxillary Width 9.2mm (+/- 0.14mm, n=2); Postorbital Constriction 4.6mm (+/- 0.21mm); Width Across Upper Molars 5.8mm (+/- 0.19mm); Width Across Upper Canines 4.1mm (+/- 0.19mm) Palatal Length 11.8mm (+/- 0.35mm); Length of Mandible 16.7mm (+/- 0.49mm, n=4); Width of Braincase 9.0mm (+/- 0.27mm).

Dias et al (2002) give the following mean and range measurements for 4 males and 3 females from São Paulo, Brazil: Greatest Length of Skull male 22.75mm (22.6-23.1mm), female 22.8mm (22.5-23.1mm); Condylobasal Length male 22mm (21.6-22.5mm), female 22.1mm (21.9-22.3mm); Basal Length male 19.98mm (19.8-20.1mm), female 19.9mm (19.7-20mm); Palate Length male 12.23mm (12-12.4mm), female 12.3mm (11.9-12.8mm); Width Across Molars male 4.9mm (4.1-5.2mm), female 5.13mm (5-5.3mm); Mandibular Length male 16.2mm (15.7-16.7mm), female 16.27mm (16.1-16.4mm); Width Across Canines male 4mm (3.6-4.2mm), female 3.93mm (3.7-4.1mm); Postorbital Constriction male 4.55mm (4-4.8mm), female 4.63mm (4.6-
DENTAL CHARACTERISTICS: I2/0 C 1/1 P3/3 M3/3 = 32. I1 and I2 are small, paired and widely separated. I1 is smaller than I2. Absence of lower incisors allows the tongue to pass through for nectar feeding. Premolars laterally compressed and increase in size from P1 to P3. P1 is reduced and separated from both the canine and P2 by a small space. P2 is also separated from P3. P3 contacts M1 at its posterior border. P2 and P3 are triangular in lateral view. Central cusps of premolars are elevated and sharp, anterior and posterior cusps being smaller. Lower premolars are thin, p1 almost contacting the canine but separated from p2. No spaces are present between the remaining premolars or lower molars. Molars with strong central depression and laterally compressed. Paraconid is smaller than the other cusps. (Barquez et al 1999). Sexual dimorphism in the size of the canines, being longer and more robust in males than females (Gardner 2007).

Barquez et al (1999) give the following measurements for individuals from Argentina: Upper Tooth Row 8.3mm (+/- 0.16mm, n=5); Lower Tooth Row 8.9mm (+/- 0.21mm, n=2).

Dias et al (2002) give the following mean and range measurements for 4 males and 3 females from São Paulo, Brazil: Upper Tooth Row male 8.38mm (8.3–8.86mm), female 8.4mm (8.1–8.7mm); Lower Tooth Row male 8.75mm (8.6–8.9mm), female 8.67mm (8.3–9mm).

Anderson (1997) gives the following measurements for 2 males and 2 females from Carnavi, Bolivia housed at AMNH: Upper Tooth Row 7.7-8.3mm; Dental Span 5.5-6mm; Molar Width 0.9-1.1mm.

GENETIC CHARACTERISTICS 2n=30. FN=56. X chromosome submetacentric, Y chromosome acrocentric. (Baker 1973). Haiduk & Baker (1982) described the G-banded karyotype and found it to be identical to that of A.geoffroyi. Arm 13/2 is present and makes up one of the arms of the largest chromosomal pair. The other arm is composed of arms 8 and 1 fused in tandem. The genus is characterised by an autapomorphic karyotype which is the result of a high rate of chromosomal evolution. The karyotype of Anoura requires a minimum of thirty rearrangements to so radically reorganise its banding pattern (Oprea et al 2009).

EXTERNAL MEASUREMENTS: A small bat with an elongated rostrum.

Barquez et al (1999) give the following measurements for individuals from Argentina (n=5 unless stated): TL 59mm (+/- 2.57mm); TA 4.7mm (+/- 0.35mm, n=2); FT 9.2mm (+/- 0.80mm); FA 38.1mm (+/- 1.24mm); EA 12.9mm (+/- 2.19mm); WT 10.4g (+/- 1.72mm, n=3).

Anderson (1997) gives the following range measurements for four females from Carnavi, Bolivia housed at LSU: TL 51-64mm; TA 2-3mm; FT 9-13mm; FA 35-37mm; EA 12-14mm; Tibia 13mm; Pollex 6mm; Third Digit First Metacarpal 37mm; Third Digit Second Metacarpal 12mm; Third Digit Third Metacarpal 19mm; WT 9-11g. The same author gives these measurements for 2 males and 2 females from the same locality at AMNH: TL 58-65mm; TA 2-7mm; FT 11-13mm; FA 34-37mm; EA 10-14mm; Tibia 11mm; Pollex 6mm; Third Digit First Metacarpal 35-37mm; Third Digit Second Metacarpal 11-12mm; Third Digit Third Metacarpal 18-20mm; WT 11-12g.

Albuja-V (1999) gives the following mean and range measurements for 9 males and 12 females in Ecuador: TL male 52.8mm (50-58mm), female 58.4mm (50-68mm); EA male 13.4mm (12-17mm), female 12.1mm (8-17mm); FA male 37.7mm (35-36.4mm), female 36.3mm (32.9-38.1mm); FT male 9.25mm (7-12mm), female 9.2mm (8-11mm); TA male 4.9mm (3.5-7mm), female 5.5mm (4-10mm).

Dias et al (2002) give the following mean and range measurements for FA of 4 males and 3 females from São Paulo, Brazil: male 36.23mm (35.5-37mm), female 35.8mm (35.3-36.4mm).

Podtiaquin (1944) gives the following measurements for two males from Concepción, and females from Saprucan and Rosario (respectively), Paraguay: TL male 54mm 56mm female 57mm 51mm; FA male 38mm 39mm female 39mm 34mm; Pollex male 6mm 6mm female 5mm 6mm; First Digit male 12mm 12mm female 11mm 10mm; Second Digit male 18mm 18mm female 19mm 17mm; Third Digit male 9mm 9mm female 10mm 9mm.

SIMILAR SPECIES: A small, delicate bat with a long snout. In Paraguay this species could only be confused with the other member of the subfamily Glossophaga soricina. This species has a slightly longer snout (so that the area above the eyes appears convex), but is most easily distinguished on account of the greatly reduced uropatagium bearing a fringe of fine hairs. The uropatagium of G.soricina is much more...
conspicuous, unfurred and supported by short calcars. As a result the very short tail reaches the border of the uropatagium in this species in live specimens, whilst it protrudes through the middle of the dorsal surface of the uropatagium in *G. soricina*. Additionally this species has more reduced nose leaf and a short, blunt tragus lacking crenulations, that of *G. soricina* is noticeably long, lanceolate and pointed.

In the north of the country Geoffroy’s Tailless Bat *Anoura geoffroyi* (Fig 2) is of hypothetical occurrence. It is a slightly larger species HB >65mm, FA >43mm and WT >13g and completely lacks a tail. Note however that preserved specimens of *A. caudifer* may also appear completely tailless. The uropatagium of *A. geoffroyi* is triangular and reduced to a narrow and densely-furred band, this in contrast to the wide, sparsely-haired, semicircular uropatagium of *A. caudifer*. This species also lacks a calcar in contrast to *A. caudifer* which has a small but well-developed calcar. Typically *A. geoffroyi* shows a greyish tone to the pelage of the venter and shoulders. On direct comparison the snout of *A. caudifer* appears longer than that of *A. geoffroyi*. (Oprea et al. 2009).

**DISTRIBUTION:** Distributed in a wide circum-Amazonian arc from Brazil through French Guiana, Surinam, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, extreme northwestern Argentina and Paraguay.

In Bolivia the species has been recorded in Departamentos Bení, La Paz, Cochabamba, Chuquisaca and Santa Cruz (Aguirre 2007). In Argentina it is known only from Provincias Jujuy and Salta in the extreme northwest of the country (Barquez et al 1999). In Brazil the species distribution is separated by the Amazon and it has been recorded in the following states: Acre, Amazonas, Amapá, Bahía, Distrito Federal, Espírito Santo, Maranhão, Goiás, Minas Gerais, Mato Grosso do Sul, Mato Grosso, Pará, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo (dos Reis et al 2007, Zórtea 2003). Zóratea (2003) had a low capture rate for the species in Goiás, Brazil (13 of 339 specimens) and did not capture any specimens in September, December, June or July.

There are no recent Paraguayan records and the species may have disappeared from the country. The only mention of the species in Paraguay comes from Podtiaguín (1944) as *Lonchoglossa ecaudata*. Podtiaguín (1944) refers to *L. ecaudata* being “distinguishable” from the “very similar” *L. caudifera (=A. caudifer)* by the fact that the latter species has a rudimentary tail and naked tail membrane. The name *Lonchoglossa ecaudata* however is a synonym of *A. caudifer* and the tail of this species is of notoriously variable length and often appears to be absent in preserved specimens.

Despite the documentation by Podtiaguín (1944) and López-González (2005) this species has been omitted from the Paraguayan mastofauna by important recent reviews (Gardner, Oprea et al. 2009). At the root of the apparent confusion are six specimens from northern Paraguay described by Rennger (1830) as a new species *Glossophaga villosa*, and included in Bertoni’s (1939) Catalogue of Vertebrates of Paraguay. *Glossophaga villosa* is described as lacking a tail, with an interfemoral membrane covered with shorts hairs and a fringe of hairs, and with a dental formula I2/2 C1/1 P3/3 M3/3.

Without further justification Podtiaguín (1944) stated that Rennger’s description “could not be a species of *Glossophaga*, and must be *Lonchoglossa*, which according to my way of seeing it must be *L. ecaudata*”. This off the cuff remark was presumably taken by Gardner (2007) to mean that the later specimens which Podtiaguín (1944) discussed in his text as *L. ecaudata* were indeed the same as Rennger’s *G. villosa*. Podtiaguín it seems overlooked the fact that Rennger’s dental formula for *G. villosa* included the presence of two lower incisors which is inconsistent with their inclusion in *Lonchoglossa (=Anoura)* (Miller 1907) and as Gardner (2007) correctly interprets, Rennger’s measurements put the total length of his bats somewhere in the region of 72mm, compared with total lengths of 51-57mm for Podtiaguín’s *L. ecaudata*. A lack of surviving specimens and further inconsistencies in Rennger’s description (a supernumerary premolar for *Glossophaga*, and the outer upper incisor being shorter and thinner than the inner for *Anoura*) led Gardner (2007) to conclude that Rennger was perhaps dealing with a mixed sample and to correctly suppress *Glossophaga villosa* as a *nomen dubium*. To confuse matters however Gardner (2007) discussed this situation under the species account for *Anoura geoffroyi*, a species of possible occurrence in Paraguay but
not yet documented, whilst simultaneously listing [Lonchoglossa] ecuadeta Trouessart 1897 as a synonym of Anoura caudifer.

Podtiaguín’s (1944) description of L.ecuadeta contains no inconsistencies with the taxon currently known as Anoura caudifer, and there is no reason to associate it with Rengger’s Glossophaga villosa other than a single unsupported remark and Bertoni’s probable confusion of it with the specimens Podtiaguín later identified as L.ecuadeta.

It was last collected in Paraguay in 1939 and the whereabouts of the collected specimens are currently unknown. Podtiaguín (1944) lists the following localities: Concepción, Departamento Concepción (males February 1900 and December 1934); Sapucai, Departamento Paraguay (female March 1903) and Rosario, Departamento San Pedro (female January 1939). Reference is also made to the presence of additional possibly Paraguayan specimens of vague and uncertain provenance in European museums “como Mus. Hist. Nat de Paris, Col. Piro, Palau etc”. Note that the dates of collection of the small sample of specimens are consistent with migratory movements in relation to inflorescences, which may help explain the scarcity of records.

HABITAT: This species often favours a higher altitudinal range resulting in a patchy distribution despite a wide geographic range (Oprea et al 2009). Gazima et al (1995) describe this species as the major, if not the only, glossophagine flower-visiting bat in Atlantic Forest above 1000m.

In Brazil however the species has been reported from all the major biomes except the Caatinga (Oliveira et al 2003) and even including the semi-arid cerrado region that spills over into Paraguay (Zortéa 2003). There are records from disturbed habitats as well as pristine areas, including primary and secondary forests (Brosset et al. 1996; Reis and Peracchi 1987), banana plantations associated with forest areas (Esbérard et al. 1996; Peracchi and Albuquerque 1971), secondary growth with islands of cerrado and gallery forest (Fischer 1992), pasture lands (Coimbra et al. 1982), and urban and rural areas (Breit and Uieda 1996). It is one of the most common species captured in surveys in karst areas (Esbérard et al. 2005). Trajano (1985) suggested that its unusual abundance in the karst area of the Rio Ribeira Valley of São Paulo may have been attributable to the apparent rarity of Glossophaga soricina in the area.

In Ecuador the species is associated with primary or only moderately disturbed humid forests, typically in areas close to streams (Albuja-V. 1999). In French Guiana Brosset et al (1996) captured 13 specimens in primary forest and 73 in secondary forest, but none in coastal savannah, coastal swamps or urban areas and 61 of those specimens were taken at roosts. In Venezuela Helversen and Reyer (1984) described a roost site at 450m located at the lower margin of deciduous forest (selva veranera) on the upper edge of dry thornbush (espinar).

One specimen in Argentina was captured almost at ground level in an open area near the banks of the Rio Pescado, whilst another specimen was netted over a calm stream at one end of a culvert under a road in forest. (Barquez et al 1999). In Bolivia the species is associated with water courses in tropical forest (Aguirre 2007).

No information on habitat usage is available for Paraguay.

ALIMENTATION: Gardner (1977) describes the diet of this species as fruit, nectar, pollen and insects. Ruschi (1953) mentions insects, soft juicy fruits, nectar and pollen in the diet in Brazil.

A. caudifer requires about 4 hours of foraging time, 800 floral visits, and in-flight commuting of about 50 km each night in order to remain in energy balance (Helversen & Reyner 1984). Using doubly labeled water injections, Helversen & Reyner (1984) calculated a daily energy expenditure (DEE) of 310% the basal rate or 12.4 kcal/day and water exchange of 13.4 ml/day. The DEE was considered to be high when compared to other bat species, small mammals and birds.

Mucchala (2006) noted that bats of the genus Anoura accounted for 75% of the conspecific pollen flow between nine species of Burmeistera (Campanulaceae) in Ecuador. No specific relationship between the bats and particular Burmeistera species were found, though they did not visit one other species B.microsepala, that was visited only by a specific species of hummingbird Adelomyia melanogenys. In a single fecal sample from the Pantanal of Mato Grosso do Sul, Munin (2008) found remains of Lepidoptera and the pollen of four plant species, Bauhinia ungulata, Bauhinia sp. (Fabaceae), Pseudobombax longiflorum (Malvaceae) and Psittacanthus corynocephalus (Loranthaceae).

Sazima (1976) captured seven specimens of the species feeding at flowers of Bahinia rufa (Leguminosae) in October and found that stomachs contained pollen and fragments of insects from the following orders: Thysanoptera, Hymenoptera, Coleoptera and Lepidoptera. It was speculated that the thrips and ants in the stomachs may have been ingested accidentally as they were small and were regularly seen on the flowers at which the bats were feeding. The Coleoptera and Lepidoptera had an inferred length of 10-15mm and were considered to have been deliberately ingested. The insect feeding behaviour was classified as being that of a “foliage-gleaner” as defined by Wilson (1973).

Fischer (1992) reported the foraging behaviour of this species in Bauhinia ungulata (Leguminosae) in disturbed but open cerrado habitat. This species visited small B.ungulata shrubs and flowers below 2.5m on taller plants, flying to and from the shrub at the same height at which they foraged. They began to forage after 8.30pm and contacted the flowers only briefly (tenths of a second), contacting several flowers on a single visit and sometimes revisiting the same flower. A.caudifer visited singly or in pairs, with visits lasting 2.5 minutes (+/-0.7, n=22) and a time between bouts of 13.5 minutes (+/-5.1, n=20). They visited a mean of 4.3 flowers (+/-1.7, n=42) per plant per night and visited the species during August only, not being present during September (towards the end of the flowering period). The foraging technique and resource usage of this species was similar to that of Glossophaga soricina and is perhaps indicative of competition. However the fact that neither species exhausts the nectar stock of a given flower may mean that the two species can coexist without competition. The larger Phyllostomus discolor fed earlier and on higher flowers during August, but utilised the whole plant during September when the other two species were absent, suggesting resource partitioning with that species.

Sazima et al (1995) stated that bat pollinated bromeliads in the genus Vriesea tended to have faint or drab-coloured flowers, with wider tubular corollas than hummingbird pollinated flowers and nocturnal blooming. The anthers are bent to the lower side of the corolla opening and dust pollen onto the chin of the bat. V.gigantea was an exception to this rule, having radially-arranged anthers that dusted pollen across the face. The flowers have a garlicky scent that increases as the nectar accumulates and sugar content of nectar is very high.

They recorded bat as arriving at Vriesea flowers shortly after nightfall and the bats made an initial flypast presumably to assess condition based on the scent of the flowers. Contact with the flower is extremely brief, lasting from 200 to 500 milliseconds. The snout is pushed inside the flower as the bat feeds, touching the reproductive organs. A single flower is visited at intervals of about 50 to 60 minutes, and generally only one bat was seen to feed at a flowering plant. The bats traced a repeated "trampoline" circuit when foraging leading to regular revisiting of a single plant and favouring cross-pollination and gene flow between populations.

Varassin et al (2001) noted that the bat-pollinated passion flower Passiflora mucronata had white, erect to slightly inclined flowers and two series of odour-producing fringes that gave a sweet scent. The flowers opened between 2.30am and 3am with a full nectar chamber and wilted by 11am. They were visited by this bat until 6am. The glucose content of the nectar of the bat-pollinated P.mucronata was slightly higher than for the other sampled members of the genus, and cholesterol levels were higher in species that were vertebrate pollinated. They concluded that bat-pollinated Passiflora flowers had shorter fringes, stronger scent, greater quantities of nectar, contained pigments in the visible spectrum and had flowers located on a long peduncle outside of the foliage so as to encourage visual location. According to
Helversen & Reyer’s (1984) calculations this species would need to visit 52 *P. mucronata* flowers in a single night in order to fulfil its energy requirements.

Sazima & Sazima (1987) note that when this species feeds on *Passiflora mucronata* it thrusts the head into the flowers so that the head brushes the anthers and stigmas but that pollen is also smeared on to the shoulders and even the back, meaning that it is not selectively placed. However the anther grouping in this plant means that the pollen is not "wasted" in so doing. A given flower could be visited as many as 30 times by bats in an hour.

Buzato et al (1989) documented the feeding behaviour of bats on *Abutilon* (Malvaceae) flowers in montane Atlantic Forest in São Paulo, Brazil. They found that flowers were visited by day by hummingbirds and by night by *A. caudifer* and that though flowers showed some characteristics of ornithophily, they tended towards chiropterophily in their physiology. The flowers of this genus remain open for almost 30 hours, allowing bat visits for two nights. The odour of the flowers is faint and smells vaguely of cabbage. Nectar production decreased throughout the day but in creased at dusk.

The bats fed by thrusting the snout into the flower above the stamen bunch and stylodia so that pollen was brushed onto the chin and throat. An *Abutilon rufinerve* plant with 10 to 15 open flowers received bat visits to 1 to 5 flowers at intervals of 15 to 30 minutes. When two individual bats visited at the same time it resulted in a chase encounter. An *Abutilon regnellii* plant with one open flower received bat visits at intervals of 8 to 25 minutes.

Fischer et al (1992) summarise the pollination of two other Malvaceae plants in São Paulo, Brazil *Bombacopsis calophylla* and *Pseudobombax grandiflorum*. The former blooms in the dry season from October to April and the latter during the dry season from June to August. Both species have brush-like flowers with a strong but unpleasant perfume. Feeding behaviour of the bats involves an initial fly past, followed by a brief hovering feeding visit in which the anthers and stamens contact the wings of the bat. In *P. grandiflorum* the first visits were at 7pm and visits diminished throughout the night, with single individuals visiting the same flower up to eight times in one night. In *B. calophylla* visitation was most frequent after midnight when more inflorescences were open.

Sazima & Sazima (1980) described bat visits to the *Marcgravia myriostigma* (Marcgraviaceae). The umbelliform flowers of this plant are slightly bent upwards and remain open for a single night. The number of open inflorescences varies from 4 to 20 flowers per plant per night and they have a weak, cabbage-like scent. The blooming period lasts 4 to 6 months. Bats make only fleeting contact with the flower, momentarily hovering in front of it. Less often the bat may grasp the plant with its claws. When approaching from below the head of the bat is thrust between the pedicels and nectariferous appendages so that the head and back are dusted with pollen. Bats approaching from above have pollen deposited on the belly and wings, and may "fall through" the flowers. On departure the bats throw themselves backwards before flying away. Considerable coordination is required on behalf of the bat to extract nectar from the relatively inaccessible nectariferous appendages in such a short visit.

Sazima et al (1994) describe the pollination biology of the plant *Siphocampylus sulfureus* (Lobeliaceae) in Brazil. The plant shows a mixture of ornithophilous (diurnal anthesis, sucrose-dominated nectar) and chiropterophilous features (yellowish flowers and strong musky odour more pronounced at night). Flowers are tubular, opening mid-afternoon with nectar readily available and pollen easily shed to the touch. Blooming period is late December to early April. Nectar is produced for three consecutive days, though none is available from mid-morning to mid-afternoon. The flowers are visited by *A. caudifer* shortly after dark, circling the flowering plants. When the bat thrusts its head into the flower the reproductive organs touch the top of the head and a cleft in the lowest corolla allows for deep penetration by the bat. Flower are arranged in whorls along a stem and a bat typically visits every open flower on a whorl during a single visit, though not in consecutive order. The bat also touched ripe buds with the snout. Intervals between feeding bouts varied greatly between two consecutive nights, about 30 minutes between 10pm and 12.05am on the first night and 15 to 250 minutes between 9.05pm and 1.30am on the second night.

Zortéa (2003) collected just four fecal samples from 17 captures in Goiás, Brazil. "Two contained insect fragments, one showed fruit pulp, and another, pollen." Muchhala & Jarrín-V (2002) note possible niche partitioning between *A. caudifer* and *A. geoffroyi* in Ecuador, with the latter preferring larger flowers than the former. Nagorsen & Tamsitt (1981) had earlier noted that *A. caudifer* and *A. geoffroyi* are frequently sympatric and that differences in size may be related to differences in resource usage.
Helversen & Reyer (1984) noted that despite the presence of flowering columnar cacti (*Lemaireocereus* and *Pilosocereus*) and treelike *Capparis* close to a roost in Venezuela, that this species was never recorded feeding at these resources. They hypothesised that the bats travelled a considerable distance to nearby rainforest to feed and that the bats roosted in the warmer coastal region by day to conserve thermoregulatory energy and commuted to the higher forests by night to forage.

The calculated basal metabolic rate for 7 specimens of average body mass 11.3 g was 28.1 ml O2/h (Cruz-Neto et al. 2001).

**Diet in Captivity** Rasweiler & de Bonilla (1972) describe husbandry methods for this species. They kept the species in wood and hardware cloth cages 80 x 92 x 138 cm with a room temperature of 21-28°C and humidity of between 55-92%. Each cage a roosting box 80 x 92 x 51 cm with an exit hole 25 x 15 cm and contained 15 to 20 bats. They used two artificial diets for the species, one in the USA and one in Colombia, and though both had the same basic ingredients the proportions differed. The diets were: USA: Peach Nectar 700ml, Beechnut Hi Protein Cereal 29.52g, Wheatgerm 4.92g, Milk Powder 12.81g, Calcium Caseinate 20.39g, Sugar 68g, Gevral Protein 3.99g, Mineral Supplement 1.68g, Vitamin Mix 0.69g, Corn Oil Mixture 9ml, Water 300ml; Colombia Guava Concentrate 194g, Cerpi Tri-Cereal 25.38g, Wheatgerm 11.93g, Milk Powder 15.9g, Calcium Caseinate 34.78g, Sugar 183.59g, Gevral Protein 4.97g, Mineral Supplement 2.15g, Vitamin Mix 0.86g, Corn Oil Mixture 11.89ml, Water 806ml. Each animal consumed approximately 24ml of food per night. Six of seven captured bats adapted to captivity and three were maintained for over 6 months in this way.

**REPRODUCTIVE BIOLOGY:** Wilson (1979) suggested a possibly asynchronous reproductive cycle because of pregnancy records from throughout the year across the range, but added that further data was required to confirm the opinion. Zortéa (2003) reported that females in the cerrado of Brazil outnumbered males by 10:3.

**Seasonality** No data available for Paraguay.

**Argentina** Barquez et al (1999) suggest that the reproductive cycle in Argentina may be long with births occurring from September through November. A juvenile in Provincia Salta in October was just beginning to fly and had deciduous teeth. Another captured nearby in mid-November had adult teeth, though the molars had not yet erupted. A female also captured in November was pregnant with a well-developed fetus. (Barquez et al 1999).

**Bolivia** Two of three females collected in July had a single embryo (Anderson 1997) and as a result Aguirre (2007) speculated that they are probably monoestrous.

**Brazil** Kuhlhorn (1953) captured a lactating female in February in Mato Grosso do Sul. Peracchi & Albuquerque (1971) captured two pregnant females in January. Taddei (1976) observed seasonal polyestry in São Paulo. In the Rio Ribeiro Valley of São Paulo Trajano (1985) reported gravid females in December, lactating females in January and pregnant and lactant females in March, indicating breeding during the rainy season. However reproductive males found in all seasons suggest that year-round breeding is also a possibility.

In the Cerrado of Goiás, Zortéa (2003) reported three pregnant females in the rainy season (November and January), a lactating female in October and a post-lactating female in May, suggestive of more than one birth peak. Only one male was reproductive (in May) and non-reproductive females were taken in August and September (end of the dry season). They considered the data suggestive of an extended birth period from September to April, with at least one peak occurring in the rainy season (November and December), but noted that more information was required to exactly define the patterns.

**Colombia** Thomas (1972) captured pregnant females in May and November and an inactive female in March in southwestern Colombia. Tamsitt & Valdivieso (1966) took a pregnant female on 29 June 1963 at Pacho which contained a 1.8g embryo with a 16.7mm crown-rump length.

**Ecuador** Two reproductive males in Rio Saloya in September 1968 and a female with a 15mm long embryo at Rio Lliquino during August 1997 (Albuja-V. 1999).

**French Guiana** Pregnant females captured in January and February by Brosset & Dubost 1967.

**Development** Trajano (1985) reported a female carrying a juvenile at 7.05pm on 28 March 1979 and another between 7pm and 8.30pm on 23 January 1979.

**GENERAL BEHAVIOUR:** Unknown in Paraguay, though this is a widespread bat that has been well-studied elsewhere.
Activity Levels

Helversen and Reyer (1984) note that bats flew from the colony together at twilight and typically returned shortly after dawn, though two territorial males frequently returned early.

Aguilar & Marinho-Filho (2004) found different capture peaks for this species when compared to two other nectarivorous bats in Minas Gerais, Brazil. This species became active an hour after sunset and the last captured were taken five hours after sunset with a peak of capture in the 4th hour after sunset. However when compared statistically the difference between activity levels of this species and the other two nectarivorous species sampled, Glossophaga soricina and Choeroniscus minor, were not significant. Though most captures of the species were in the dry season in May and June, there was no significant difference in capture rate between the dry and wet season.

Pedro & Taddei (2002) caught this species throughout the night in Minas Gerais, Brazil. Though this was the least captured of the five Phyllostomids sampled it showed a similar capture pattern to the others with peaks of capture in the first two hours after sunset, then again during the 5th and 6th hours after sunset with a smaller peak at dawn. The species showed highest capture rates at the beginning of the rainy season from October to December.

Flight Pattern

Wings narrower and more pointed than the related Glossophaga soricina resulting in faster flight and perhaps an adaptation to longer foraging flights. (Helversen and Reyer 1984)

Roosts

Caves, tunnels and tree holes have been reported as roosts (Helversen and Reyer 1984, Barquez et al 1999). Brosset & Charles Dominique (1990) found colonies of a few to 100 individuals in French Guiana, some being nursing colonies and other harems. The species was found in culverts in association with Carollia perspicillata. Lemke & Tamsitt (1979) report huge mixed colonies including this species from abandoned rail-road tunnels in Colombia.

Helversen and Reyer (1984) note a cavern colony of 13 individuals (9 females, 2 males with enlarged testes and 2 males without externally visible testes) shared with 10 Carollia perspicillata in Venezuela. They observed no conflict between males. The bats were awake by day, hanging singly or in small, loose groups and would fly around the cavern when disturbed, but were unwilling to leave it by day. Females did not return to the roost at night to groom or rest.

In Brazil it roosts in caves (Esbéárd et al. 2005), rock crevices (Peracchi and Albuquerque 1971), holes in fallen trees (Reis and Peracchi 1987) and a variety of man-made structures (Esbéárd et al. 1996). Ruschi (1953) notes roosts in the foliage of trees such as Mangifera indica and plants including Livistona and Attalea.

Aggressive Behaviour

Handled individuals are extremely excitable (Trajano 1985).

Parasites

Webb & Loomis (1977) list the following ectoparasites: Labidocarpidae: Alabidocarpus furmani (Venezuela); Spinturnicidae: Periglischrus caligus (Venezuela), P. vargasi (Venezuela); Streblidae: Anastroblea mattadeni (Colombia), Paraenestodes longipes (Brazil), Strebla wiedemanni (Brazil); Trombiculidae: Parascoschoengastia aemulata (Venezuela).

Additional Streblidae species subsequently recorded for this species include Trichobius tuptoni (Brazil) (Komeno & Linhares 1999) and the newly described Strebla carvalhoi (Brazil) (Graciolli 2003).

UBelaker et al (1977) list the protozoa Trypanosoma vespertilionis and Trypanosoma (megadermae-type) as endoparasites. Mourão et al (2002) redescribe the nematode Litomosoides brasiliensis (Filarididae) from Amapá, Brazil.

Physiology

Members of the genus Anoura have the 3rd largest brains in the subfamily Glossophaginae (Baron et al. 1996), and the fundamental, telencephalon, and brainstem areas are large. The brain of A. caudifer is similar to that of A. geoffroyi but smaller (Baron et al. 1996). The vomeronasal organ of is asymmetrical (right vomeronasal organ, 3.72 mm; left vomeronasal organ, 3.97 mm) in anteroposterior length (Bhatnagar and Smith 2007) and the lumen is crescentric or nearly round. The ratio between the vomeronasal neuroepithelium and the receptor-free epithelium is estimated to be 3:1. The vomeronasal organ retains a cartilaginous capsule anteriorly, becoming partially ossified posteriorly and ending as a small remnant next to the palate. The nasal septum is thick and contains glands that also are
observed in the lateral nasal wall. A large blood sinus is present lateral to the receptor-free epithelium. The vomeronasal neuroepithelium is approximately 38 mm in height, whereas the nonciliated receptor-free epithelium is approximately 12 mm. Large vomeronasal nerve fascicles are seen under the vomeronasal neuroepithelium (Bhatnagar and Smith 2007).

The basal metabolism of 178% is the highest reported for any glossophagin bat (McNab 1969) and the species remains homeothermic at cool ambient temperatures both in the laboratory and in natural conditions (McNab 1969). The higher basal metabolism may thus be necessary given the differential between ambient and body temperatures (Arends et al. 1995).

VOCALISATIONS: No information available.

HUMAN IMPACT: None in Paraguay where the species has not been recorded since 1939.

CONSERVATION STATUS: Globally considered to be of Low Risk Least Concern by the IUCN, see http://www.iucnredlist.org/apps/redlist/details/1565/0 for the latest assessment of the species. The species is widespread but abundance decreases in the south of the range where the large colonies of tropical regions do not form. Oprea et al (2009) state that misdirected campaigns aiming to control vampire bats represent a general threat to this species which frequently shares its roosts.

The lack of recent Paraguayan records led López-González (2005) to speculate that the species may have disappeared from Paraguay or that its populations may have declined significantly as a result of habitat loss. However capture rates of this species are often reported to be low (Zortéa 2003) and the lack of modern records may also be indicative of a lack of sufficient sampling effort.

The timing of the confirmed specimens in Paraguay, being collected from December to March, may perhaps reflect migratory movements associated with temporal inflorescences. Sample size is small and no data is available to support this theory but, coupled with the fact that this species is apparently difficult to catch (Barquez et al 1999) it may explain the scarcity of records.

Sazima et al (1995) note that Atlantic Forest bromeliads, which are a principal food source for this species, are being increasingly sought for their ornamental value in urban landscaping and hence are being illegally removed from their native habitats. They suggest that this may have conservation repercussions both for the bromeliads and their pollinator bat species. Similarly Sazima & Sazima (1987) attributed prolonged visitation rates and attempts to open flower buds of Passiflora mucronata as possibly related to a decline in the flower population as a result of increased urbanisation.

Oprea et al (2009) note that the species is listed as data deficient on most regional conservation lists. The species is perhaps best considered Data Deficient at national level, though it was rated as critically endangered by SEAM (2006) and listed as in danger of extinction by SEAM (2010).

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FIGURE 2 - Geoffroy’s Tailless Bat *Anoura geoffroyi* (©Marco Mello www.casadosmorcegos.org).