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New Genus and Species of Nectar-Feeding Bat from the Atlantic Forest of Southeastern Brazil (Chiroptera: Phyllostomidae: Glossophaginae)

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ABSTRACT

The lowland Atlantic Forest of southeastern Brazil is well known for its biological diversity and numerous endemic taxa. Among bats collected recently at the Reserva Natural Vale and previously in the Floresta Nacional de Goytacazes, in the state of Espírito Santo, are specimens easily recognized as nectar-feeding glossophagines, but that exhibit a suite of morphological traits that preclude assignment to any of the 10 genera currently recognized in the subfamily Glossophaginae. Here we describe a new genus and species based on this material. This new taxon, named *Dryadonycteris capixaba*, is diagnosed based on both external and craniodental features, including traits not seen in other nectar-feeding phyllostomids, such as similar-sized calcar and foot and inflated maxillary bones. The combination of character states seen in *Dryadonycteris* suggests that it belongs in the Tribe Choeronycterini, subtribe Choeronycterina, but the mosaic nature of primitive and derived states seen in this taxon precludes easy assessment of its relationships to other choeronycterine genera. Future explicit phylogenetic analyses of morphological data and DNA sequencing studies will be necessary to resolve its phylogenetic position within Choeronycterini.

KEYWORDS: Atlantic Forest, endemic, Glossophaginae, morphology, Espírito Santo.

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INTRODUCTION

Specialized nectar-feeding bats, characterized by long and narrow snout, reduced postcanine dentition, and a prolonged and protusible tongue, have evolved independently in both the New World and the Old World (Koopman, 1981; Hill and Smith, 1984; Freeman, 1995). In the Neotropical region, these bats belong to the highly diversified family Phyllostomidae, in which they have been recognized as comprising either a single subfamily (Glossophaginae: Wetterer et al., 2000; Carstens et al., 2002), or, more recently, two independent lineages (Glossophaginae and Lonchophyllinae: Baker et al., 2003; Griffiths and Gardner, 2008; Datzmann et al., 2010; Rojas et al., 2011). According to the latter interpretation, which is strongly supported by molecular sequence data, several shared conspicuous traits associated with nectarivory in these lineages are the result of convergent evolution. Despite considerable morphological convergence, the separate evolutionary pathways of these lineages are marked by unique anatomical modifications related to the process of nectar acquisition. Lonchophyllinae is characterized by a deep groove along each side of the tongue (completely absent in glossophagines), whereas in Glossophaginae the anterior portion of the tongue resembles a “paintbrush” consisting of numerous long hairlike papillae with filamentous tips (in lonchophyllines hairlike papillae are present but have conical tips and are distributed in a few lines; Griffiths and Gardner, 2008). Additionally, lonchophyllines are the only nectar-feeding bats in which the inner and outer upper incisors differ markedly in size, a feature that facilitates their recognition and differentiation from glossophagines even under field conditions.

Ten genera are currently recognized within Glossophaginae sensu stricto: *Anoura*, *Choeroniscus*, *Choeronycteris*, *Glossophaga*, *Hylonycteris*, *Leptonycteris*, *Lichonycteris*, *Monophyllus*, *Musonycteris*, and *Scleronycteris* (Simmons, 2005; Griffiths and Gardner, 2008). Most of these are monotypic or include only a few described species, with *Anoura* (10 species) as a notable exception (Mantilla-Meluk and Baker, 2010). More than in other phyllostomid subfamilies, dental formula is paramount for taxonomic identifications among glossophagine genera. The dentition in this group ranges from 26 to 34 teeth, with incisors and molars most frequently varying in number (Griffiths and Gardner, 2008). Other striking differences among genera include differences in banding pattern of dorsal fur (bicolored versus tricolored), level of posterior insertion of the plagiopatagium, relative size of foot and calcar, presence and development of the tail and uropatagium, development of the zygomatic arch, and morphology of the pterygoids (Wetterer et al., 2000; Griffiths and Gardner, 2008).

Recent fieldwork conducted at a lowland rainforest site in southeastern Brazil resulted in the collection of three glossophagine species, two of which, *Anoura geoffroyi* and *Glossophaga soricina*, are common and widespread (Griffiths and Gardner, 2008). The third species, however, exhibits a unique combination of characters that does not allow inclusion in any of the previously described genera of nectar-feeding bats. A review of material from the same region allowed us to place in this new taxon a third specimen, which was collected in 1977 but previously identified as *Choeroniscus minor* in faunal reports (i.e., Peracchi and Albuquerque, 1993; Peracchi et al., 2011a). Herein, these three specimens are described as a new genus and species.

MATERIAL AND METHODS

STUDY SITE

The two recently collected specimens here assigned to a new genus and species were captured at the Reserva Natural Vale, a private protected natural area with most of its 22,000 ha located in the municipality of Linhares, in the north of the state of Espírito Santo, southeastern Brazil (fig. 1). This reserve is half of a larger forest fragment whose other half consists of the Reserva Biológica de Sooretama. A federal road—BR 101—separates the two reserves. Together, these reserves harbor ca. 45,000 ha of forest and represent the largest remnant of Atlantic Forest located north of 22° S latitude (SOSMA and INPE, 2011). These reserves are covered by *tabuleiro* (tableland) forests, a particular type of Atlantic Forest vegetation that evolved in association with Tertiary (Pliocene) sediments of the Barreiras series (Joly et al., 1990; Rizzini, 1997; Peixoto et al., 2002, 2008). This group of geological formations extends to the Amazon Basin, which, in part, explains the similarities between the *tabuleiro* forests and the terra firme forests of the Amazon Basin (Rizzini, 1997). These affinities were expressed by Heinsdijk et al. (1965) and Andrade-Lima (1966), who referred to the *tabuleiro* forests, respectively, as tall terra firme forest and *hiléia baiana*. Many plant genera and some tree species are shared between these forests (Peixoto and Gentry, 1990; Peixoto et al., 2002). In terms of species richness of trees, the *tabuleiro* forests are also considered the richest forest formation in the Atlantic Forest (Peixoto et al., 2002). Phyto-geographically, the *tabuleiro* forests found at the Reserva Natural Vale have been classified as semideciduous seasonal forest (Peixoto and Gentry, 1990; Massad et al., 2011).

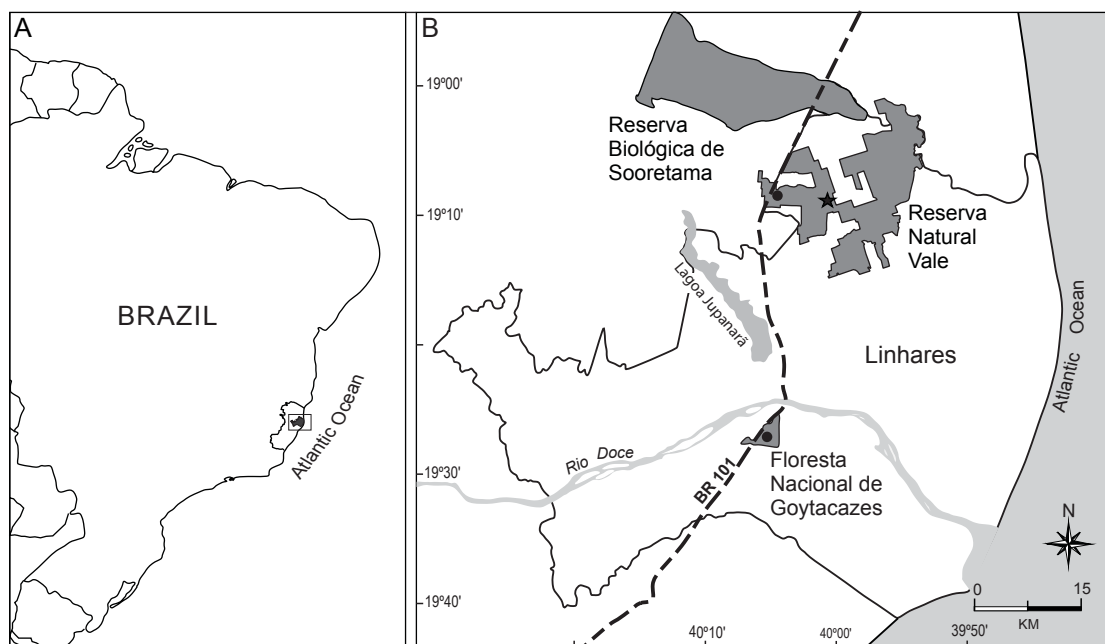


FIGURE 1. Map showing the municipality of Linhares in the northern part of the state of Espírito Santo in southeastern Brazil (A), and the collecting sites of *Dryadonycteris capixaba* at the Reserva Natural Vale and Floresta Nacional de Goytacazes (B). The symbols mark the collecting localities of the holotype (filled star) and paratypes (filled circles).

The third specimen of the new genus and species of nectar-feeding bat was collected at the Floresta Nacional de Goytacazes, a 1400 ha federal reserve located about 30 km south the Reserva Natural Vale, on the right bank of the Rio Doce, also in the municipality of Linhares (fig. 1). The forest at this reserve, recognized as alluvial semideciduous seasonal forest, is developed on fluvial sediments of Holocene origin, but is floristically similar to the tabuleiro forests at Reserva Natural Vale. Dozens of species found at the Floresta Nacional de Goytacazes and on adjacent alluvial floodplain areas of the Rio Doce are rare and probably endemic to the Atlantic Forest (Rolim et al., 2006). The climate in the municipality of Linhares is tropically warm and wet (Aw in the Köppen's classification), with a drier season from May to August and an annual mean precipitation of 1277 mm (Nóbrega et al., 2008). Data from the Reserva Natural Vale indicate an annual mean temperature of 23.3° C (mean minimum temperature, 14.8° C; mean maximum temperature, 34.2° C) (Jesus and Rolim, 2005).

DATA ACQUISITION

All specimens whose measurements are provided here were considered adults based on epiphyseal fusion of the manual phalanges and metacarpals, and complete closure of basicranial sutures. Hair and ear length were measured with a ruler, and other linear measurements were taken with digital calipers. Measurements of the head and body, tail, foot, and ear of the holotype were taken prior to the preparation of the specimen as skin and skull. Data on hair length and pelage coloration of the two fluid-preserved specimens of the new bat were recorded by briefly drying the carcasses. Tooth morphology was described using the terminology applied by Phillips (1971). Our measurement protocol, presented below, is based on Simmons and Voss (1998) with some modifications.

Total length (ToL) – from the tip of the snout to the distal tip of the tail.

Tail length (TaL) – from the base of the tail where it originates on the body to the distal tail tip.

Hindfoot length (HFL) – from the anterior edge of the base of the calcar, at its junction with the tibia, to the tip of the claw of the longest toe.

Calcar length (CL) – from the ventral point of the junction of the calcar with the tibia to the distal tip of the calcar.

Ear length (Ear) – from the notch to the distal tip of the pinna.

Tibia length (TiL) – from the proximal end of the tibia where it articulates with the femur to its distalmost point at the junction with the calcar.

Forearm length (FAL) – from the elbow (tip of the olecranon process) to the wrist, including the carpals (measurement taken with the wing folded).

Thumb length (ThL) – from the metacarpal-phalangeal joint to the tip of the claw.

Metacarpal length (ML–III, IV, and V) – from the proximal end of the bone where it articulates with the carpals to the center of its articulation with the first phalanx (measurement taken with the wing folded).

Phalangeal length (PL) – from the proximal to the distal end of the phalanx; in the case of the first phalanx (1PL) and the proximal end of the second phalanx (2PL), the centers of articulation with adjacent bones were used as reference points.

Greatest length of the skull (GLS) – from the anteriormost point of the premaxillae (excluding the incisors) to the posteriormost point of the cranium.

Condylolincisive length (CIL) – from the anteriormost point of the upper inner incisors to the posteriormost point on the occipital condyles.

Condyllocanine length (CCL) – from the anteriormost point on the upper canines to the posteriormost point on the occipital condyles.

Postorbital constriction breadth (POC) – least breadth across the frontals posterior to the postorbital processes or bulges.

Braincase breadth (BB) – greatest breadth of the globular part of the braincase.

Mastoid breadth (MB) – greatest cranial breadth across the mastoid region.

Maxillary tooththrow length (C-M) – from the anteriormost edge of the crown of the upper canine to the posteriormost edge of the crown of the last upper molar.

Breadth across molars (BAM) – greatest breadth across the outer edges of the crowns of the upper molars.

Breadth across canines (BAC) – greatest breadth across the outer edges of the crowns of the upper canines (taken with the caliper perpendicular to the longitudinal axis of the skull).

Mandibular length (MaL) – from the anteriormost point (excluding the incisors) to the posteriormost point (angular process or mandibular condyle).

Mandibular tooththrow length (c-m) – from the anteriormost edge of the crown of the lower canine to the posteriormost edge of the crown of the last lower molar.

Our comparative analyses included material from all genera currently recognized in the subfamily Glossophaginae (sensu Baker et al., 2003, and Griffiths and Gardner, 2008) plus specimens of the genus *Lonchophylla* (subfamily Lonchophyllinae; sensu Baker et al., 2003, and Griffiths and Gardner, 2008) (see appendix). This material is deposited in the following institutions (names followed by acronyms used in the appendix): American Museum of Natural History, New York (AMNH); Museu Nacional, Universidade Federal do Rio de Janeiro, municipality of Rio de Janeiro, Brazil (MN); Museu Paraense Emílio Goeldi, Pará, Brazil (MPEG); National Museum of Natural History, Washington, D.C. (USNM); and Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil (ALP – Coleção Adriano Lúcio Peracchi). Comparative information gained from direct examination of specimens was supplemented by literature accounts (e.g., Phillips, 1971; Carter and Dolan, 1978; Koopman, 1994; Reid, 1997; Wetterer et al., 2000; Carstens et al., 2002; LaVal and Rodriguez-H., 2002).

SYSTEMATICS

Family Phyllostomidae Gray, 1825

Subfamily Glossophaginae Bonaparte, 1845

Dryadonycteris capixaba, gen. and sp. nov.

Figures 2–9, tables 1–3

HOLOTYPE: An adult female (fig. 2), preserved as skin and cleaned skull, deposited at the Coleção Adriano Lúcio Peracchi (ALP 9667), in the Laboratório de Mastozoologia of the Uni-

versidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil. It was collected on June, 3, 2011, by Adriano L. Peracchi, Marcelo R. Nogueira, Isaac P. Lima, and Paulo Cesar at the Estrada Oiticica (19°09'17" S and 40°00'18" W), Reserva Natural Vale, in the municipality of Linhares, state of Espírito Santo, southeastern Brazil (field number AP 2847). Liver tissue is preserved in ethanol at the Coleção Adriano Lúcio Peracchi. Skull and mandible in good condition, but the left upper canine and the left first premolar are both missing, the anterolabial portion of the left first upper molar is broken, and the distal portion of both pterygoids is broken.

PARATYPES: Two adult males, both also collected in the municipality of Linhares. The first specimen was collected on December 15, 1977, at the Floresta Nacional de Goytacazes (fig. 1) (19°25'51" S and 40°04'20" W) by Adriano L. Peracchi, Sila T. Albuquerque, Sansão D.L. Raimundo, and Onézimo F. Fraga (field number AP 1782). It is a dried skin with skull, initially deposited at the Coleção Adriano Lúcio Peracchi, under the number ALP 3268, but now incorporated into the mammal collection of the Museu Nacional, Universidade Federal do Rio de Janeiro, municipality of Rio de Janeiro, Brazil, under the accession number MN 78305. The skin is in good condition (except for some patches lacking fur on the ventral region), but the skull is



FIGURE 2. Right oblique view of the head of *Dryadonycteris capixaba* (holotype, ALP 9667), from Reserva Natural Vale, municipality of Linhares, northern state of Espírito Santo, southeastern Brazil.

in poor condition: the basicranium, the occipital region, and the left basal portion of the braincase are broken. The mandible is represented only by the left dentary, in which the ascending ramus is missing. The second specimen is preserved in fluid, with skull removed and cleaned, and was deposited at the Coleção Adriano Lúcio Peracchi under the number ALP 9599. It was collected on November 9, 2010, at 22:30 hours, by Isaac P. Lima (field number IPL 1285). The skull and mandible are in perfect condition, and the tongue is preserved separately in fluid. A photograph of this specimen appeared in Peracchi et al. (2011b: 166) under the name *Choeroniscus minor*.

TYPE LOCALITY: Brazil, state of Espírito Santo, municipality of Linhares, Reserva Natural Vale, 19°08'29" S and 40°04'08" W, approximately 60 m elevation.

ETYMOLOGY: In the first phytogeographic system proposed for Brazilian vegetation, the 19th-century German naturalist Karl Friedrich Philipp von Martius ascribed names of nymphs from Greek mythology to each of the major provinces he described (Martius, 1824). To the province we now recognize as Atlantic Forest, he gave the name "Dryades" (from the Greek *Dryas*, a wood nymph) for the immortal nymphs of the forest. The generic epithet proposed here means, therefore, "bat from Dryades," hence "bat from the Atlantic Forest," in reference to the endemic character of this taxon. The species name *capixaba*, a noun in apposition, is from the Tupi language and designates natives from the state of Espírito Santo.

DESCRIPTION: Body size small (forearm 29–32 mm; tables 1–2) for a Glossophaginae and for bats in general; muzzle elongated, but shorter than braincase; mandibular prognathism evident; spear of noseleaf nearly triangular (3 mm wide \times 3.38 mm tall in the fluid paratype) with no central rib; internarial region with narrow, unbeaded ridge along midsagittal line; horseshoe of noseleaf continuous with upper lip with no ridges or other structures separating it from lip; lateral edges of horseshoe confluent with face inferiorly, but with superior edge free; dorsal snout with pair of well-developed padlike papillae separated from each other and located just behind noseleaf; two columns of vibrissae present at each side of snout, lateral to noseleaf, the more anterior with its two vibrissae standing entirely on the padlike papilla, and the more posterior with three of its four vibrissae standing on this pad (the lowest vibrissa stands on its own smaller pad); anterior half of the upper lip, at each side of mouth, also ornamented with well-developed vibrissae, five of which are nearly evenly distributed in an irregular line parallel to lip, beginning close to posterior border of the large padlike papilla described above, and one located just above the more posterior of these vibrissae; one genal vibrissa present halfway between the corner of the mouth and the base of the ear notch; chin with deep central cleft and with a pair of narrow, scalloped dermal pads, one on each side of the cleft; two interramal vibrissae located posterior to the chin cleft; chin skin adjacent to the cleft, along each side of the mandible, ornamented with five well-developed vibrissae arranged, from anterior to posterior region, in a 1-2-1-1 scheme (additional, smaller vibrissae also present); ears small, with rounded distal tip, strongly convex inner margin, and outer margin nearly straight; tragus about one third the length of the pinna, spatulate in form, noticeably thicker medially, thinner and translucent laterally, bearing a basal expansion with a lobule on its upper margin that is folded posteriorly; forearm with basal two-thirds covered with fur on both the dorsal and ventral surfaces; metacarpal and proximal phalange of thumb nearly equal in length; metacar-

TABLE 1. Selected external and craniodental measurements¹ of a female *Dryadonycteris capixaba* (holotype) from the municipality of Linhares, state of Espírito Santo, southeastern Brazil, and comparative data from females of related species from Venezuela (Soriano et al., 2005), French Guiana (Simmons and Voss, 1998), Pará, in northern Brazil (USNM 239520 – holotype, from Swanepoel and Genoways, 1979; MPEG 1251), and Bahia, in northeastern Brazil (Taddei and Pedro, 1993).

	<i>Dryadonycteris capixaba</i>	<i>Choeroniscus minor</i>	<i>Lichonycteris degener</i>			
	SE Brazil	French Guiana	Venezuela	N Brazil		NE Brazil
	ALP 9667		CVULA I-2650	USNM 239520	MPEG 1251	
Weight	5.0	9.8 (8.0–12.0) 7	—	—	7.2	—
ToL	56.4	68.1 (65.0–70.0) 7	—	—	—	—
TaL	6.3	7.8 (6.0–9.0) 7	—	—	8.9	—
HFL	8.3	9.0 (9.0–9.0) 7	—	—	—	—
CL	8.0	—	—	—	—	—
Ear	10	12.3 (8.0–13.0) 7	—	—	8.0	—
FL	32.3	34.3 (33.0–36.0) 6	32.3	—	34	34
TiL	10.13	—	—	—	—	—
ThL	4.86	—	—	—	—	—
ML-III	33.3	—	—	—	—	—
1PL-III	13.4	—	—	—	—	—
2PL-III	15.9	—	—	—	—	—
ML-IV	30.9	—	—	—	—	—
1PL-IV	9.7	—	—	—	—	—
2PL-IV	10.2	—	—	—	—	—
ML-V	28.7	—	—	—	—	—
1PL-V	7.6	—	—	—	—	—
2PL-V	9.7	—	—	—	—	—
GLS	20.2	23.36 (22.62–23.99) 7	19.38	18.8	17.06	19.3
CiL	19.8	—	—	—	16.43	—
CCL	19.08	—	—	—	16.02	—
C-M	6.81	8.08 (7.87–8.46) 7	6.27	6.0	5.37	6.3
BB	7.75	8.59 (8.41–8.94) 7	8.22	7.9	8.05	8.2
MB	8.25	8.59 (8.44–9.07) 7	8.19	—	8.06	8.5
POC	3.95	—	4.01	3.8	3.66	3.9
BAM	4.05	4.25 (3.96–4.39) 7	4.29	4.2	—	4.7
BAC	—	4.14 (3.74–4.4) 6	—	—	3.6	—
MaL	14.29	—	—	—	11.95	13
c-m	7.02	—	—	—	5.66	—

¹Weight (body mass) is reported in grams; other measurements in millimeters. Measurements of multiple individuals are presented as follows: mean (minimum–maximum) number of individuals.

TABLE 2. Selected external and craniodental measurements¹ of male *Dryadonycteris capixaba* (paratypes) from the municipality of Linhares, state of Espírito Santo, southeastern Brazil, and comparative data from males of related species from French Guiana (Simmons and Voss, 1998), and from Minas Gerais (Aguilar et al., 1995) and Espírito Santo (MZUSP 2253, Zortéa et al., 1998), in southeastern Brazil.

	<i>Dryadonycteris capixaba</i>		<i>Choeroniscus minor</i>	<i>Lichonycteris degener</i>	
	SE Brazil		SE Brazil	French Guiana	SE Brazil
	ALP 9599	MN 78305			MZUSP 2253
Weight	5	4.1	—	8.0 (7.0–8.8) 4	—
ToL	49.9	50.6	—	63.8 (61.0–68.0) 4	—
TaL	6.4	4.4	—	8.0 (7.0–9.0) 4	—
HFL	7.8	7.5	—	9.1 (8.5–10.0) 4	—
CL	7.3	7.8	—	—	—
Ear	10	9	—	12.3 (12.0–12.5) 4	—
FL	29.1	30.5	29.5 (28.6–30.4) 5	34.3 (33.0–35.0) 4	35.3
TiL	7.1	10.0	11.6 (11.2–11.8) 5	—	—
ThL	4	4.0	—	—	—
ML–III	30.8	31.4	30.9 (29.2–32.2) 5	—	—
1PL–III	12.1	12.1	12.1 (11.3–12.6) 5	—	—
2PL–III	15.3	15.3	15.2 (14.4–15.7) 5	—	—
ML–IV	28.0	29.0	29.0 (27.1–30.0) 5	—	—
1PL–IV	8.2	8.2	8.5 (7.9–9.0) 5	—	—
2PL–IV	9.7	10.4	9.1 (8.6–9.9) 5	—	—
ML–V	27.4	27.3	27.2 (26.0–27.8) 5	—	—
1PL–V	6.8	7.4	7.5 (6.9–8.1) 5	—	—
2PL–V	9.3	9.7	9.2 (8.5–10.0) 5	—	—
GLS	19.58	—	—	22.19 (21.76–22.36) 4	—
CIL	18.99	19.05	—	21.76 (21.16–21.85) 4	—
CCL	18.3	18.41	18.0 (17.8–18.2) 3	—	—
C-M	6.18	6.28	6.3 (6.1–6.4) 3	7.74 (7.50–7.99) 4	5.5
BB	7.66	7.71	7.5 (7.3–7.6) 3	8.65 (8.50–8.87) 4	9.2
MB	7.89	—	7.7 (7.7–7.8) 3	8.40 (8.22–8.62) 4	—
POC	4.29	3.86	4.0 (3.9–4.1)	—	4.3
BAM	4.1	4.05	3.7 (3.7–3.7) 2	4.08 (3.98–4.25) 3	4.3
BAC	3.3	3.45	3.0 (3.0–3.0) 3	3.92 (3.75–4.00) 4	—
MaL	13.95	—	13.1 (12.9–13.2) 2	—	—
c-m	6.27	6.5	6.5 (6.5–6.5) 2	—	—

¹Weight (body mass) is reported in grams, other measurements in millimeters. Measurements of multiple individuals are presented as follows: mean (minimum–maximum) number of individuals.



FIGURE 3. Dorsal fur (A) and palmar view of left hind foot (B) of *Dryadonycteris capixaba* (holotype, ALP 9667). Note the tricolored banding pattern of the fur and the nearly equal length of the foot relative to the length of the calcar.

pal formula $V < IV < III$; plagiopatagium dark brown and inserted at the base of toes (fig. 3); uropatagium relatively long (15 mm at midline), dark brown, bearing sparse, short hairs on dorsal surface and on upper one-third of ventral surface, and naked along its posterior border (no fringe of hairs); calcar length nearly equal to that of foot (fig. 3); tail short (6.50 mm); dorsal fur about 7 mm long on upper back, tricolored, with pale brown base, wide beige middle band, and narrow dark brown band distally (fig. 3); dorsal fur with additional pale frosting at tips; ventral fur on upper chest similar to dorsal fur in both length and banding pattern, but distal band similar in color to basal band, leading to a slightly paler general ventral appearance to the bat (brown venter versus dark brown in the dorsum).

Skull (figs. 4–5) with rostrum shorter than braincase; rostrum gently tapering anteriorly to a marked constriction at level of P4, then expanded in an unusual, autapomorphic inflation of anterior portion of maxillary bones (less developed in males); postorbital constriction present in the female (holotype), but poorly developed or absent in males (paratypes); premaxillae relatively well developed and with two circular and small midline foramina, the more posterior of which is small and located between antero-internal margin of incisive foramina; orbital portion of frontal marked by five diagonal lines marking the internal insertion points of nasal turbinates; braincase oval in dorsal view and low in lateral view; sagittal crest absent, but lambdoidal crests developed; anterior border of foramen magnum V-shaped; basisphenoid pits shallow and separated by low and wide septum; palate almost flat from premaxillae to the level of P3, then concave until the end of anterior portion of palate (just behind the dentition); posterolateral border of palate, behind molars, concave; posterior (interorbital) palate long and with U-shaped posterior border; pterygoid wings short, not touching the tympanic bulla (visible only in the paratypes; wings broken in holotype); presphenoid with a central ridge; basisphenoid smooth except for a small central ridge at junction with the wide interbasiooccipital septum; zygomatic arches incomplete, small anterior projection of the zygoma turned upward.

Dentary (fig. 4) long and delicate; anterior extremity of dentary projected well beyond canines, but in the same plane with the body of the dentary (not downturned ventrally); mandibular condyle and coronoid process extend dorsally to approximately the same level above the dentary; angular region with discrete angular process at posterior extremity and no ventral projection (as a consequence, the ventral margin of the ascending ramus forms an almost straight line with the body (tooth-bearing portion) of the mandible).

Dentition (figs. 5–6) with dental formula $I\ 2/0$, $C\ 1/1$, $P\ 2/3$, $M\ 3/3 \times 2 = 30$; upper incisors small, inner pair mesiodistally wider than outer and with flat crowns; outer incisors varying from pointed to peglike (variation probably related to wear); both upper incisor teeth completely visible in lateral view; upper canines delicate, laterally compressed, with flat anterior face, and strongly recurved posterior edge; lingual surface of upper canines slightly concave, whereas anterior surface lacks any longitudinal ridge or groove; posterior accessory cusp of upper canines poorly developed or absent; upper canines laterally bowed (more conspicuous in holotype than paratypes); two upper premolars, the second (P4) larger than first (P3) in anteroposterior length (0.79 versus 0.65 mm in the holotype) and also slightly higher; P3 with anterior and posterior cuspules usually absent or, when present, poorly

developed; P4 similar to P3 with respect to presence and development of cusps, but posterior crest of P4 protocone longer and less steeply inclined than anterior crest; both P3 and P4 laterally compressed; M1 and M2 greater in mesiodistal length than M3; all upper molars relatively similar in structure, with parastyle as main cusp, paracrista, paracone, and post-paracrista (= precentrocrista of Philips, 1971) either reduced to a single low ridge (holotype) or with poorly defined, anteriorly displaced paracone (paratypes); precentrocrista runs toward lingual side of tooth almost parallel to the labial margin of the tooth, so that the anterior half of the W-shaped ectoloph essentially is not discernible; anterolabial portion of right M1 in the holotype (the left is broken) with an anterior basal projection or shelf that is absent in both M1s of paratypes; anterolabial portion of M3 retaining a nearly triangular shape, with paracone always present and not anteriorly displaced as in M1 and M2 of paratypes; posterolabial portion of all upper molars less laterally compressed than the anterior one and also retaining a nearly triangular shape typical of the ectoloph dentition (poorly defined in MN 78305, but clear in the holotype); metacone conspicuous on all upper molars,



FIGURE 4. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of specimens of *Dryadonycteris capixaba* (holotype, ALP 9667, on the left; paratype ALP 9599, on the right) (scale bar = 5 mm).

but mesostyle and metastyle variable in development (both conspicuous in the holotype, but less developed or reduced to a low ridge in paratypes); protocone relatively low, but present on all upper molars and connected to the base of metacone via postprotocrista; hypocone and hypoconal shelf absent.

Lower incisors absent; lower canines simple and small, straight and not recurved in lateral view, straight at outer margin and slightly recurved internally in anterior view, with poorly developed cingular shelf on the posterior side of the tooth; first lower premolar (p2) characterized by a low central cusp, only slightly higher than anterior and posterior styler cusps, which are also poorly developed; p2 with lingual outline concave in occlusal view (more pronounced in the holotype); second lower premolar (p3) with central cusp conspicuously higher than anterior and posterior styler cusps, both of which are better developed than those on first premolar; third lower premolar (p4) with the main cusp similar in size to the main cusp of p3, and with posterior crest dorsoventrally compressed and ending in a conspicuous posterior cuspule; degree of slope of anterior crest of the primary cusp of p4 varying from steep (anterior style visible; ALP 9599) to more gradual in most specimens (no anterior style visible); the three lower molars are laterally compressed, but retain all typical cusps; first two lower molars (m1 and m2) similar in mesiodistal length and slightly longer than m3; metaconid is the most prominent cusp in the lower molars; m1 with paralophid (connecting paraconid and protoconid) higher than on other molars; metacristid (connecting paraconid and metaconid) low on all molars; hypoconid and entoconid low but distinct; hypoconulid absent.

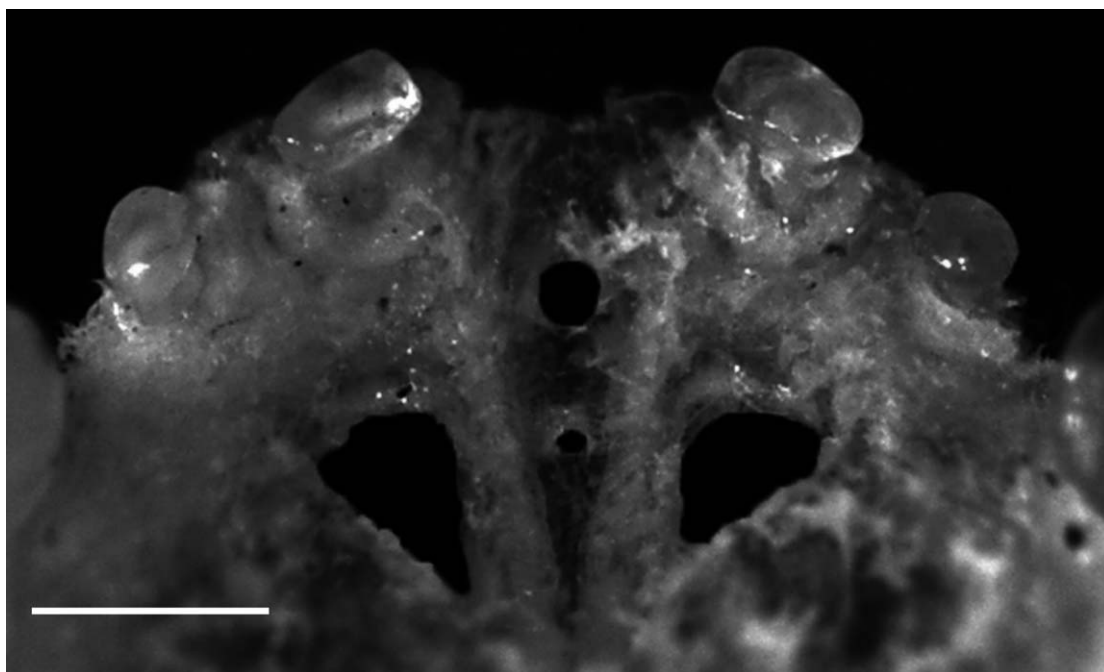


FIGURE 5. Occlusal view of the well-developed premaxillae and upper incisors of *Dryadonycteris capixaba* (holotype, ALP 9667). Note the presence of two small foramina between the premaxillae (scale bar = 0.5 mm).

Multiple diastemata present in both upper and lower dentitions; upper incisors clearly separated by a wide median gap; diastema between inner and outer upper incisors slightly smaller than that between outer incisor and canine, which is about the same size as the mesio-distal length of inner incisor; both P3 and P4 widely separated from adjacent teeth; distance between canine and P3 large, similar to anteroposterior length of canine; diastema between P3 and P4 similar to anteroposterior length of P3; diastema between P4 and M1 similar to that between P3 and P4; three upper molars separated by conspicuous diastemata, the second (between M2 and M3) smaller than the first; first lower premolar (p2) separated from canine by a small diastema (usually smaller than those separating the lower premolars from each

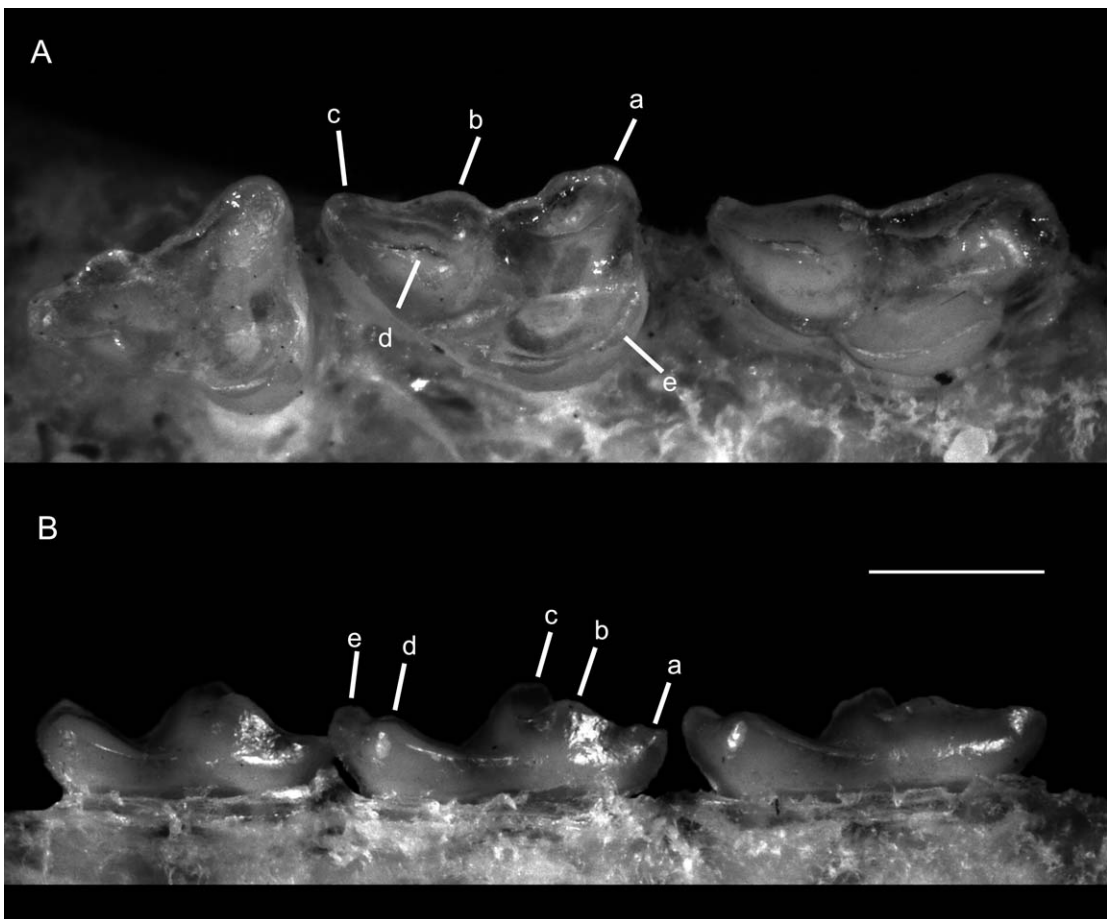


FIGURE 6. Oblique occlusal view of the upper molars (A) and lateral labial view of the lower molars (B) of *Dryadonycteris capixaba* (holotype, ALP 9667). Cusps indicated in the second upper molar are as follows: parastyle (a), mesostyle (b), metastyle (c), metacone (d), and protocone (e). In the second lower molar, cusps are as follows: paraconid (a), protoconid (b), metaconid (c), hypoconid (d), and entoconid (e). Note the absence of a distinct paracone on the upper molars. This trait is variable in *Dryadonycteris*, with the paratypes exhibiting somewhat better development of this cusp (see text for discussion) (scale bar = 0.5 mm).

other); m1 separated from m2 by a conspicuous gap, and m2 separated from m3 by a small gap or in contact with this latter tooth (holotype).

COMPARISONS AND DIAGNOSTIC TRAITS: *Dryadonycteris capixaba* can be easily differentiated from all other described Neotropical nectar-feeding bats on the basis of external and craniodental morphology (table 3). The absence of lower incisors is shared only with members of the tribe Choeronycterini (sensu Baker et al., 2003), to the exclusion of all Lonchophyllini (*Lionycteris*, *Lonchophylla*, *Platalina*, and *Xeronycteris*) and Glossophagini (*Glossophaga*, *Monophyllus*, and *Leptonycteris*). Within the tribe Choeronycterini, two subtribes were recognized by Baker et al. (2003): Anourina and Choeronycterina. The former includes only the genus *Anoura*, from which *Dryadonycteris* is promptly differentiated by its long uropatagium and tail. *Dryadonycteris* is also distinguished from *Anoura* by morphology of the upper part of the lateral edges of the horseshoe, which are free from the face in *Dryadonycteris* instead of being confluent with skin of the face as in *Anoura*. In this respect *Dryadonycteris* resembles members of the subtribe Choeronycterina (data not available for *Scleronycteris*) (Wetterer et al., 2000). Among the seven genera currently recognized as comprising Choeronycterini, *Musonycteris* and *Choeronycteris* are remarkably different and are easily distinguished from all other genera, including *Dryadonycteris*, by virtue of possessing greatly elongated rostra that are approximately equal to or longer than their respective braincases (fig. 7). This character results in a very long muzzle in *Musonycteris* and *Choeronycteris*, which contrasts with the moderately long muzzle of *Dryadonycteris* (rostrum shorter than braincase). Externally, *Dryadonycteris* is also differentiated from *Musonycteris* and *Choeronycteris*, as well as from *Choeroniscus* and *Scleronycteris*, by the color banding pattern of dorsal fur. *Dryadonycteris* shares exclusively with *Lichonycteris* and *Hylonycteris* a tricolored fur pattern, i.e., each hair has a pale middle band and darker basal and distal bands. The condition present in most glossophagines and lonchophyllines is a bicolored pattern in which each hair has a pale base and a dark tip (Wetterer et al., 2000; Carstens et al., 2002). A tricolored dorsal pelage is also found in other genera of Phyllostomidae, but only outside the lineages of specialized nectar-feeding bats (e.g., *Carollia*). It must be noted, however, that the basal band in the dorsal fur of *D. capixaba* is paler than the distal band, which leads to a less visible contrast between the two basal bands. This is similar to the condition reported for *Hylonycteris* (Reid, 1997), while the prevalent condition in *Lichonycteris* is a more clearly tricolored pattern (Reid, 1997). A particular caution is, therefore, necessary when analyzing this character, particularly under field conditions.

Dryadonycteris capixaba has calcar and foot subequal in length, which departs from the condition reported for all other glossophagines and lonchophyllines, in which the calcar is shorter than the foot (Wetterer et al., 2000; Carstens et al., 2002). Additionally, in most glossophagines the insertion of the posterior edge of the plagiopatagium occurs at the ankle, whereas in *Dryadonycteris* it extends distally to the base of the toes. This latter condition is also found in *Lichonycteris* (Reid, 1997; LaVal and Rodriguez-H., 2002), which is the genus most prone to be externally confused with *Dryadonycteris*. The similarity between *Dryadonycteris*

TABLE 3. Characters Distinguishing Genera of the Tribe Choeronycterini¹

	<i>Anoura</i>	<i>Choeromiscus</i>	<i>Choeronycteris</i>	<i>Dryadonycteris</i>	<i>Hylonycteris</i>	<i>Lichonycteris</i>	<i>Musonycteris</i>	<i>Scleronycteris</i>
Forearm length	33–48 mm	28.6–42 mm	42–47 mm	29–32 mm	31–37 mm	31–35.5 mm	40–43 mm	34.5–35.5 mm
Body weight²	8.5–23 g	5–13 g	14–19 g	4–5 g	6–12 g	6–10.5 g	6–12.6 g	9 g ³
Lateral edges of horseshoe	Confluent with face along entire length	Confluent with face inferiorly, superior edge free	Confluent with face inferiorly, superior edge free	Confluent with face inferiorly, superior edge free	Confluent with face inferiorly, superior edge free	Confluent with face inferiorly, superior edge free	Confluent with face inferiorly, superior edge free	Data not available
Dorsal fur	Bicolored	Bicolored	Bicolored	Tricolored	Tricolored	Tricolored	Bicolored	Bicolored
Plagiopatagium insertion	At ankle	At ankle	At ankle	At base of toes	At ankle	At base the toes	At ankle	At ankle
Uropatagium	Virtually absent or narrow	Extends past knees	Extends past knees	Extends past knees	Extends past knees	Extends past knees	Extends past knees	Extends past knees
Calcar	Shorter than foot	Shorter than foot	Shorter than foot	Subequal with foot	Shorter than foot	Shorter than foot	Shorter than foot	Shorter than foot
Rostrum	Shorter than braincase	Shorter than braincase	Subequal to braincase	Shorter than braincase	Shorter than braincase	Shorter than braincase	Shorter than braincase	Shorter than braincase
Premaxilla	Relatively short	Relatively short	Relatively short	Well developed	Relatively short	Relatively short	Relatively short	Relatively short
Foramen (foramina) between premaxillae	1	1	1	2	1	0	1	0
Anterior maxilla	Not inflated	Not inflated	Not inflated	Inflated	Not inflated	Not inflated	Not inflated	Not inflated
Diagonal lines on orbital portion of frontal	Varies from poorly to well developed	Absent	Absent	Well developed	Absent	Absent	Absent	Well developed
Posterior palate	Relatively short	Relatively short	Relatively short	Relatively long	Relatively short	Relatively short	Relatively short	Relatively short

	<i>Anoura</i>	<i>Choeromiscus</i>	<i>Choeromycteris</i>	<i>Dryadomycteris</i>	<i>Hylomycteris</i>	<i>Lichomycteris</i>	<i>Musomycteris</i>	<i>Scleromycteris</i>
Pterygoid wings at distal margin	Not inflated	Inflated	Inflated	Not inflated	Not inflated	Not inflated	Inflated	Not inflated
Mandibular condyle	Lower than coronoid process	Lower than coronoid process	Lower than coronoid process	As high as the coronoid process	Lower than coronoid process	Lower than coronoid process	Lower than coronoid process	Lower than coronoid process
Upper incisor arcade	Relatively straight (I1 obscured by I2 in lateral view)	Relatively straight (I1 obscured by I2 in lateral view)	Relatively straight (I1 obscured by I2 in lateral view)	U-shaped (I1 visible in lateral view)	Relatively straight (I1 obscured by I2 in lateral view)	Relatively straight (I1 obscured by I2 in lateral view)	Relatively straight (I1 obscured by I2 in lateral view)	Relatively straight (I1 obscured by I2 in lateral view)
First lower premolar lingual surface	Flat	Flat	Flat	Concave	Concave	Flat	Flat	Flat
Premolars	3/3	2/3	2/3	2/3	2/3	2/3	2/3	2/3
Molars	3/3	3/3	3/3	3/3	3/3	2/2	3/3	3/3
Paracone	Present	Absent	Absent	Variable	Absent	Variable	Absent	Absent
Mesostyle	Present	Absent	Absent	Variable	Absent	Present but poorly developed	Absent	Present

¹The inclusion of *Dryadomycteris* in the Tribe Choeromycterini is supported by the complete absence of lower incisors. In the glossophagine genera *Glossophaga*, *Lep-
tonycteris*, and *Monophyllus* there are two lower incisors on each side of the mandible.

²Data compiled by Simmons and Wetterer (2002).

³E. Bernard (personal commun.).

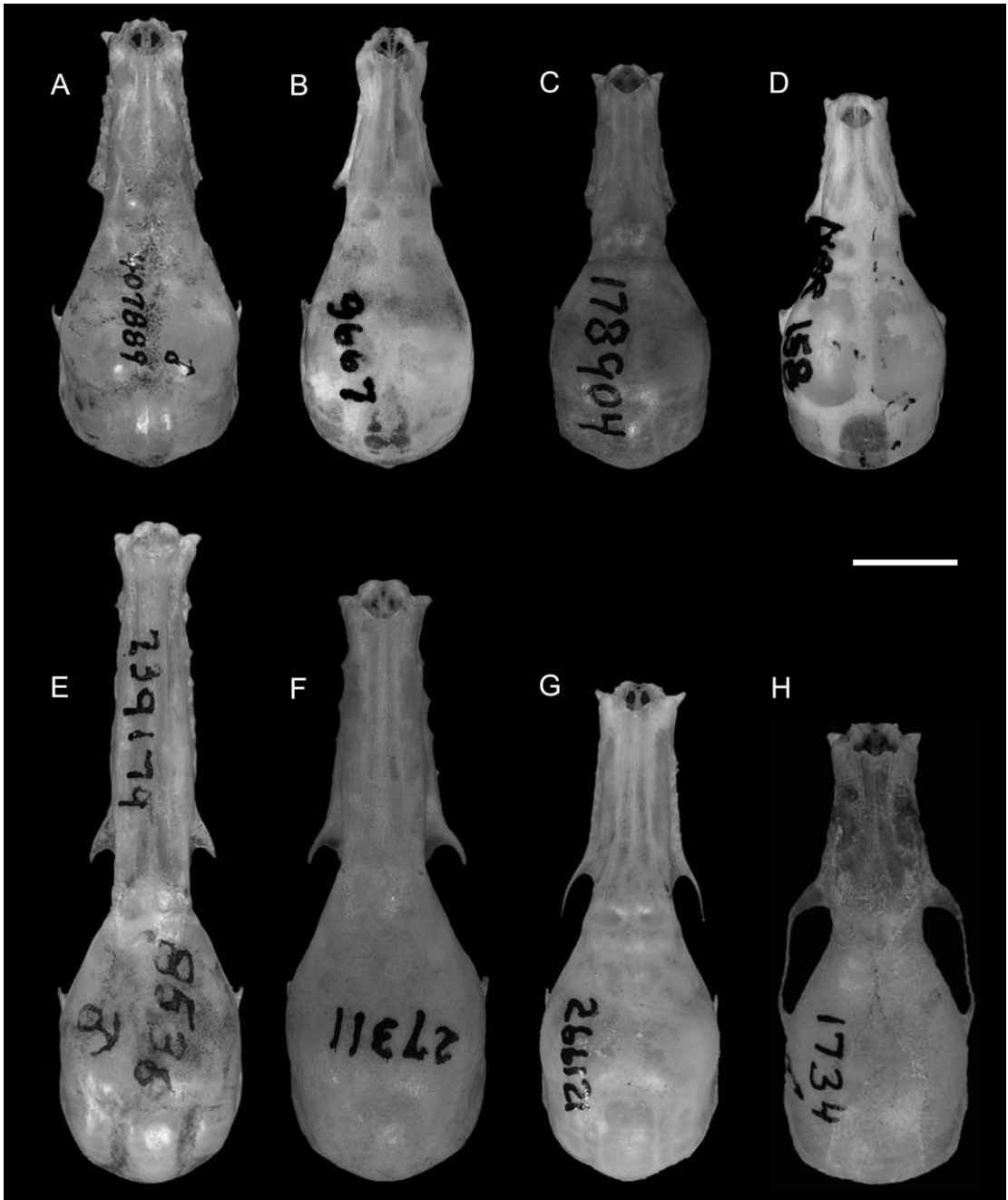


FIGURE 7. Dorsal view of the skull of the choeronycterine bats (A) *Scleronycteris ega* (USNM 407889), (B) *Dryadonycteris capixaba* (ALP 9667), (C) *Hylonycteris underwoodi* (AMNH 178904), (D) *Lichonycteris degener* (ALP 5990), (E) *Musonycteris harrisoni* (AMNH 235179), (F) *Choeronycteris mexicana* (AMNH 27311), (G) *Choeroniscus minor* (AMNH 266121), and (H) *Anoura caudifer* (ALP 1734) (scale bar = 5 mm).



FIGURE 8. Ventral view of the skull of the choeronycterine bats (A) *Scleronycteris ega* (USNM 407889), (B) *Dryadonycteris capixaba* (ALP 9667), (C) *Hylonycteris underwoodi* (AMNH 178904), (D) *Lichonycteris degener* (ALP 5990), (E) *Musonycteris harrisoni* (AMNH 235179), (F) *Choeronycteris mexicana* (AMNH 27311), (G) *Choeroniscus minor* (AMNH 266121), and (H) *Anoura caudifer* (ALP 1734) (scale bar = 5 mm).

and *Lichonycteris* is particularly relevant because these taxa are the same general size and potentially occur sympatrically in the Atlantic Forest of eastern Brazil. *Hylonycteris* is also small sized and has tricolored dorsal fur, but its wings attach to the ankle, its calcar is shorter than its foot, and its known distribution is restricted to Central America.

Though generally similar to *Lichonycteris* in external characters, *Dryadonycteris* is markedly different from this genus in several craniodental features. The most obvious are: rostral length (shorter in *Lichonycteris*) and shape (anteriorly inflated in *Dryadonycteris*, but not in *Lichonycteris*); development of the premaxillae (well developed in *Dryadonycteris*, but not in *Lichonycteris*); position of upper incisors (separated by a wide median gap and convergently positioned in *Dryadonycteris*, versus evenly spaced and forming an almost straight line in *Lichonycteris*); and number of upper molars (only two in *Lichonycteris*, but three in *Dryadonycteris*). Though some of these features will not be evident in the field, we expect that the relatively longer muzzle, well-developed premaxillae, and convergently positioned upper incisors (both outer and inner incisors are visible in lateral view) will prove useful in field identification.

The skull of *Dryadonycteris capixaba* can be promptly differentiated from those of all other glossophagines by its unique inflation of the anterior maxillary bones, anterior to a conspicuous constriction of the rostrum (fig. 7). Among Choeronycterini genera, it is also unique in having well-developed premaxillae (figs. 7, 8), with both inner and outer incisors visible in lateral view (fig. 9). *Dryadonycteris* also has two small foramina on the midline of the premaxillae (in addition to the two larger foramina located more laterally), while in most glossophagines a single foramen is present or, as in the case of *Scleronycteris ega* and *Lichonycteris obscura*, no foramina are present in the midline (fig. 8) (Carstens et al., 2002). The diagonal lines present in the orbital region of *Dryadonycteris* seem to be shared only with *Anoura geoffroyi* and with the rare Amazonian endemic *Scleronycteris ega*, which makes this another character useful for distinguishing the skull of *Dryadonycteris* (fig. 9). In *Anoura caudifer* and *Glossophaga soricina* some lines are present, but they are not developed as in the aforementioned species. The posterior palate in *Dryadonycteris* is proportionally longer than that in all other Choeronycterini, and the pterygoid wings are short and not inflated at the distal margin as is the case in *Choeroniscus*, *Choeronycteris*, and *Musonycteris* (fig. 8).

In *Dryadonycteris* the paracone is subject to individual variation. The holotype lacks a distinct paracone on M1 and M2 (fig. 6), but this cusp is more evident in the paratypes, where it appears as a low cusp adjacent to the parastyle. This type of within-taxon variation in cusp development has also been described for *Lichonycteris* (Phillips, 1971). In contrast, the paracone is uniformly absent in *Scleronycteris*, *Choeroniscus*, *Hylonycteris*, *Choeronycteris*, and *Musonycteris* (Phillips, 1971), and it is uniformly present in *Anoura*, which retains a conspicuous W-shaped ectoloph in the upper molars. The mesostyle is another character that is typically informative regarding the evolution of Choeronycterini, as it is present in *Anoura* and *Scleronycteris*, poorly developed in *Lichonycteris*, and absent in *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris* (Phillips, 1971; Jones and Carter, 1976; Koopman, 1994). In this respect, the female of *Dryadonycteris capixaba* (holotype; fig. 6) described here is more similar

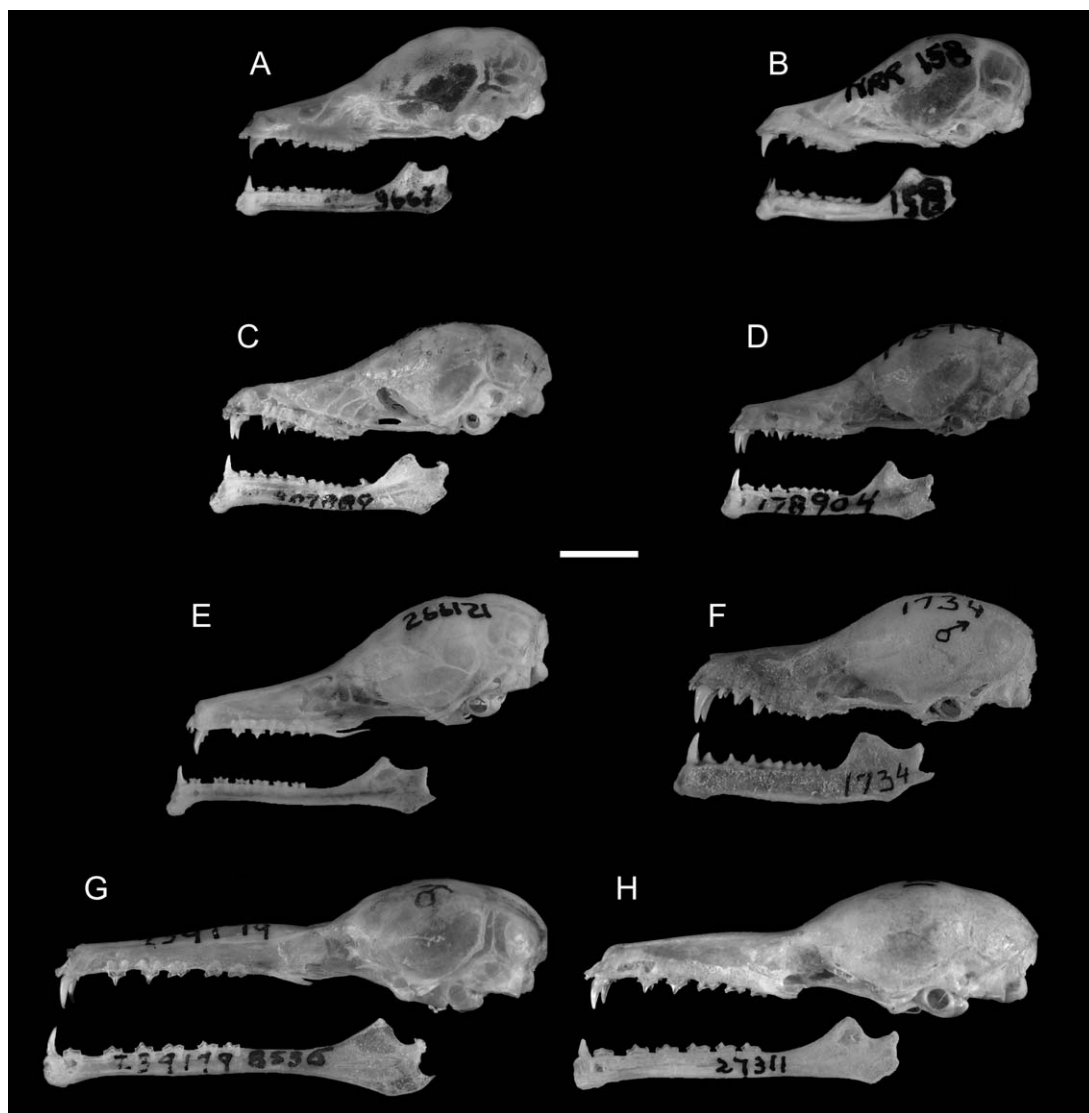


FIGURE 9. Lateral view of the skull and mandible of the choeronycterine bats (A) *Dryadonycteris capixaba* (ALP 9667), (B) *Lichonycteris degener* (ALP 5990), (C) *Scleronycteris ega* (USNM 407889), (D) *Hylonycteris underwoodi* (AMNH 178904), (E) *Choeroniscus minor* (AMNH 266121), (F) *Anoura caudifer* (ALP 1734), (G) *Musonycteris harrisoni* (AMNH 235179), (H) *Choeronycteris mexicana* (AMNH 27311) (scale bar = 5 mm).

to *Scleronycteris*, whereas the two males resemble *Hylonycteris* and the other taxa listed above. In the lower dentition, the first premolar of *Dryadonycteris* is separated from adjacent canine by a small but conspicuous diastema, whereas in *Lichonycteris*, *Scleronycteris*, and *Hylonycteris* this gap is barely visible or absent (fig. 9). In *Anoura*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris*, the development of this diastema seems to be variable. *Dryadonycteris capixaba* is similar to *Lichonycteris*, *Scleronycteris*, and *Hylonycteris* in having small diastemata separating the lower premolars, whereas in *Anoura*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris* the

diastema between the first two molars is generally larger than that separating the second and third premolars. Still in relation to lower dentition, *Dryadonycteris* is similar to most Choeronycterini in having a low main cusp on the first lower premolar (fig. 9). In *Anoura* and in most *Hylonycteris* we were able to examine, however, the main cusp is conspicuously higher than the adjacent styler cusps. In describing the first lower premolar of glossophagines, Phillips (1971) reported that the lingual surface of this tooth is concave in *Hylonycteris*, a condition that is shared only with *Dryadonycteris*.

The mandible of *Dryadonycteris* exhibits a unique feature: the mandibular condyle is positioned approximately at the same height as the upper border of the coronoid process, whereas in all other Choeronycterini the condyle is lower (more ventral) than the coronoid process (fig. 9). The projection of the anterior part of the mandible is directed relatively ventrally in most Choeronycterini (*Scleronycteris*, *Lichonycteris*, *Choeroniscus*, *Hylonycteris*), but projects straight forward in *Dryadonycteris*. In most Choeronycterini, the angular process is also poorly developed (exception in *Anoura* and *Musonycteris*), and there is a secondary process on the ventral surface of the angular region. *Dryadonycteris capixaba* is similar to *Lichonycteris* in having a poorly developed angular process with no secondary process on the ventral aspect of this region.

Size is another important character in the discrimination of *Dryadonycteris* and other Choeronycterini. The range for forearm length of *D. capixaba* (29–32 mm) overlaps only with those for *Lichonycteris* (31–35.5 mm; Griffiths and Gardner, 2008), *Hylonycteris* (31–37 mm; Koopman, 1994), and *Choeroniscus* (26.5–42 mm; Genoways et al., 1973; Griffiths and Gardner, 2008). Some members of *Anoura* (33–48 mm; Griffiths and Gardner, 2008) also are near *Dryadonycteris* in forearm length, but the lowest value reported for the smaller species living in eastern Brazil, *Anoura caudifer*, is 35 mm (Taddei, 1975; Dias et al., 2002; Dias and Peracchi, 2008), which is significantly larger than *D. capixaba*. The poorly known *Scleronycteris ega* seems to be similarly larger (34.5–35.5 mm; Griffiths and Gardner, 2008; E. Bernard, personal commun.), and the other Choeronycterini are much larger than *Dryadonycteris*, e.g., *Choeronycteris* (42–47 mm) and *Musonycteris* (40–43 mm; Koopman, 1994). *Lichonycteris degener*, which according to Griffiths and Gardner (2008) is the only representative of this genus in eastern Brazil, can be confused with *Dryadonycteris capixaba* in forearm size, but these two species exhibit no overlap in cranial measurements (tables 1–2). *Dryadonycteris* has a longer but thinner skull, which is clearly reflected in linear measurements related to these aspects (e.g., condylocanine length, maxillary tooththrow length, and braincase breadth). *Hylonycteris* is from Central America and will not be considered in detail here, but *Choeroniscus* deserves particular attention. The relevant species in this case is *C. minor*, which occurs in eastern Brazil (Aguilar et al., 1995; Faria et al., 2006) and is potentially syntopic with *Dryadonycteris capixaba*. Specimens of *Dryadonycteris* described here are consistently smaller than specimens of *Choeroniscus* collected by Simmons and Voss (1998) in French Guiana, but agree in all respects with those found at an Atlantic Forest site in the state of Minas Gerais, 200 km westward from the type locality of *Dryadonycteris capixaba* (Aguilar et al., 1995) (tables 1–2). It may be the case that *Choeroniscus minor* is geographically variable in size—smaller in the southern part of its range—but a taxonomic reevaluation of the sample from Minas Gerais is advisable.

NATURAL HISTORY

The specimens of *Dryadonycteris capixaba* described here were captured in ground-level mist nets placed at the border of the forest (ALP 9599) and inside the forest (MN 78305). In the first case, the net was set at the center of a clearing bordered by *mata alta* (tall forest) on one side (about 50 m away) and cultivated trees and a dam on the other. In the second, nets were set along small dirt roads crossing the forest tracts. The specimen from the clearing was captured at 22:30 hours, while the one from inside the forest at the Reserva Natural Vale was captured at 18:05 hours (no information is available for the specimen MN 78305). Other species sampled at the clearing during the same night we captured *Dryadonycteris capixaba* were *Desmodus rotundus*, *Glossophaga soricina*, *Artibeus lituratus*, *Platyrrhinus recifinus*, *Myotis nigricans*, and *Molossus molossus*. During the night we captured specimen ALP 9667, the additional species sampled were *Saccopteryx leptura*, *Desmodus rotundus*, *Chrotopterus auritus*, *Lamproncycteris brachyotis*, *Micronycteris microtis*, *Rhinophylla pumilio*, *Dermanura gnoma*, and *Artibeus obscurus*.

Dryadonycteris capixaba was captured in both dry and wet seasons. No evidence of feeding habits was obtained, but the morphology of the skull and dentition of this bat is clearly indicative of nectarivory. At the Reserva Natural Vale, the guild of nectar-feeding bats includes at least two other species: *Glossophaga soricina* and *Anoura geoffroyi*. Based on frequency of captures, *Dryadonycteris capixaba* appears to be less abundant than sympatric nectar-feeding species. *Dryadonycteris* (3 individuals captured) comprised only 0.2% of the 1501 total bat captures at the site, whereas in the same sample *Anoura geoffroyi* was represented by 46 individuals (3.1%) and *Glossophaga soricina* by 84 (5.6%). In the sample obtained at the Floresta Nacional de Goytacazes in the 1970s, the single *Dryadonycteris capixaba* obtained corresponded to 0.5% of the 191 individuals captured (A.L. Peracchi, unpublished data). *Anoura caudifer* was similarly rare at this site (0.5%), and *Glossophaga soricina* was, again, the most common glossophaginae, accounting for 3.7% of the captures. *Dryadonycteris capixaba* seems, therefore, to represent a relatively rare species.

As reported in the study site section, the Reserva Natural Vale is covered by tabuleiro forests. Four natural vegetation types are identified in the tabuleiro forests of northern Espírito Santo; the *mata alta*, where *Dryadonycteris* was found, is the most prevalent. About 70% of the vegetation cover of the Reserva Natural Vale is composed of this type of forest (Peixoto et al., 2008). The *mata alta* occurs on clay or sandy-clay soils and exhibits a thick canopy layer with most trees reaching around 30 m, and emergent trees towering up to 40 m (Peixoto et al., 1995, 2008). There are two other lower arboreal strata, with average heights of 14 and 9 m, respectively (Peixoto et al., 1995). The understory is relatively open, probably as a result of the intense shade from the closed canopy (Peixoto et al., 1995, 2008). The forest at the Floresta Nacional de Goytacazes, where an additional specimen of *D. capixaba* was collected, is floristically similar to the *mata alta* of the Reserva Natural Vale, but it occurs in a much more fragmented landscape influenced by the proximity of the urban area of Linhares. The potential of *D. capixaba* to persist in such fragmented landscapes needs to be further investigated, particularly considering the fact that in the 1970s, when the specimen was captured, the forests covering the region were more extensive than they are today.

DISCUSSION AND CONCLUSIONS

Dryadonycteris represents a new genus-level taxon based on the clearly divergent morphology of the specimens available. Species-level taxonomy, as currently applied to both glossophagines and lonchophyllines, generally relies on subtle differences (see keys in Griffiths and Gardner, 2008), including size and quantitative traits, some of which appear here as intraspecific variation in *Dryadonycteris* (e.g., degree of development of a postorbital process). In contrast, generic distinctions are typically based on more clear-cut qualitative traits including dental formulae and fur-banding patterns. The unique shape of the skull of *Dryadonycteris*, together with its dental characters and external morphology, preclude its inclusion in any described genus, at least without requiring major revisions in the definition and diagnosis of existing taxa. The mosaic of traits seen in this taxon precludes easy assessment of its relationships, but several characters suggest that it belongs to the tribe Choeronycterini and subtribe Choeronycterina (table 3). Future explicit phylogenetic analyses of morphology and DNA sequences of *Dryadonycteris* will be necessary to elucidate the details of its relationships to other glossophagines.

The available evidence suggests that *Dryadonycteris capixaba* is a sexually dimorphic species, at least in wing dimensions, with females larger than males. This pattern has been reported for *Choeroniscus minor* (Genoways et al., 1973; Simmons and Voss, 1998). In *Anoura* an inverse tendency has been documented for upper canine size, with males having larger and more massive teeth (Griffiths and Gardner, 2008). It is possible that additional variation described here for important characters in *Dryadonycteris*, such as the expansion of the anterior maxillary bones (much more conspicuous in the female), will show that these traits are also sexually dimorphic. Until more material is available, however, the significance of the variation in these characters cannot be assessed.

Our samples from Reserva Natural Vale (RNV) and Floresta Nacional de Goytacazes (FNG) show that *Dryadonycteris* shares its habitat with two nectar-feeding species in each area: *Glossophaga soricina* and *Anoura geoffroyi* at RNV and *Glossophaga soricina* and *Anoura caudifer* at FNG. From the literature, however, it seems that at least two additional species, *Lonchophylla mordax* (Pedro and Passos, 1995) and *L. bokermanni* (Pimenta et al., 2010) occur at RNV, and there is also a record for the presence of *Lichonycteris degener* in the forests of the northern state of Espírito Santo, probably in the vicinity of Lagoa Juparanã (Zortéa et al., 1998), close to our study site (fig. 1). With the only specimen of *Choeroniscus minor* available for the state of Espírito Santo now correctly recognized as *Dryadonycteris capixaba*, the closest records for the former species are in eastern Minas Gerais and southern Bahia (Aguilar et al., 1995; Faria et al., 2006). Because the southern Bahia region shares the same forest formation found in northern Espírito Santo, the presence of *Choeroniscus minor* at our study site remains possible.

The discovery of *Dryadonycteris* in the forests of Linhares, namely at RNV, reinforces the importance of this site for the conservation of Atlantic forest vertebrates in general (e.g., Chiarello, 2000; Marsden et al., 2005; Srbek-Araújo and Chiarello, 2006; Galetti et al., 2009) and for bats in particular. We recently reported that this protected natural area is the richest site for Chiroptera in the entire Atlantic Forest biome, with 50 recorded species (Peracchi et al., 2011a). This number represents 70% of the species recorded in the state of Espírito Santo and

about half the number reported for the Atlantic Forest of southeastern Brazil (Peracchi and Nogueira, 2008). As currently known, *Dryadonycteris* represents the first bat genus endemic to the Atlantic Forest, and *D. capixaba* is the third species of bat apparently restricted to this biome. The other two bats, both Vespertilionidae, are the enigmatic *Lasiurus ebenus*, known only from the holotype collected in the state of São Paulo, and the recently described *Myotis izecksohni*, recorded from the states of Rio de Janeiro and Paraná (Moratelli et al., 2011). The Atlantic Forest is one of the 35 world's biodiversity hotspots (Mittermeier et al., 2011), and it is the most threatened Brazilian biome, with the remains of its forest highly fragmented and representing no more than 10% of the original distribution (Ribeiro et al., 2009; SOSMA and INPE, 2011). Any evolutionary lineage endemic to this biome should, therefore, be carefully evaluated for its conservation status.

At the present, the limited information available on the natural history of *Dryadonycteris capixaba* suggests that this bat is locally rare and occurs in only two vegetation formations, both now highly fragmented. Most tabuleiro forests still in existence today are found between northern Rio de Janeiro and southern Bahia, and the majority of fragments are around 1000 ha in extent (Silva and Nascimento, 2001). The RNV/Reserva Biológica de Sooretama, with ca. 45,000 ha, is a unique exception. Fragments of semideciduous seasonal forests are similarly small, but they are more widespread, occurring from northeastern to southern Brazil and reaching the eastern Paraguay and northeastern Argentina (Oliveira-Filho and Fontes, 2000). The significance of this wider distribution for the conservation of *Dryadonycteris* remains unclear, however, because the semideciduous seasonal forests at Rio Doce valley are floristically more similar to those over the tabuleiros than to other semideciduous forests of more austral distribution (e.g., at the state of São Paulo) (Rolim et al., 2006). The extent to which *Dryadonycteris* is dependent on specific floras or forest fragments of particular sizes remains to be determined, as does the full extent of its geographic range. Additional field studies and a review of eastern Brazilian glossophagines currently deposited in museum collections could help clarify the ecological requirements of *D. capixaba* and guide consistent assessments of its conservation status.

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APPENDIX

SPECIMENS EXAMINED

The following list includes all the specimens used in this study; see Material and Methods for acronyms.

Anoura caudifer – Brazil, Acre, Parque Nacional da Serra do Divisor (ALP 7035, 7055, 7169, 7292); São Paulo, Botucatu (ALP 1734).

Anoura geoffroyi – Brazil, Espírito Santo, Reserva Natural Vale (ALP 9218).

Choeroniscus minor – Brazil, Acre, Parque Nacional da Serra do Divisor (ALP 7048). Trinidad and Tobago, Trinidad, Saint George County (AMNH 207065). French Guiana, Paracou, Sinnamary (AMNH 266120, 266121, 266124, 267153, 267946, 267947, 267948).

Choeronycteris mexicana – Mexico, Jalisco, Tuxpan (AMNH 27309, 27311, 27319, 27366); Oaxaca, Centro (AMNH 208229, 212358, 213004, 213762); Puebla, Tepeyahualco (AMNH 237361, 237362).

Dryadonycteris capixaba – Brazil, Espírito Santo, Reserva Natural Vale (ALP 9667, holotype; ALP 9599, paratype), Floresta Nacional de Goytacazes (MN 78305, former ALP 3268, paratype).

Glossophaga soricina – Brazil, Minas Gerais, Jaíba (ALP 6902); Acre, Parque Nacional da Serra do Divisor (ALP 7185).

Hylonycteris underwoodi – Panama, Chiriquí, Bugaba (AMNH 178904); Darién, Cerro Mali (AMNH 238199). Belize, Toledo District, Quebrada de Oro (AMNH 256826). Mexico, Oaxaca, Tuxtepec (AMNH 189687, 189688).

Lichonycteris degener – Brazil, Pará, Belém (MPEG 1251); Amazonas, Parque Nacional da Amazônia (ALP 5990, filed number NRR 158).

Lonchophylla bokermanni – Brazil, Rio de Janeiro, Jardim Botânico do Rio de Janeiro (ALP 7954).

Lonchophylla mordax – Brazil, Minas Gerais, Jaíba (ALP 6841).

Musonycteris harrisoni – Mexico, Colima, Armeria (AMNH 235179), Pueblo Juarez (USNM 314689), Mixcuate (USNM 324971).

Scleronycteris ega – Venezuela, Amazonas, Rio Orinoco, Tamatama (USNM 407889).

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