

AMERICAN MUSEUM  
*Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024  
Number 3239, 28 pp., 8 figures, 3 tables August 27, 1998

A Revision of *Centronycteris* Gray  
(Chiroptera: Emballonuridae) with Notes on  
Natural History

NANCY B. SIMMONS<sup>1</sup> AND CHARLES O. HANDLEY, JR.<sup>2</sup>

CONTENTS

Abstract .....	2
Introduction .....	2
Historical Background .....	2
Materials and Methods .....	5
Gazetteer .....	6
Systematics .....	9
<i>Centronycteris</i> Gray .....	9
<i>Centronycteris maximiliani</i> Fischer .....	14
<i>Centronycteris centralis</i> Thomas .....	19
Phylogenetic Relationships .....	22
Natural History .....	24
Acknowledgments .....	25
References .....	26
Appendix: Specimens Examined .....	28

<sup>1</sup> Associate Curator, Department of Mammalogy, American Museum of Natural History.

<sup>2</sup> Curator, Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

## ABSTRACT

*Centronycteris* is a genus of rare Neotropical emballonurid bats that ranges from southern Mexico to southeastern Brazil. Although this taxon has been known to scientists for over 175 years, few specimens exist in museum collections. The last revision of the genus (Sanborn, 1936) recognized one species and two subspecies. Based on a sample of specimens four times greater than was available to Sanborn, we find that *Centronycteris* comprises at least two species, *C. maximiliani* Fischer and *C. centralis* Thomas, which are easily distinguished on the basis of craniodental morphology. *Centronycteris maximiliani* ranges from

southeastern Brazil to the Guianas, and west through northern Brazil and southern Venezuela; *C. centralis* ranges from Peru north through Central America to southern Mexico. Both species are known principally from lowland primary rainforest habitats, although *C. centralis* also occurs up to 1450 m. Aside from limited information on roost sites and reproduction, little else is known about the natural history of these rare bats. A review of published hypotheses of phylogenetic relationships of emballonurids suggests that *Centronycteris* is most closely related to other Neotropical taxa, but there is no consensus regarding identity of its sister taxon.

## INTRODUCTION

Bats of the genus *Centronycteris* are among the rarest of Neotropical Emballonuridae. Although *Centronycteris* ranges from southern Mexico to southeastern Brazil, fewer than 50 specimens exist in museum collections. Consequently, variation within the genus has been poorly understood. Sanborn (1936, 1937) referred all specimens of *Centronycteris* to a single species, *C. maximiliani*, and subsequent authors have followed this arrangement (e.g., Goodwin, 1947; Dalquest et al., 1950; Husson, 1962; Handley, 1966; Baker and Jones, 1975; Barghoorn, 1977; La Val, 1977; Carter and Dolan, 1978; Greenbaum and Jones, 1978; Hall, 1981; Albuja, 1982; Lemke et al., 1982; Williams et al., 1983; Reis and Peracchi, 1987; Griffiths and Smith, 1991; McCarthy and Ochoa, 1991; Koopman, 1993, 1994). However, our study of 37 specimens of *Centronycteris* reveals that *C. maximiliani* is a composite of at least two species. The goals of this contribution are to (1) provide a systematic revision of *Centronycteris* with diagnoses of all taxa, (2) review the literature on phylogenetic affinities of *Centronycteris* to other Neotropical emballonurids, and (3) summarize what is known about the natural history of each species of *Centronycteris*.

## HISTORICAL BACKGROUND

The type species of *Centronycteris* Gray, 1838, is *Proboscidea calcarata* (Schinz, 1821). Schinz (1821) originally described this species as *Vespertilio calcaratus* in a

German translation of Cuvier's treatise on the Animal Kingdom. As was common at that time, Schinz added names and descriptions of taxa that were not present in Cuvier's original work. Although libraries typically catalog this publication under Cuvier's name, authorship of new taxa (e.g., *Vespertilio calcaratus*) described therein is properly attributed to Schinz (1821). Additional confusion concerning authorship was introduced by Schinz's (1821: 180) attribution of *V. calcaratus* to "P. Max." (Maximilian, Prinz zu Wied-Neuwied). While it is possible that Wied-Neuwied used the name *V. calcaratus* on specimen labels or in letters or manuscripts seen by Schinz, Wied-Neuwied was not the first to publish this name. Nevertheless, many subsequent workers have incorrectly cited Wied-Neuwied as the author of *V. calcaratus* (e.g., Fischer, 1829; Gervais, 1856; Peters, 1867, 1872; Palmer, 1898, 1904; Trouessart, 1904; Thomas, 1913; Hall, 1981; McKenna and Bell, 1997). Wied-Neuwied (1822–31, 1826) himself cited Schinz (1821) as the source of this name, and we agree with Carter and Dolan (1978) that Schinz must be regarded as the author of *Vespertilio calcaratus*.

Schinz (1821) provided a brief description of *V. calcaratus* and noted that it was from Brazil. The name *V. calcaratus* seems to have been derived from the unusually long calcar mentioned in all early descriptions of this taxon. Carter and Dolan (1978) identified an unnumbered specimen in the Zoologisch-

es Museum der Humboldt Universität zu Berlin as either the holotype or a syntype of *V. calcaratus*. This specimen was collected by Wied-Neuwied at Fazenda Cordoba, Rio Jucú, near Rio do Espírito Santo, Espírito Santo, Brazil (Wied-Neuwied, 1826). Wied-Neuwied (1826) provided a more detailed account of *Vespertilio calcaratus*, including selected measurements, and in 1827 he published a color plate showing a dorsal view of the animal (in Wied-Neuwied 1822–31).

Fischer (1829) discovered that *Vespertilio calcaratus* Schinz, 1821, was preoccupied by *Vespertilio calcaratus* Rafinesque, 1818, and provided a replacement name, *Vespertilio maximiliani* Fischer, 1829. Apparently unaware of Fischer's work, Temminck (1841) moved this taxon to the genus *Emballonura* as *E. calcarata*.

Gray (1838) proposed the name *Centronycteris* for this bat, under which he listed three name combinations: *Proboscidea calcarata*, *Vesp. calcaratus* Pr. Max., and *Vesp. maximiliani* Fischer. Many subsequent authors (e.g., Sanborn, 1937) have interpreted Gray's citation as indicating that he intended to use the name *Centronycteris calcarata* for this species. However, Gray's text suggests otherwise. *Centronycteris* appeared in Gray (1838) under the numbered, capitalized heading *Proboscidea* Spix. Gray (1838: 499–500) listed three subdivisions under this heading: (1) "Interfemoral membrane truncated. (*Proboscidea*, Spix)"; (2) "Interfemoral membrane produced conical; heel-bone very long, *Centronycteris*"; and (3) "Interfemoral membranes, & c. \_\_\_\_\_? (*Emballanura*, Kuhl)." Gray went on to note the species included under each of these subdivisions. Each species was listed on a separate indented line, and the preferred name was apparently given first, followed by synonyms. Because only one species was noted under *Centronycteris*, and the first name listed for this taxon was *Proboscidea calcarata*, it seems likely that Gray (1838) intended *Centronycteris* as a subgeneric subdivision of *Proboscidea* that included only one species, *Proboscidea calcarata*. Palmer (1904) and Miller (1907) suggested this interpretation, noting that Gray (1838) named *Centronycteris* as a subgenus of *Proboscidea*. In spite of indications to the contrary by Sanborn

(1937), Gray (1838) did not explicitly use the combination *Centronycteris calcarata*. However, a few years later Gray (1843) raised *Centronycteris* to genus rank in a summary of genera of Neotropical bats.

Gervais (1856) used *Centronycteris* as a generic name, but retained Schinz's (1821) species epithet rather than using Fischer's (1829) replacement name. He was the first to explicitly use the combination *Centronycteris calcarata*.

Peters (1867, 1872) also used the name *Centronycteris calcarata*. Peters (1867) provided a detailed description of the holotype together with more measurements than had been provided by Wied-Neuwied (1826). Subsequently Peters (1872) described an additional specimen from Peru<sup>3</sup> and provided a comprehensive description of the species. Finding several points of disagreement between the new Peruvian specimen and the holotype of *C. calcarata* (which at that time was dried and in poor condition), Peters soaked the latter in a weak solution of alum in order to soften it. In contrast to earlier descriptions, Peters (1872) found the calcar of *C. calcarata* to be comparable in relative length to that of *Saccopteryx* rather than unusually long (see footnotes to table 1). He also noted that *C. calcarata* has only one pair of upper incisors, not two pairs as reported by Wied-Neuwied (1826). Peters' (1872) description provided the basis for most subsequent treatments of *Centronycteris*.

Between 1865 and 1883, Peters commissioned a series of plates to illustrate a monograph on bats in the Berlin Museum, "Museum Zoologicum Berolinese. Chiroptera" (Matschie, 1899: v). Peters died before completing this work, but the plates were published posthumously in 1906 (Thomas, 1909). One of these plates (Taf. 17Aa) illustrated external, cranial, and dental morphology of *Centronycteris calcarata* (fig. 1). The peculiar swelling on the leading edge of the propatagium (antebrachial membrane) and external measurements of the bat shown in this plate agree exactly with comments and

<sup>3</sup>This specimen was described by Peters (1872) as a female preserved in alcohol sent to him by Dr. L. Taczanowski of the Warsaw Museum. The locality was reported as "high plains of Peru" (Peters, 1872: 700).

Museum Zoologic Berolinense

Chiroptera Taf 17Aa

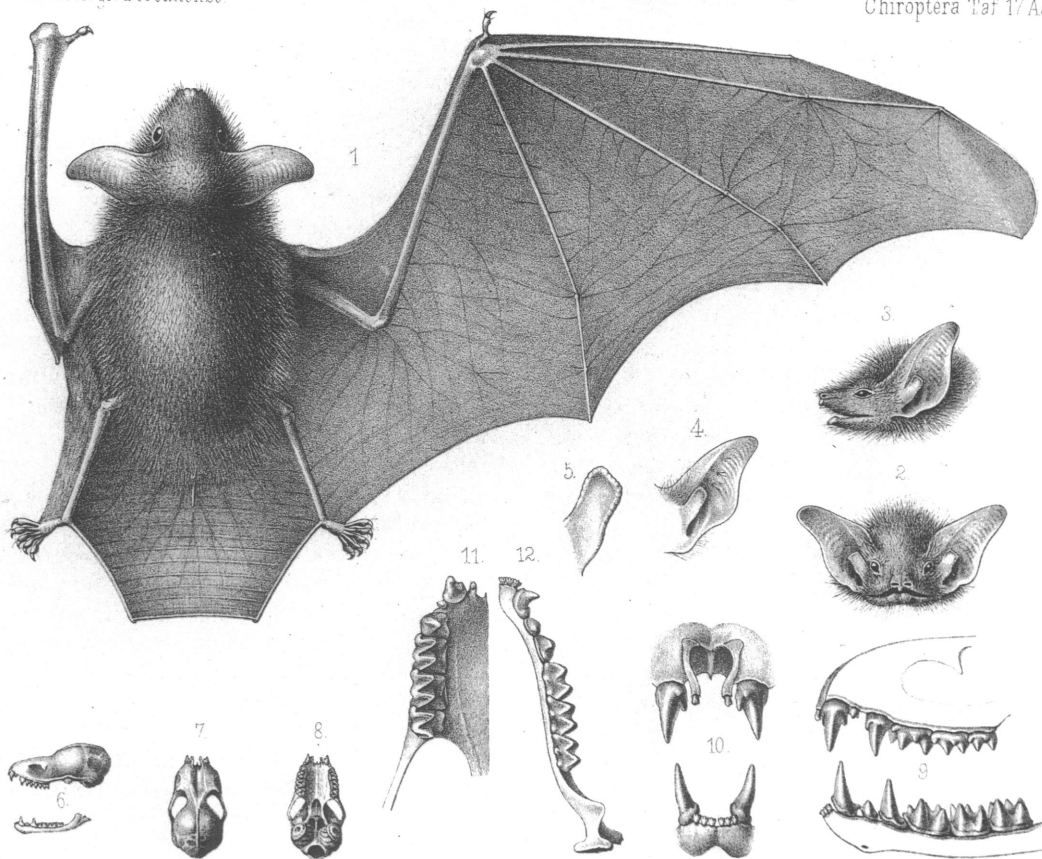
*Centronycteris calcarata.*

Fig. 1. Plate illustrating external and craniodental morphology of *Centronycteris calcarata*. This plate was commissioned in the late 1800s by Wilhelm K. H. Peters to illustrate his monograph on bats in the Berlin Museum, which was never published (see text for discussion). Measurements and craniodental morphology of the bat in the plate show it to be unquestionably *C. centralis* Thomas as recognized in the present study.

measurements reported by Peters (1872) for his Peruvian specimen (see footnote 3).

Dobson (1878) placed *Vespertilio calcaratus* Schinz, 1821, in the genus *Saccopteryx*, thus creating the new combination *Saccopteryx calcarata*. He recognized four subgenera in *Saccopteryx*: *Centronycteris* (including only *Saccopteryx calcarata*), *Balantiopteryx*, *Peropteryx*, and *Saccopteryx*. Dobson's inclusion of *Vespertilio calcaratus* in this complex was based on cranial similarities and the mistaken impression (obtained from his misreading of Peters, 1872) that a wing sac was present in the female *Centronycteris* from Peru described by Peters (1872). Dobson

(1878: 354) placed *Saccopteryx* in his "Group Emballonurinae" together with *Rhynchonycteris*, *Coleura*, *Emballonura*, and *Taphozous*. He placed *Diclidurus* in its own taxon, "Group Diclidurinae."

Palmer (1898), following Dobson (1878) but unaware of Fischer (1829), proposed a second replacement name for *Vespertilio calcaratus* Schinz, 1821. This new name, *Saccopteryx wiedi* Palmer, 1898, is an junior objective synonym of *Vespertilio maximiliani* Fischer, 1829.

Trouessart (1897) followed Gervais (1856) and Peters (1867, 1872) in using the name *Centronycteris calcarata*. However, in a later

edition of the same work, Trouessart (1904) accepted Palmer's (1898) replacement name *wiedi* but retained *Centronycteris* as the generic epithet. The resulting binomial, *Centronycteris wiedi*, is a junior objective synonym of *Vespertilio maximiliani* Fischer, 1829. Miller (1907) was the first to note this synonymy, and he firmly established *Centronycteris maximiliani* as the valid name for this taxon in his monograph on families and genera of bats. All subsequent authors have followed Miller's usage.

Thomas (1912) described a second species, *Centronycteris centralis*, from Panama. A year later, Thomas (1913) discussed an additional specimen of *Centronycteris maximiliani* from the Brazilian state of Pará, and reconfirmed his conclusion that *C. maximiliani* and *C. centralis* represented distinct species. He also summarized all known records for *Centronycteris*, four specimens altogether: (1) the holotype of *C. maximiliani*, a male from southeastern Brazil (described in detail by Peters, 1867); (2) a female from Peru (described by Peters, 1872); (3) the holotype of *C. centralis*, a male from Panama (described by Thomas, 1912); and (4) a female specimen of *C. maximiliani* from Pará.

In his account of the mammals of Panama, Goldman (1920) repeated Thomas' (1912) description of *Centronycteris centralis* but did not report any new specimens or information. Allen and Barbour (1923) subsequently reported discovery of another specimen of *C. centralis* among material collected by C. F. Underwood in Costa Rica. This specimen had gone undetected in the Museum of Comparative Zoology, Harvard University, for many years after its collection in 1908, and was identified only after Thomas' (1912) and Goldman's (1920) descriptions were published.

No additional specimens of *Centronycteris* were reported until Sanborn (1936) described a specimen collected in Guatemala. This was followed by Sanborn's (1937) revision, which included reference to the six specimens mentioned above as well as an additional specimen from Brazil and two from Ecuador. Sanborn's (1937) revision was thus based on nine specimens, only five of which he examined personally.

Contrary to Thomas's (1912, 1913) con-

clusions, Sanborn (1937) was not convinced that *C. centralis* represented a species distinct from *C. maximiliani*. Sanborn (1936) gave no justification for reducing *C. centralis* to a subspecies of *Centronycteris maximiliani*. However, a year later he provided a brief explanation under his description of *C. maximiliani centralis*:

In his original description Thomas said of *Centronycteris centralis* "Mainly distinguishable from *C. maximiliani* by its very different basisphenoid pits." None of the specimens examined seem to agree with Thomas' characterization of the typical form, so all are referred to *centralis*. (Sanborn, 1937: 339)

We have examined all of the specimens seen by Sanborn, and find that four of these (from Guatemala, Costa Rica, and Ecuador) correspond perfectly with Thomas' (1912) description of *C. centralis*. The skull of the fifth specimen, a male from central Brazil (AMNH 78858), was poorly prepared and the basicranial region is damaged. We suspect that Sanborn (1937) misinterpreted the crushed basisphenoid pits in this specimen as being intermediate in form between the morphology Thomas (1912, 1913) described for *C. maximiliani* in eastern Brazil and the morphology typical of *C. centralis* in western South America and Central America. Nevertheless, Sanborn's (1937) usage has been followed by all subsequent authors.

## MATERIALS AND METHODS

We examined most of the specimens of *Centronycteris* currently available in museum collections in the United States and Europe, and reviewed all literature accounts of this taxon. Unless otherwise indicated, all observations reported here are based on adults with closed epiphyses. Measurements of the holotypes and other specimens available to us are provided in tables 1 and 2. External and craniodental measurements are in millimeters; body mass (weight) in grams. The first five measurements listed below were taken from skin tags or other records made by the collector of each specimen; other dimensions were measured with dial or digital calipers. Measurements are defined as follows:

*Weight*: Body mass in grams.

*Total length*: Distance between the tip of the

snout and the tip of the last caudal vertebra.

**Tail length:** Combined length of the caudal vertebrae measured from the posteriormost point on the rump to the tip of the last caudal vertebra.

**Hind foot length:** Distance from the anterior (inner) edge of the base of the calcar to the tip of the claw of the longest toe. Some European collectors may have omitted the length of the claw from this measurement.

**Ear length:** Distance from the ear notch to the distal tip of pinna. Instances in which original measurements were obviously made using a different protocol are not included in our summary tables.

**Forearm length:** Distance from the elbow (measured from the tip of olecranon process) to the distal end of the forearm including carpals. This measurement is made with the wing at least partially folded.

**Tibia length:** Distance from the proximal end of the tibia to the posterior (outer) base of the calcar.

**Condylacanine length:** Distance between the posteriormost point on the occipital condyles and the anteriormost point on the upper canines as measured in a parasagittal plane. This measurement was used as an alternative to other measures of skull length because emballonurids (including *Centronycteris*) have a movable premaxilla that is often missing or distorted in museum preparations.

**Basisphenoid pit length:** Greatest length of the basisphenoid pits as measured in a parasagittal plane.

**Lacrima breadth:** Greatest breadth across the lacrimal (= anteorbital) ridges.

**Postorbital breadth:** Least breadth across the constriction of the frontals, posterior to the postorbital processes.

**Zygomatic breadth:** Greatest breadth between the outer edges of the zygomatic arches.

**Mastoid breadth:** Greatest breadth of the skull as measured across the mastoid region.

**Maxillary tooththrow length:** Greatest crown length of the maxillary tooththrow measured from the anteriormost surface of the canine to the posteriormost surface of M3.

**Breadth across molars:** Greatest breadth between the outer margins of the crowns of the upper second molars.

**Length of lower molar row:** Greatest length of the lower molar row measured from the anteriormost surface of m1 to the posteriormost surface of m3.

## GAZETTEER

The following gazetteer provides locality information for all specimens of *Centronycteris* examined by us or reported in the literature. Collection localities are listed by country; italic type identifies subordinate political units (departments, states, provinces, etc.), and boldface identifies locality names as cited in the text and appendix. Latitude and longitude are given in parentheses, followed by supplementary information including museum catalog numbers (when known), sex of specimens, and the earliest published references to each specimen (when applicable). Locality numbers refer to figures 2 and 3. Specimens we examined are listed in the appendix.

The following institutional abbreviations are used in this report: **AMNH**, American Museum of Natural History, New York, New York, USA; **BMNH**, British Museum of Natural History (= Natural History Museum, London), London, England; **CM**, Carnegie Museum, Pittsburgh, Pennsylvania, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **INPA**, Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil; **KU**, University of Kansas Museum of Natural History, Lawrence, Kansas, USA; **LACM**, Los Angeles County Museum of Natural History, Los Angeles, California, USA; **LSU**, Louisiana State University Museum of Zoology, Baton Rouge, Louisiana, USA; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MEPN**, Museo de la Escuela Politécnica Nacional, Quito, Ecuador; **MUSM**, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **MVZ**, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; **RMNH**, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; **ROM**, Royal Ontario Museum, Toronto, Canada; **TTU**, Texas Tech University, Lubbock, Texas, USA; **USNM**, National Museum of

Natural History, Washington, D.C., USA; **UWZM**, University of Wisconsin Zoological Museum, Madison, Wisconsin, USA; **ZMB**, Zoologisches Museum der Humboldt Universität zu Berlin, Berlin, Germany.

## MEXICO

1. *Veracruz*, **35 km SE of Jesus Carranza** (17°28'N/95°01'W), elevation 350 ft; KU 32088 (female), reported by Dalquest et al. (1950) and skull illustrated by Hall (1981).

## BELIZE

2. *Orange Walk*, **Gallon Jug** (17°56'N/89°03'W); AMNH 269848 (female); and **Chan Chich**, near Gallon Jug (17°53'N/89°11'W); AMNH 269847 (female).

3. *Toledo*, **Double Falls** (16°42'N/88°38'W); FMNH 63949 (female), reported by Sanborn (1941).

## GUATEMALA

4. *Escobas*, **Izabal** (15°22'N/89°09'W), near San Tomas; FMNH 41558 (male), reported by Sanborn (1936).

## NICARAGUA

5. *Zelaya*, **9.5 mi. NW Rama** (13°22'N/85°54'W); TTU 30670 (female), reported by Greenbaum and Jones (1978); and **9.0 mi. E Rama**; TTU 13419 (female), reported by Baker and Jones (1975).

## COSTA RICA

6. *Alajuela*, **Vijagua** (10°44'N/85°06'W), = La Bijagua, a small town on the Caribbean slope of Volcán Miravalles (Starrett and Casebeer, 1968); MCZ 7092 (female), reported by Allen and Barbour (1923) without locality data, later listed with misspelled locality name "Viragua" by Sanborn (1937).

7. *Heredia*, **La Selva** (10°26'N/83°59'W), vicinity of Puerto Viejo de Sarapiquí; KU 127971 (female), reported by LaVal (1977).

8. *Puntarenas*, **Rincón de Oso** (ca. 08°34'N/83°31'W); elevation 0 m; LSU 9338; and **Camp Seattle**, Osa Productos Forestales, Rincón de Oso, 35 m, two females deposited in the LACM (Starrett and Casebeer, 1968); and near **Headquarters of Osa Productos Forestales**, Rincón de Oso, 10 m, one female deposited in the LACM (Starrett and Casebeer, 1968).

## PANAMA

9. *Chiriquí*, **Bogava** (08°31'N/82°40'W), = Bugaba, 250 m; BMNH 0.7.11.3 (male), holotype

of *Centronycteris centralis*, described by Thomas, 1912.

10. *Colon*, **Barro Colorado Island** (09°10'N/79°50'W), USNM 304864 (male), 503827 (female), and 535021 (male); and **Bohio Peninsula** (09°12'N/79°50'W), Gatún Lake, USNM 514956 (female).

11. *Panama*, **Ft. Clayton** (08°56'N/79°34'W), Concrete building #519; USNM 311571 (female), first reported by Handley (1966) but no specimen number given.

12. *Panama*, **5 mi E of Gamboa** (09°07'N/79°42'W), MVZ 108943 (sex unknown).

13. *Darién*, **4 mi. W of Cerro Malí** (08°07'N/77°14'W), on ridge, elevation 4750 ft; USNM 339021 (female), first reported by Handley (1966) but no specimen number given.

## COLOMBIA

14. *Antioquia*, **La Tirana**, 25 km S and 22 km W of Zaragoza (ca. 07°21'N/75°03'W); UWZM-NEP 291170-07 (male); collected by N. Peterson.

15. *Valle del Cauca*, **Río Achicaya**, 8 km W of Danubio (03°37'N/76°53'W), elevation 300 m; KU 135138 (female).

~. *Cordoba*, **Alto Ure** (not located); FMNH 98230 (female), reported by Lemke et al., 1982.

## ECUADOR

16. *Manabi*, **Mongoya** (00°10'S/79°39'W); elevation 200 m; FMNH 53421 (female).

17. *Pichincha*, **Río Toachi** (00°08'N/79°18'W); MEPN E-55.3.1 (female), reported by Albuja (1982).

18. *Pastaza*, **Montalvo**, Río Bobonazo (02°04'S/76°58'W); elevation 250 m; FMNH 41431 (female), reported by Sanborn, 1937; and **Río Copataza** (02°07'S/77°27'W); MEPN E-39.4.1 (male), reported by Albuja (1982).

19. *Pastaza*, **Mera** (01°28'S/78°08'W); elevation 1,160 m; USNM 548065 (male); and **Mera, Río Alpayacu** (01°28'S/78°07'W); AMNH 63663 (male), reported by Sanborn, 1937.

## PERU

20. *Junin*, **Chanchamayo** (ca. 11°03'S/75°19'W), elevation 1250 m; MUSM 1078 (female).

~. High plains of Peru (not located); purported source of a female specimen described by Peters (1872) as having been collected by Dr. Taczanowski; specimen mentioned by Thomas (1913) as being in the ZMB, but could not be located in 1996.

## VENEZUELA

21. *Amazonas*, **Buena Vista** (01°58'N/66°42'W); left bank of Río Casiquaire, elevation

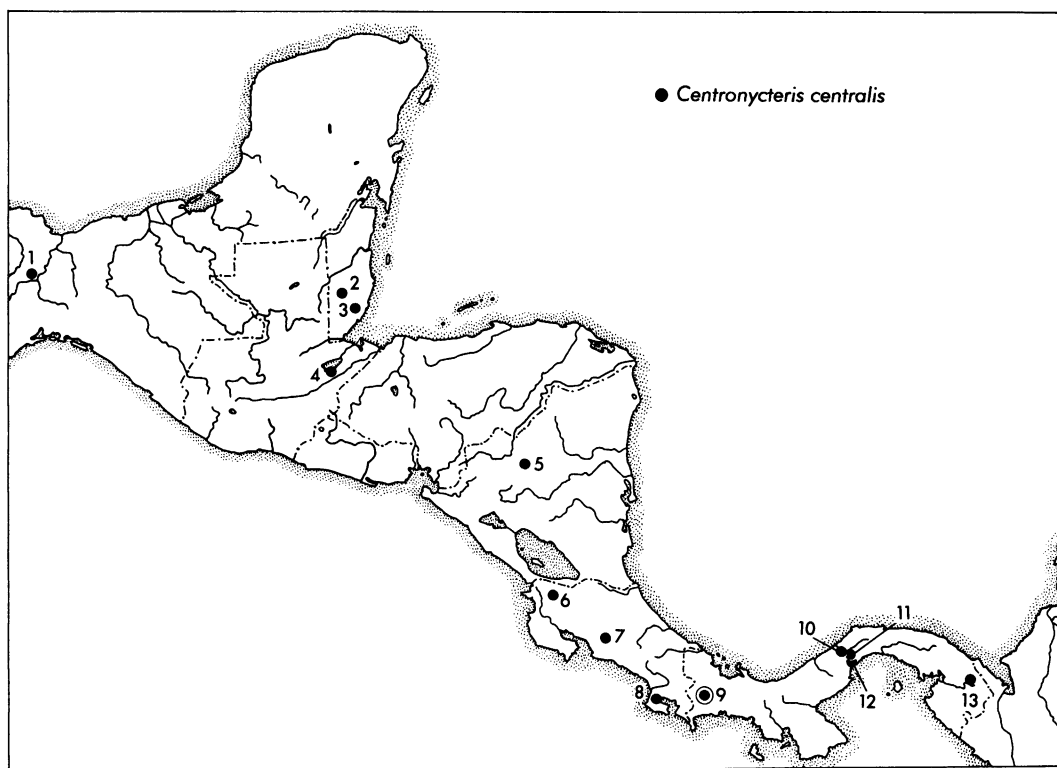


Fig. 2. Map of Central America showing collection localities for *Centronycteris centralis*. The symbol indicating the type locality is circled. Names and geographic coordinates of numbered localities are provided in the gazetteer.

100 m (McCarthy and Ochoa, 1991); 45 km above confluence of Río Casiquaire and Río Guainia (Paynter, 1982); AMNH 74820 (male), reported by McCarthy and Ochoa (1991).

#### GUYANA

22. *Potaro-Siparuni*, **Burro Burro River** (04°44'N/58°51'W), 25 km WNW Kurupukari, KU 156014 (female); and **Pakatau Falls** (04°44'N/59°01'W), 42 km WNW Kurupukari, ROM 107081 (female) and ROM 107082 (female).

#### SURINAM

23. *Saramacca*, **Tibiti** (05°33'N/55°54'W), savanna forest; RMNH 12111 (female); reported and illustrated by Husson (1962).  
24. *Marowijine*, **Oelemarie** (03°06'N/54°31'W); CM 76749 (male); reported by Williams et al., 1983.

#### FRENCH GUIANA

25. *Cayenne*, **Paracou** (05°23'N/52°57'W), near Sinnamary; AMNH 267397 (male).

#### BRAZIL

26. *Amazonas*, **Santo Isadoro Tefé** (03°22'S/64°42'W), cited as *Sitío Isado*, near Tefé by Sanborn (1937); AMNH 78858 (male).  
27. *Amazonas*, **Colosso** (ca 02°25'S/59°52'W), 82 km N Manaus (BDFFP Reserve), INPA 2495 (female); **Fazenda Dimona** (ca 02°20'S/60°07'W), 89 km N Manaus (BDFFP Reserve), INPA 2541 (female); **Gavaio** (ca 02°26'S/59°50'W), 79 km N Manaus (BDFFP Reserve), INPA 2502 (female); **ZF-2 Tower** (ca 02°28'S/60°07'W), 78 km N Manaus (Apoio Forestry Research Station), field number NRR 128 (male); deposited in the Instituto de Biologia da Universidade de Federal Rural do Rio de Janeiro; reported by Reis and Peracchi (1987).  
28. *Pará*, **Belém** (01°27'S/48°29'prW); cited as *Pará*, *Utinga* by Thomas (1913); BMNH 12.11.4.3 (female).  
29. *Pernambuco*, **Recife** (08°03'S/34°54'W); BMNH 44.6.9.9 (sex unknown).  
30. *Espírito Santo*, **Rio Jucú** (20°24'S/40°19'W), near Rio de Espírito Santo, Fazenda



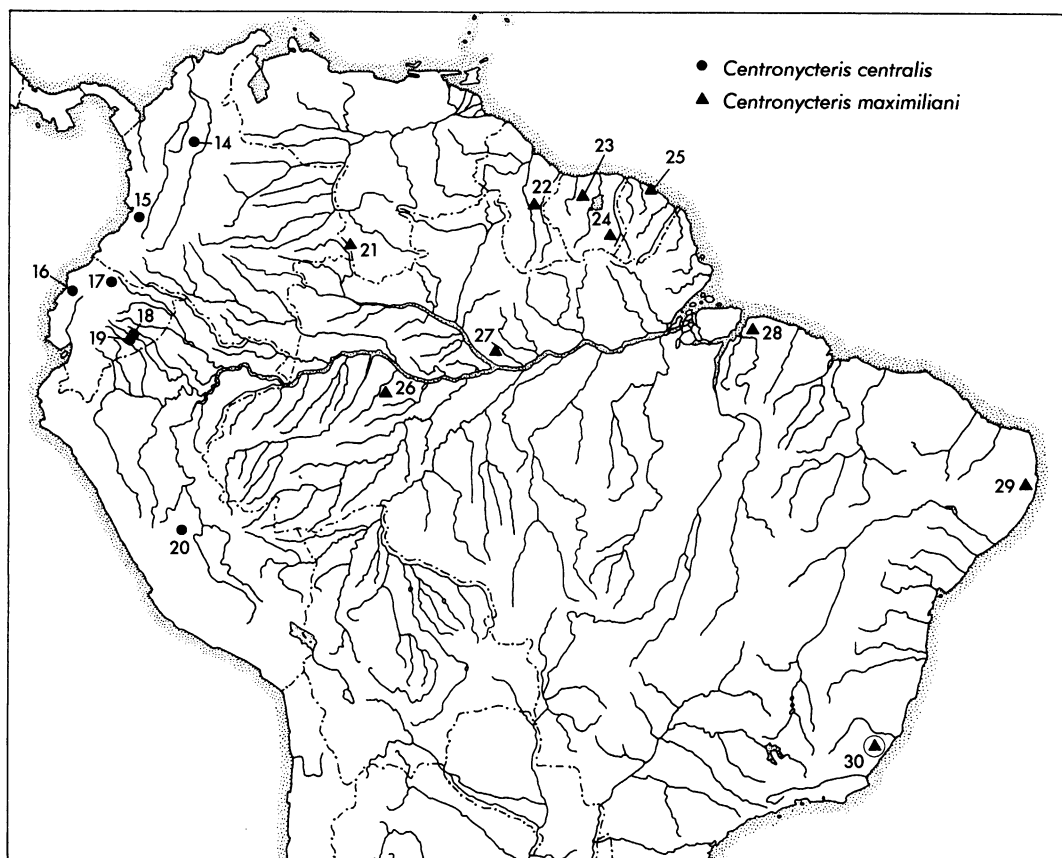


Fig. 3. Map of South America showing collection localities for *Centronycteris centralis* and *C. maximiliani*. The symbol indicating the type locality for *maximiliani* is circled. Names and geographic coordinates of numbered localities are provided in the gazetteer.

Coroaba; ZMB 54654 (sex unknown), holotype of *Vespertilio calcarata*.

## SYSTEMATICS

### FAMILY EMBALLONURIDAE

#### Genus *Centronycteris* Gray

*Vespertilio*: Schinz, 1821: 180 (part).

*Proboscidea*: Gray, 1838: 499 (part).

*Centronycteris* Gray, 1838: 499 (subgenus of *Proboscidea*).

*Emballonura*: Temminck, 1841: 299 (part).

*Centronycteris*: Gray, 1843: 23 (raised to generic rank).

*Saccopteryx*: Dobson, 1878: 371 (part).

*Centronycteris*: Dobson, 1878: 371 (subgenus of *Saccopteryx*).

TYPE SPECIES: Gray (1838) designated

*Proboscidea calcarata* (Schinz, 1821) as the type species of *Centronycteris*. This species is now known as *Centronycteris maximiliani* (see below).

DIAGNOSIS: Dorsal fur bicolored with dark gray-brown bases and paler brown to brownish-orange tips, no sharp division between colors; venter somewhat paler than dorsum; ventral fur bicolored with fuscous bases and paler brown tips, colors sharply divided; no dorsal stripes; dorsal fur extends onto uropatagium to approximately the level of knees and halfway along tail; ventral fur extends onto uropatagium as a small patch at base of tail; ventral uropatagium with parallel rows of short, bristle-like hairs; no uropatagial sacs; wing membranes and uropatagium dark brown or fuscous; no wing sacs; forearm and

propatagium virtually naked; calcar slightly longer than tibia, approximately 2.5 times length of foot; posterior edge of wing membrane attaches to side of foot at level of metacarpophalangeal joints (base of toes); nostrils tubular with circular external openings; no sharp angle between rostrum and braincase; anterior root of zygoma little expanded; maxilla does not form lateral shelf above tooth row; sagittal crest moderately well developed in both sexes; premaxillae well developed dorsally with platelike expansions that overlap anterior maxillaries; posterior border of hard palate v-shaped; basisphenoid pits deep and separated by a median septum; dental formula I 1/3, C 1/1, P 2/2, M 3/3; small anterior upper premolar with distinct anterior and posterior cusps.

MORPHOLOGICAL COMPARISONS WITH OTHER NEOTROPICAL EMBALLONURIDS: Independent studies of allozymes (Robbins and Sarich, 1988) and morphology of the hyoid apparatus (Griffiths and Smith, 1991) have strongly supported monophyly of Neotropical Emballonuridae relative to Old World members of the family. Accordingly, we compare *Centronycteris* only with other Neotropical genera.

The dorsal fur in *Centronycteris* is bicolored with dark gray-brown bases that blend gradually into paler brown or brownish-orange tips. The ventral fur is slightly paler and more sharply bicolored, with fuscous bases and paler brown tips. This combination of color and banding pattern is seen among other Neotropical emballonurids only in *Saccopteryx canescens*, which has a frosted appearance not found in *Centronycteris*. Dorsal stripes are absent in *Centronycteris* as they are in most Neotropical emballonurids. A pair of white or cream-colored dorsal stripes are present only in *Rhynchonycteris* and *Saccopteryx* (very faint in *S. gymnura*).

Fur extends beyond the body onto both surfaces of the uropatagium in *Centronycteris*. The fur on the dorsal surface extends to about the level of the knees and halfway along the tail. Fur on the ventral surface is confined to a small patch at the base of the tail. Rows of short, bristle-like hairs cover the remaining uropatagium distal to the ventral fur patch. This pattern of fur on the uropatagium is similar to that seen in other Neo-

tropical emballonurids with the exception of *Cyttarops* and *Diclidurus* (both of which have more fur on the ventral uropatagium and lack the bristle-like hairs), *Balantiopteryx plicata* (which has more fur on the ventral uropatagium), and *Saccopteryx leptura* and *Cormura* (which have only sparse fur on the dorsal uropatagium).

The forearm in *Centronycteris* is naked except for a few widely scattered fine hairs. This is similar to the condition seen in *Peropteryx*, *Cormura*, *Saccopteryx bilineata*, *S. leptura*, *Balantiopteryx io*, *Diclidurus ingens*, and *Cyttarops*. The forearm of the remaining Neotropical emballonurids is covered with a thin coat of fur.

The propatagium is naked in *Centronycteris* as it is in *Balantiopteryx*, *Saccopteryx*, *Peropteryx*, and *Cormura*. In contrast, the propatagium is densely furred in *Rhynchonycteris*, *Cyttarops*, and *Diclidurus*. Propatagial wing sacs are present in many Neotropical emballonurids including all members of *Balantiopteryx*, *Saccopteryx*, *Cormura*, and *Peropteryx*. Wing sacs are absent in *Centronycteris*, *Rhynchonycteris*, *Cyttarops*, and *Diclidurus*. Uropatagial sacs are present only in *Diclidurus*.

The wing membranes in *Centronycteris* are dark, varying between brown and fuscous depending on preparation type and preservation. This color pattern is also seen in *Peropteryx* (except *P. leucoptera*). *Rhynchonycteris*, *Balantiopteryx*, *Saccopteryx*, *Cormura*, and *Cyttarops* have dark wing membranes that are blackish rather than fuscous. In contrast, the wing membranes are transparent pale gray in *Peropteryx leucoptera*. *Diclidurus isabellus* has pale brown wing membranes, and the remaining species of *Diclidurus* have transparent yellowish membranes.

Relative length of the calcar (compared with length of the hind foot) varies enormously among Neotropical emballonurids. The calcar in *Centronycteris* is approximately 2.5 times the length of the hind foot (fig. 1). A similarly long calcar is seen in *Rhynchonycteris*, *Cyttarops*, and most species of *Peropteryx* and *Diclidurus*. In contrast, the calcar is less than or equal to twice the length of the hind foot in *Balantiopteryx*, *Saccop-*

*teryx*, *Cormura*, *Peropteryx kappleri*, and *Diclidurus isabellus*.

The site of attachment of the posterior edge of the wing membrane to the hindlimb varies widely among emballonurid genera and species (for an illustration see Husson, 1962: fig 2, or 1978: fig. 9). In *Centronycteris* the edge of wing membrane attaches to the side of the foot at the level of metacarpal-phalangeal joint (fig. 1). This unusually distal attachment is unique among Neotropical emballonurids. The posterior edge of the wing membrane attaches near the midpoint of the metatarsus in *Cormura*, *Peropteryx kappleri*, *Saccopteryx gymnura*, *Diclidurus*, and *Cyttarops*. The wing membrane attaches at the base of the metatarsus or at the ankle (difficult to distinguish due to elasticity of the skin) in *Rhynchonycteris*, *Peropteryx leucoptera*, *P. macrotis*, *P. trinitatus*, *Saccopteryx leptura*, and *S. bilineata*. The posterior edge of the wing membrane attaches on the tibia well proximal to the ankle in *Balantiopteryx*.

The nostrils in *Centronycteris* are tubular with circular external openings. This arrangement is similar to that seen in *Peropteryx leucoptera*, *Saccopteryx gymnura*, and *Rhynchonycteris*. The nostrils are somewhat less tubelike in *Balantiopteryx*, the remaining species of *Saccopteryx*, and *Cormura*, and they are not tubular in *Diclidurus*, *Cyttarops*, and the remaining species of *Peropteryx*. The external openings of the nostrils are long and flat rather than circular in the latter two taxa.

The skull of *Centronycteris* (figs. 4, 5) has an expanded lacrimal region similar to that seen in other Neotropical emballonurids. There is no sharp break in slope between the rostrum and braincase in *Centronycteris*, *Rhynchonycteris*, *Cormura*, and *Saccopteryx*. In contrast, there is a sharp break in slope between the dorsal surface of the rostrum and the plane of the forehead in *Peropteryx*, *Balantiopteryx*, *Cyttarops*, and *Diclidurus*.

The anterior root of the zygomatic arch in *Centronycteris* is not expanded laterally and the maxilla does not extend laterally beyond the edges of the toothrow. The zygomatic arches are slender and easily damaged in museum specimens. In these respects *Centronycteris* resembles *Rhynchonycteris*, which also has slender zygomatic arches with little expansion of the anterior root. In contrast, in

*Saccopteryx*, *Cormura*, *Peropteryx*, and *Balantiopteryx* the zygomatic arch is more robust, the anterior portion of each arch is expanded, and the maxilla forms a shelf that extends laterally well beyond the edges of the tooth row. *Cyttarops* and *Diclidurus* have relatively robust zygomatic arches, but lack any lateral expansion of the anterior root or maxilla.

Both sexes of *Centronycteris* have a moderately well-developed sagittal crest, as do most other Neotropical emballonurids. *Rhynchonycteris* is the only taxon that consistently lacks a sagittal crest in adults.

The premaxilla in *Centronycteris* is well developed dorsally and has a platelike expansion that overlaps the maxilla near the nasal aperture. A similar condition is seen in *Rhynchonycteris*, *Saccopteryx*, *Cormura*, and *Peropteryx*. The premaxilla lacks a platelike dorsal expansion in *Balantiopteryx*, *Cyttarops*, and *Diclidurus*.

The posterior border of the palate is v-shaped in *Centronycteris* as it is in *Rhynchonycteris*, *Saccopteryx*, and *Cormura*. In contrast, the posterior border of the palate is u-shaped or w-shaped in all other Neotropical emballonurids.

The basisphenoid pits in *Centronycteris* are deep and always separated by a thin median septum. Most other Neotropical emballonurids also have deep basisphenoid pits; the only exceptions are *Cyttarops* and *Rhynchonycteris*, which have very shallow pits that are little more than depressions. A median septum is always present in *Diclidurus* and most species of *Saccopteryx*, and is variably present (entirely absent in some individuals) in *Cormura*, *Balantiopteryx io* and *Saccopteryx canescens*. A septum is apparently always absent in *Rhynchonycteris*, *Peropteryx*, *Balantiopteryx plicata*, and *B. infusca*. A low ridge separates the shallow basisphenoid pits in *Cyttarops*.

All Neotropical emballonurids share the same dental formula: I 1/3, C 1/1, P 2/2, M 3/3 = 32. The only tooth that exhibits significant variation is the anterior upper premolar, often identified as P2 (Miller, 1907; Slaughter, 1970) but probably homologous with P1 of other mammals (Thomas, 1908; Handley, 1959). In *Rhynchonycteris* this tooth is relatively large, triangular in lateral

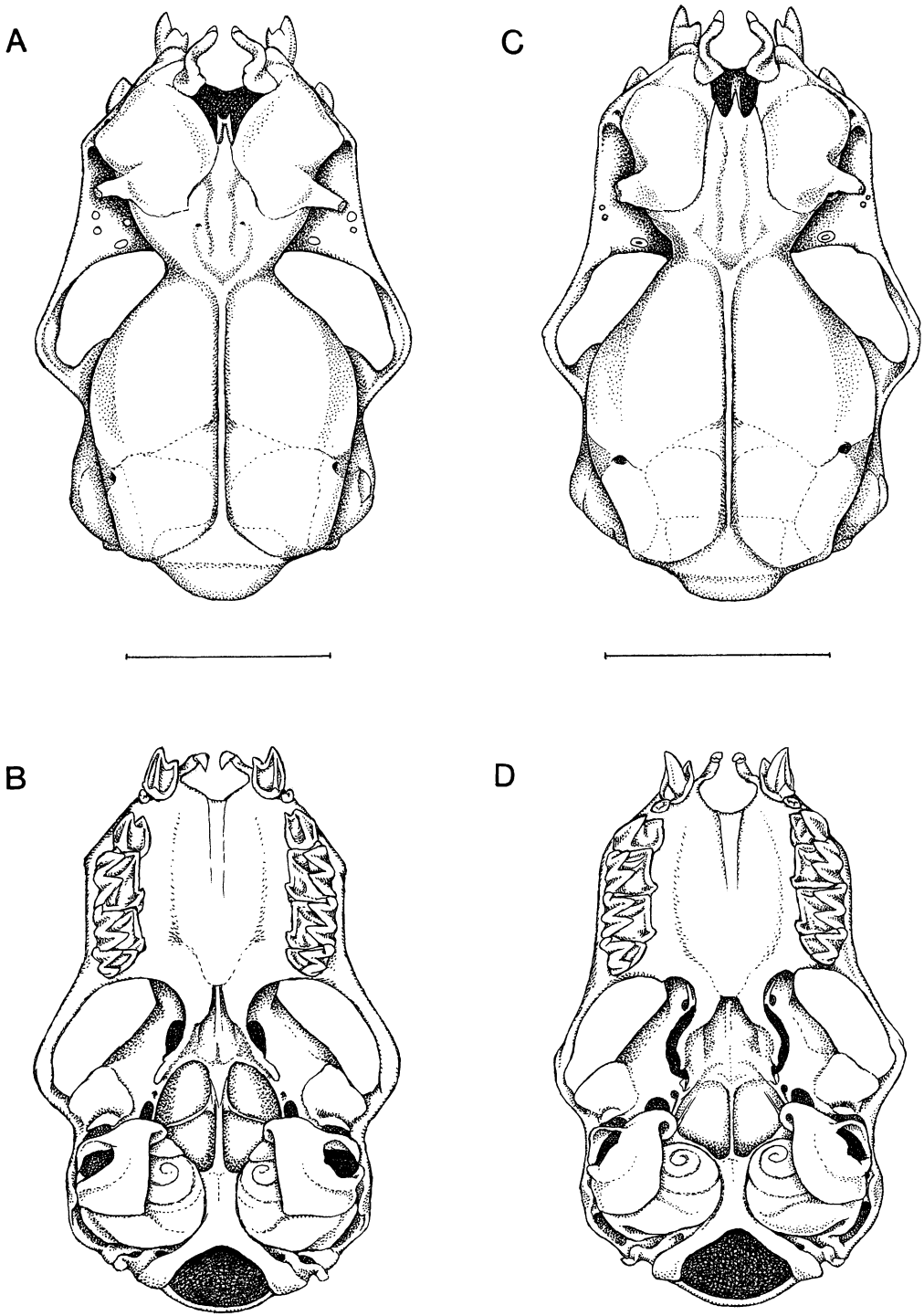


Fig. 4. Dorsal (A) and ventral (B) views of the skull of *Centronycteris maximiliani* (AMNH 267397; male). Dorsal (C) and ventral (D) views of the skull of *Centronycteris centralis* (LSU 9338; male). Scale bars = 5 mm.

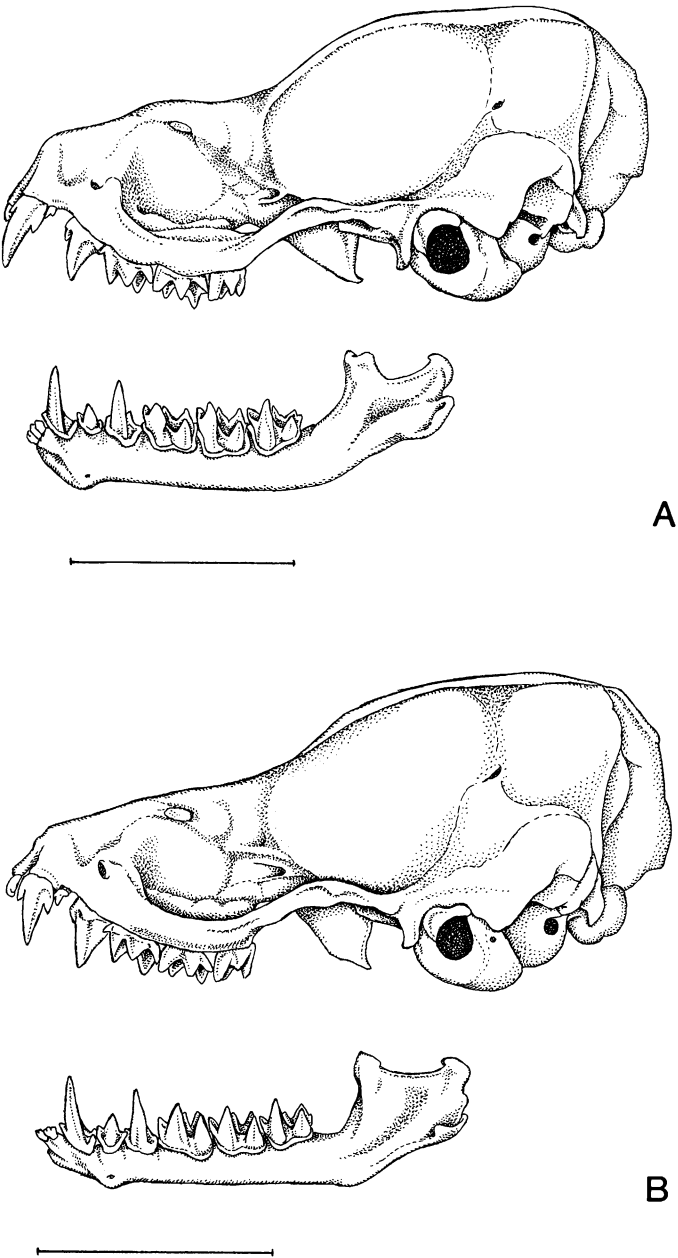


Fig. 5. Lateral views of the skull and lower jaw of (A) *Centronycteris maximiliani* (AMNH 267397; male) and (B) *Centronycteris centralis* (LSU 9338; male). Scale bars = 5 mm.

view, and has small anterior and posterior cingular cusps but no lingual cingulum. It is smaller in *Centronycteris*, *Cormura*, *Cyttarops*, and *Didlidurus*, but retains distinct anterior and posterior cusps, both of which are

located on the margin of a well-developed lingual cingulum. P1 is a tiny, featureless spicule in *Balantiopteryx*, *Saccopteryx*, and *Peropteryx*. Otherwise, apart from size, dental differences between taxa are minimal.

*Centronycteris maximiliani* Fischer

*Vespertilio calcaratus* Schinz, 1821: 180 (not *Vespertilio calcaratus* Rafinesque, 1818).

*Vespertilio maximiliani* Fischer, 1829: 112-113 (replacement name for *Vespertilio calcaratus* Schinz, 1821, which is preoccupied).

*Emballonura calcarata*: Temminck, 1841: 299 (new combination).

*Proboscidea calcarata*: Gray, 1838: 499 (new combination).

*Centronycteris calcarata*: Gervais, 1856: 69 (new combination).

*Saccopteryx calcarata*: Dobson, 1878: 376 (new combination).

*Saccopteryx wiedi* Palmer, 1898: 110 (replacement name for *Vespertilio calcaratus* Schinz, 1821).

*Centronycteris wiedi*: Trouessart, 1904: 98 (new combination).

*Centronycteris maximiliani*: Miller, 1907: 91 (new combination).

TYPE MATERIAL: Carter and Dolan (1978: 21) identified and described the holotype of *Vespertilio calcaratus* as follows:

ZMB (not numbered): adult of undetermined sex; in alcohol; Brazil [Fazenda Coroaba, Rio Jucú, near Rio do Espírito Santo (Wied-Neuwied, 1826: 271)]; Maximilian, Prinz zu Wied-Neuwied; date of capture not specified. Holotype or syntype.

Skin. — Condition poor, originally a mounted skin. Ears relatively long and rather pointed.

Skull. — Partial skull, now in alcohol.

Remarks. — The specimen was collected by Wied-Neuwied and must be one of those on which the name *V. calcaratus* was based.

This is presumably the same specimen described by Schinz (1821), Wied-Neuwied (1826), and Peters (1867). There is no evidence that Schinz (1821) based his description on more than one specimen, and in view of the rarity of this animal more than one is unlikely, so we accept this as the holotype rather than a syntype. Measurements of this specimen provided by Peters (1867, 1872) and Carter and Dolan (1978) are given in table 1.

At our request, Robert Voss examined this specimen in November 1996 at the Zoologisches Museum der Humboldt Universität zu Berlin. He found that this specimen had been cataloged since Carter and Dolan's (1978) publication, and is now labeled ZMB 54654. Voss (personal commun.) found the skin, floating in alcohol, to be in poor condition, but with one forearm still intact. He

measured the forearm according to our instructions and found it to be 45.5 mm in length, not 44.5 mm as reported by Peters (1867), or 46.2 mm as reported by Carter and Dolan (1978).

Voss (personal commun.) noted that the remains of the skull of ZMB 54654 consist of a large piece of the palate bearing the incomplete left maxillary dentition, a bit of the right maxilla with several teeth, and a few isolated maxillary teeth. The rostrum, braincase, and basicranial region are missing. Both mandibles are present and are still joined at the symphysis but they are broken off behind the last molars and the ascending rami are missing. The mandibular tooth rows are intact, but they are imbedded in dried tissue and thus could not be accurately measured.

DISTRIBUTION: Southern Venezuela, Surinam, French Guiana, northern Brazil along the Amazon River, and eastern and southeastern Brazil (fig. 3).

DIAGNOSIS: Rostrum with dorsolateral swelling at base of postorbital process, swellings visible in both dorsal and lateral view; nasals strongly constricted anteriorly between medially expanded maxillae and terminating at level of anterior borders of orbits; basisphenoid pits large, extending anteriorly between the pterygoid processes, each pit divided by a lateral septum into subequal anterior and posterior cells; posterolateral border of palate smoothly curved, not notched; ectotympanic with angular "corner" on posteromedial margin; upper canines somewhat procumbent; P1 small, anteroposterior crown length less than one-fourth of the length of P4; diastema between P1 and P4 large, length greater than or equal to the crown length of P1; mandible robust, depth of ramus at p4/m1 juncture approximately equal to height of p4; anterior border of ascending ramus of coronoid process rises in a gentle curve from immediately behind m3.

COMPARISONS: We are unaware of any external features other than minor size differences that consistently distinguish *Centronycteris maximiliani* from *C. centralis*. Pelage differences may exist, but most specimens of *C. maximiliani* have been preserved in alcohol, thus precluding precise color comparisons. One dry skin of *C. maximiliani*

TABLE 1  
Measurements of Holotypes of *Centronycteris*

	<i>Vespertilio calcaratus</i> ZMB 54654 (= <i>Centronycteris maximiliani</i> ) adult; sex unknown			<i>Centronycteris centralis</i> BMNH 0.7.11.3 adult male		
	Peters (1867, 1872)	Carter and Dolan (1978)	This study <sup>a</sup>	Thomas (1912)	Carter and Dolan (1978)	This study <sup>b</sup>
Total length	75.0 <sup>c</sup>	—	—	70.0	—	[60.0]
Tail length	15.0	—	—	18.0	—	[20.0]
Hind foot length	7.5	—	—	—	—	8.0
Ear length	—	15.0	—	—	—	15.0
Forearm length	44.5	46.2	45.5	45.0	44.8	44.7
Tibia length	—	—	—	—	20.4	19.6
Calcar length	18.0 <sup>c</sup>	—	—	—	—	19.2
Skull length <sup>d</sup>	—	—	—	15.0	—	—
Basisphenoid pit length	—	—	—	1.8	—	1.88
Postorbital breadth	—	—	—	—	3.1	3.06
Lacrimal breadth	—	—	—	—	—	5.85
Zygomatic breadth	—	—	—	10.0	—	—
Maxillary toothrow length	—	—	—	6.1	6.0	5.93
Breadth across molars	—	—	—	6.6	6.6	6.63

<sup>a</sup> Specimen measured by R. Voss at our request; see text for additional discussion.

<sup>b</sup> External measurements given here were recorded by one of us (COH) in 1967. The craniodental measurements were taken by A. Ditchfield in 1997 following a protocol provided by us; see text for a description of measurement methods.

<sup>c</sup> Peters (1867) reported a measurement of 95.0 mm for total length and 31.0 mm for calcar length based on examination of the dried holotype. He subsequently soaked this specimen in an alum solution, remeasured it, and reported revised measurements (given here) in 1872.

<sup>d</sup> This measurement, which was reported by Thomas (1912), is probably equivalent to maximum skull length as measured from the most posterior point on the skull to the most anterior point on the skull. It is not clear whether this included or excluded the premaxillae and incisors, which are often missing in museum specimens of emballonurids.

(BMNH 44.6.9.9) has somewhat darker brown fur than typical of *C. centralis*; however, significance of this difference remains unclear in the absence of additional specimens.

Measurements (table 2) show at least some overlap between *Centronycteris maximiliani* and *C. centralis* in most external and craniodental dimensions. When males and females are considered separately, mean values for *C. maximiliani* are typically smaller than those of *C. centralis* (table 2). Small sample sizes for *C. maximiliani* make meaningful comparisons difficult, but our data indicate non-overlapping differences between *C. maximiliani* and *C. centralis* in forearm length (males only), length of the maxillary toothrow (males only), zygomatic breadth (males only), and length of the basisphenoid pits

(both sexes; table 2). Of these, the only clear difference between the species (which we would expect to be consistently maintained in both sexes even with large sample sizes) is in the length of the basisphenoid pits. This measurement reflects a major morphological difference between *C. maximiliani* and *C. centralis* (see below).

Several craniodental differences clearly distinguish *C. maximiliani* and *C. centralis*. The most obvious of these, originally described by Thomas (1912, 1913), involves the size and extent of the basisphenoid pits. These pits are large and extend anteriorly between the pterygoid processes in *C. maximiliani* (fig. 4B). In contrast, the basisphenoid pits are shorter (table 2) and do not extend anteriorly between the pterygoid processes in *C. centralis* (fig. 4D). The principal

TABLE 2  
Comparative Measurements<sup>a</sup> of *Centronycteris*

	<i>Centronycteris maximiliani</i>			<i>Centronycteris centralis</i>	
	3 males <sup>b</sup>	8 females <sup>c</sup>	8 males <sup>d</sup>	14 females <sup>e</sup>	
Number/Sex	4.5 (4.5)1	6.0 (5.0–9.0)4	4.5 (4.0–5.0)3	5.7 (5.0–6.0)3	
Weight	67.0 (67.0)1	75.0 (63.0–87.0)2	70.0 (60.0–78.0)7	77.0 (70.0–93.0)5	
Total length	26.0 (26.0)1	21.5 (20.0–23.0)2	22.5 (18.0–32.0)6	24.8 (20.0–40.0)5	
Tail length	7.0 (7.0)1	7.0 (6.0–8.0)6	7.3 (7.0–8.5)8	7.8 (7.0–9.0)9	
Hind foot length	17.0 (17.0)1	15.5 (14.0–17.0)4	16.8 (15.0–18.0)5	16.8 (11.0–20.0)5	
Ear length	41.5 (41.5)1	43.6 (42.2–44.7)7	44.9 (42.0–49.0)7	45.9 (42.9–48.1)13	
Forearm length	16.6 (16.6)1	17.7 (17.0–18.3)8	18.4 (16.0–19.7)7	18.5 (18.1–19.2)5	
Tibia length	13.74(13.38–14.11)2	13.62(12.80–14.39)6	13.91(13.38–14.38)3	14.44(13.58–15.39)7	
Condylolcanine length	2.81 (2.76–2.85)2	2.80 (2.50–3.14)5	1.92 (1.78–2.03)5	2.01 (1.84–2.24)10	
Basisphenoid pit length	3.13 (2.95–3.30)2	3.00 (2.90–3.20)7	3.12 (2.86–3.44)5	3.17 (2.89–3.51)9	
Interorbital breadth	6.54 (6.42–6.66)2	6.40 (6.07–6.64)5	6.75 (6.33–6.78)5	6.84 (6.46–7.09)6	
Lacrimal breadth	8.93 (8.93)1	8.86 (8.70–9.31)7	9.38 (9.06–9.66)3	9.51 (8.72–10.11)8	
Zygomatic breadth	7.69 (7.29–8.09)2	7.51 (7.27–8.03)6	7.57 (7.43–7.80)3	7.74 (7.29–8.03)5	
Mastoid breadth	5.62 (5.57–5.67)2	5.78 (5.62–6.00)7	6.11 (5.68–6.56)6	6.17 (5.72–6.53)8	
Maxillary tooththrow length	6.73 (6.73)1	6.56 (6.20–6.77)7	6.94 (6.52–7.55)6	7.08 (6.71–7.52)8	
Breadth across molars	3.87 (3.71–4.07)3	3.71 (3.59–3.90)5	4.06 (3.82–4.30)5	4.06 (3.71–4.42)9	
Length of lower molar row					

<sup>a</sup> Summary statistics (mean, observed range, and sample size) of measurements for each species. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

<sup>b</sup> AMNH 74820, 78858, 267397.

<sup>c</sup> BMNH 12.11.4.3; INPA 2495, 2502, 2541; KU 156014, RMNH 12111; ROM 107081, 107082. Measurements of the RMNH specimen were taken from Husson (1962).

<sup>d</sup> AMNH 63663; BMNH 0.7.11.3; FMNH 41558; LSU 9338; USNM 304864, 535021, 548065; UWZM-NEP 291170-07.

<sup>e</sup> AMNH 269847, 269848; FMNH 41431, 53421, 63949, 98230; KU 32088, 127971; MCZ 7092; MUSM 1078; TTU 30670; USNM 339021, 503827, 514956.



difference between these conditions seems to involve relatively greater development of the anterior section of each pit in *C. maximiliani*. In this species, a low septum extends laterally and somewhat posteriorly across the middle of each pit to a point near the anteromedial corner of the ectotympanic. This septum is also visible in *C. centralis*, but it extends only a short distance into the pit from the lateral wall. The posterior portion of each basisphenoid pit (delineated anteriorly and laterally by the lateral septum and the lateral border of the pits, medially by the median septum, and posteriorly by the posterior border of the pits) is approximately the same size in *C. maximiliani* and *C. centralis*. In contrast, the anterior portions (which lie anterior and lateral to the lateral septum) are of contrasting sizes in these taxa. The anterior portion of each basisphenoid pit is relatively large (subequal to the posterior portion) in *C. maximiliani* (fig. 4B), while it is very small (less than or equal to one-sixth of the area of the posterior portion) in *C. centralis* (fig. 4D).

The functional implications of differences in structure of the basisphenoid pits remain unclear. The basisphenoid pits in *Centronycteris* and other emballonurids partially enclose epithelium-lined air spaces that open ventrally into the nasopharynx, dorsal to the epiglottis (T. Griffiths, personal commun.). These air spaces may function in some way to modify vocalizations, perhaps including those used for echolocation. However, this has never been investigated experimentally, so the function(s) of these airspaces—and the reasons why they vary—remain unknown.

The posterolateral border of the palate is smoothly curved in *C. maximiliani* (fig. 4B). In contrast, a distinct notch is present in the posterolateral border of the palate in *C. centralis* (fig. 4D). The posteromedial outline of the ectotympanic bulla also differs in *C. maximiliani* and *C. centralis*. The ectotympanic forms an angular "corner" posteromedially in *C. maximiliani* (fig. 4B). In contrast, in *C. centralis* the medial margin curves more evenly into the posterior border and the ectotympanic lacks an angular posteromedial corner (fig. 4D).

In lateral view the rostrum in *C. centralis* tapers smoothly from forehead to external

nares with no noticeable break in slope (fig. 5B). In contrast, a dorsolateral swelling is present in the maxilla near the base of the postorbital process in *C. maximiliani* (fig. 5A). While this swelling is not large, it is obvious in lateral view because it protrudes above the otherwise flat rostral profile. Another difference between the species is readily apparent in dorsal views of the skulls (fig. 4). In *C. maximiliani* the nasals are strongly constricted anteriorly between medially expanded maxillae, and they terminate at the level of anterior borders of the orbits (fig. 4A). In contrast, the nasals in *C. centralis* are not constricted between the maxillae and they extend somewhat further anteriorly (fig. 4C).

Dental differences between *C. maximiliani* and *C. centralis* are found principally in the anterior dentition (figs. 4–6). The upper canines are more procumbent in *C. maximiliani* than in *C. centralis* (fig. 5). P1 in *C. maximiliani* is a tiny tooth with a maximum crown length that is less than one-fourth the length of P4 (fig. 6A). In contrast, crown length of P1 is greater than one-fourth (usually approximately one-third) the length of P4 in *C. centralis*. Consequently, P1 in *C. centralis* appears almost twice as large its homolog in *C. maximiliani* (fig. 6B). Largely as a result, the diastema between P1 and P4 is large in *C. maximiliani* (equal to or longer than the crown length of P1), while it is small in *C. centralis* (less than half the length of P1).

The mandible of *C. maximiliani* is robust, with depth of the ramus at the p4/m1 juncture approximately equal to the height of p4 (fig. 5A). The ramus is less robust in *C. centralis*, with depth of the ramus equal to approximately two-thirds the height of p4 (fig. 5B). The anterior border of the ascending ramus of the coronoid process rises in a gentle curve from immediately behind m3 in *C. maximiliani*. In contrast, in *C. centralis* there is a gap between m3 and the anterior border of the ascending ramus, which rises at a steeper angle from the body of the mandible.

**INTRASPECIFIC VARIATION:** Only a few specimens of *Centronycteris maximiliani* are known, so it is difficult to assess within-species variation in this taxon. However, we have noted some differences between speci-

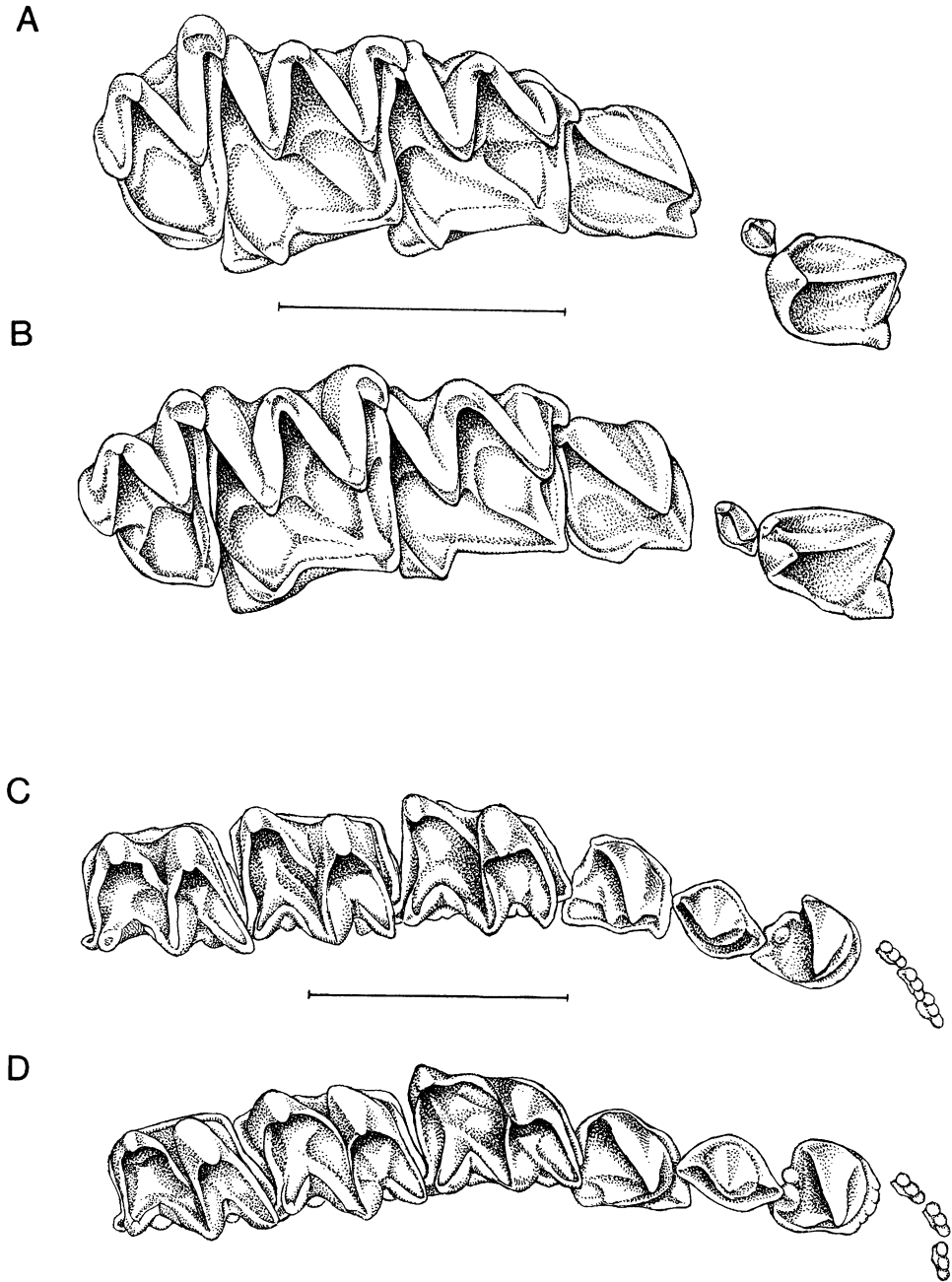


Fig. 6. Close-up occlusal views of the upper right dentition of (A) *Centronycteris maximiliani* (AMNH 267397; male) and (B) *Centronycteris centralis* (LSU 9338; male). Occlusal views of the lower left dentition (C) *Centronycteris maximiliani* (AMNH 267397) and (D) *Centronycteris centralis* (LSU 9338) are shown below. Scale bars = 2 mm.

mens. One of the only females in our sample (INPA 2495) has a somewhat larger, more robust braincase and a stronger sagittal crest than does the male illustrated in figures 4 and 5 (AMNH 267397). P1 is absent and there is no alveolus on one side in INPA 2495; the tooth on the other side is essentially identical to that of AMNH 267397. The anterolabial basal cusp on M1 is relatively large in INPA 2495, but is smaller in AMNH 267397. In the lower dentition, p1 is crowded between the canine and p4 in AMNH 267397. As a result, p1 has an oblique orientation relative to the long axis of the mandible. In contrast, the anterior tooththrow is less crowded and p1 is oriented parallel to the long axis of the mandible in INPA 2495. It is not clear whether these differences are related to age, sex, or simply individual variation; we interpret them as representing normal intraspecific variation of the sort that is common in bats.

**DISCUSSION:** The damaged condition of the holotype (ZMB 54654, described above) raises an important issue not yet addressed: the nature of the evidence that links specimens we have identified as *Centronycteris maximiliani* with the holotype. Unfortunately, this evidence is sparse. The basicranial region and much of the palate of the holotype have been destroyed, so the form of basisphenoid pits and shape of the lateral edges of the posterior palate cannot be observed. Breakage, loss of teeth, and presence of dried tissue obscuring many of the remaining teeth in ZMB 54654 currently preclude meaningful comparisons and craniodental measurements. We assume that our specimens from the Guianas and central and eastern Brazil are conspecific with the holotype of *C. maximiliani* (from southeastern Brazil) principally because of geographic proximity of collecting localities, rather than the presence of known shared diagnostic characters. In this we follow Thomas (1912, 1913: 133), who assumed that a specimen from Pará (BMNH 12.11.4.3) was an "example of the typical Brazilian *C. maximiliani* (*Vespertilio calcarata*, Wied, *nec* Raf; *C. wiedi* Palmer)." Future studies of the damaged holotype of *C. maximiliani* may ultimately reveal diagnostic characters missed in previous examinations of this specimen.

### *Centronycteris centralis* Thomas

*Centronycteris centralis* Thomas, 1912: 638.

*Centronycteris maximiliani centralis*: Sanborn, 1936: 94.

**TYPE MATERIAL:** The holotype of *C. centralis* is BMNH 0.7.11.3, an adult male preserved as a dry skin and skull. It was collected by H. J. Watson on 20 October 1898 at Bogava, Chiriquí. The skin is moderately well preserved but the forearms are broken. The skull is badly damaged and is missing the occiput, zygomatic arches, and postorbital processes. Both mandibles are also broken.

**DISTRIBUTION:** Southern Mexico to Ecuador on the west side of the Andes, and to west-central Peru on the east side of the Andes.

**DIAGNOSIS:** Rostrum without dorsolateral swelling at base of postorbital process, rostral profile tapers smoothly from forehead to external nares without a noticeable break in slope when seen in lateral view; nasals not constricted anteriorly between maxillae, nasals extend anteriorly slightly beyond anterior edges of orbits; basisphenoid pits relatively short, not extending anteriorly between the pterygoid processes and not divided by a lateral septum into subequal anterior and posterior cells; posterolateral border of palate notched; medial and posterior margins of ectotympanic merge in a gentle convex curve with no angular posteromedial "corner;" upper canines not procumbent; anteroposterior crown length of P1 greater than one-fourth (usually approximately one-third) the length of P4, diastema between P1 and P4 small, less than half the crown length of P1; mandible gracile, depth of ramus at p4/m1 juncture approximately equal to two-thirds of the height of p4; gap present between m3 and anterior border ascending ramus, which rises at a steep angle from body of mandible.

**COMPARISONS:** See discussion under *C. maximiliani*. A summary of characters distinguishing *C. centralis* from *C. maximiliani* is given in table 3.

**INTRASPECIFIC VARIATION:** Numerous specimens of *C. centralis* have been prepared as dry skins with skulls, so pelage and craniodental comparisons are possible within this species. Most specimens have dorsal fur that

TABLE 3  
Characters Distinguishing *Centronycteris maximiliani* and *C. centralis*

<i>Centronycteris maximiliani</i>	<i>Centronycteris centralis</i>
Rostrum with dorsolateral swelling at base of postorbital process	Rostrum without dorsolateral swelling at base of postorbital process
Nasals strongly constricted anteriorly between medially expanded maxillae, terminate at level of anterior borders of orbits	Nasals not constricted anteriorly, extend beyond anterior borders of orbits
Basisphenoid pits large, extending anteriorly between pterygoid processes, each pit divided by a lateral septum into subequal anterior and posterior cells	Basisphenoid pits small, not extending anteriorly between the pterygoid processes and not divided by lateral septa into subequal anterior and posterior cells
Posterolateral border of palate smoothly curved, not notched	Posterolateral border of palate notched
Ectotympanic with angular "corner" on posteromedial margin	Ectotympanic without angular posteromedial "corner"
Upper canines somewhat procumbent	Upper canines not procumbent
P1 small, maximum crown length less than one-fourth that of P4; diastema between P1 and P4 large, diastema length equal to or greater than the crown length of P1	Maximum crown length of P1 greater than one-fourth (usually approximately one-third) that of P4; diastema between P1 and P4 small, length less than one-half the crown length of P1
Mandible robust, depth of ramus at p4/m1 juncture approximately equal to height of p4	Mandible gracile, depth of ramus at p4/m1 juncture approximately equal to two-thirds of the height of p4
Ascending ramus of coronoid process rises in gentle curve from immediately behind m3	Gap present between m3 and anterior border of ascending ramus of coronoid process, ascending ramus rises at steep angle from body of mandible

is dull brown with hints of orange (fig. 7). Some individuals are less orange and more gray-brown, but these differences are relatively minor and are difficult to detect unless comparative specimens are in hand.

The most noticeable within-species variation in *C. centralis* involves size. Individuals from Peru and Ecuador are larger than most specimens from Central America. For example, in our sample the only male from Ecuador with an intact forearm (USNM 548065) has a forearm measurement of 49.0 mm, compared with 42.0–45.8 mm. for male specimens from Colombia and Central America (n = 5). Another male from Ecuador (AMNH 63663) has a maxillary tooththrow length of 6.56 mm, compared with 5.68–6.28 mm in Colombian and Central American males (n = 5). However, the pattern is not so clear in females, of which we have a larger sample. Those from Peru and Ecuador are large (forearm 46.4–48.1 mm, maxillary tooththrow 6.11–6.53 mm, n = 3), but not markedly larger than specimens from Colombia (forearm 45.9 mm), Panama (forearm

45.6–47.7 mm, maxillary tooththrow 6.14–6.23 mm, n = 3), Belize (forearm 46.0–47.6 mm, n = 2) and Mexico (forearm = 47.9 mm, maxillary tooththrow 6.15 mm). The smallest female in our sample is from Nicaragua (TTU 30670), which falls between collection localities of larger individuals. We compared the largest and smallest individuals of each sex, but did not find any consistent correlation between morphological variation and geography. Given these findings, the absence of other consistent variation, and the relatively small sample size available, we see no justification for recognizing subspecies at the present time.

We encountered one anomalous specimen during our study: KU 135138, a juvenile female from the Pacific coast of Colombia that exhibits a mosaic of character states not entirely consistent with the diagnoses of either *C. centralis* or *C. maximiliani*. This specimen consists of a relatively well-preserved fluid body (with skin) and a cleaned skull. Measurements are as follows: hind foot length (in alcohol), 7.0 mm; forearm, 42.3 mm; con-



Fig. 7. Photograph of *Centronycteris centralis* taken by M. B. Fenton. This nonreproductive female (7.0 g; forearm 41.0 mm) was captured in a mist net on 17 February 1998 at the Cana Palma Biological Station, Tortuguero, Costa Rica. The capture site was on a narrow trail through secondary growth approximately 20 m from a cleared field next to the ocean. The bat was flying approximately 3 m above the ground at the time of her capture at 18:05 h. She was released after this photograph was taken.

dylocanine length, 13.32 mm; basisphenoid pit length, 2.19 mm; interorbital breadth, 3.05 mm; zygomatic breadth, 8.25 mm; maxillary tooththrow length, 5.85 mm; breadth across molars, 6.09 mm; and length of lower molar row, 3.70 mm. The geographic location of the collection locality and the small size of the basisphenoid pits (which do not extend anteriorly between the pterygoids) lead us to tentatively identify this specimen as *C. centralis*. However, some morphologi-

cal features are not consistent with this identification. The forearm measurement of this specimen (42.3 mm) is smaller than found in any adult female *C. centralis* (42.9–48.1 mm; table 2), and is much smaller than seen in any of the South American specimens that we examined (45.9–48.1 mm). This difference may be due to age, as some of the epiphyses in KU 135138 are not yet closed. However, other measurements of this specimen are also unusually small, including some

that should not be affected by further ontogenetic changes (e.g., length of the lower molar row). P1 is very small and lateral edge of the posterior palate lacks a notch in KU 135138, more closely resembling the condition in *C. maximiliani* than that of *C. centralis*. It is possible that the mosaic of features seen in this specimen is diagnostic of an unrecognized third species of *Centronycteris*. However, testing this hypothesis will require additional specimens not available at present, and/or application of molecular systematic methods beyond the scope of the current study.

**DISCUSSION:** So few specimens of *Centronycteris* are known that it is probable that the geographic ranges of both species are larger than indicated in figures 2 and 3. Although *C. centralis* and *C. maximiliani* have never been collected in sympatry, no known biogeographic barriers separate these taxa. We would not be surprised to find the two species in sympatry in the Amazon basin (e.g., in northeastern Peru) or in the evergreen forests of Venezuela. It is hoped that continued collecting will lead to future improvements in our knowledge of both geographic distribution patterns and morphological variation in *Centronycteris*.

## PHYLOGENETIC RELATIONSHIPS

Monophyly of *Centronycteris* (including *C. maximiliani* and *C. centralis*) is suggested by the suite of characters discussed previously under the generic account for *Centronycteris*. This mosaic of characters includes at least one unambiguous synapomorphy shared by both species: attachment of the edge of wing membrane to the side of the foot at the level of metacarpal-phalangeal joint. This derived feature is not seen in any other emballonurid bat (J. Dunlop, personal commun.).

The phylogenetic relationships of *Centronycteris* to other emballonurids have been addressed in only a few studies. It has long been recognized that *Centronycteris* is related to other Neotropical emballonurids, but there has been little agreement about which taxa are its closest relatives. Peters (1872) suggested that *Centronycteris* resembles *Saccopteryx* in the shape of the ears, tragus, and overall form of the skull, but is more like

*Peronymus* and *Rhynchonycteris* in having a broad mesopterygoid fossa and weak zygomatic arches. Dobson (1878) cited Peter's (1872) observations, added his own (mistaken) conclusion from misreading Peters that *Centronycteris calcarata* (= *Centronycteris maximiliani*) had a wing sac, and transferred this species to the genus *Saccopteryx* along with species previously referred to *Balaniopteryx*, *Peropteryx*, and *Peronymus*. The general conclusion that *Centronycteris* (recognized as either a distinct genus or subgenus) was closely related to *Saccopteryx* and/or other sac-winged Neotropical emballonurids was widely accepted for most of the next half-century (e.g., Palmer, 1898; Miller, 1907; Goldman, 1920; Allen and Barbour, 1923).

Miller (1907) contrasted *Centronycteris* to a group including *Saccopteryx*, *Cormura*, *Peropteryx*, and *Peronymus* in a key in his influential monograph on the families and genera of bats. All five taxa were noted as having wing sacs and "premaxillaries well developed above, their extremities lying distinctly on upper surface of rostrum" (Miller, 1907: 85). Within this group, *Centronycteris* was distinguished from the other genera on the basis of form of the zygomatic arch, which is greatly expanded anteriorly and covers the toothrow in dorsal view in *Saccopteryx*, *Cormura*, *Peropteryx*, and *Peronymus* but not in *Centronycteris*.

Almost 60 years after Dobson (1878) mistakenly attributed wing sacs to *Centronycteris*, Sanborn (1937: 324) corrected this error and, in a key based on external characters, grouped *Centronycteris* with *Rhynchonycteris* because these are the only "emballonurines" that lack a wing sac. In a subsequent key based on craniodental morphology, Sanborn (1937: 324) grouped *Centronycteris* with *Cormura* because they share a common morphology of the anterior upper premolar ("round, with anterior and posterior cusps"). In another key based on skull morphology, Dalquest et al. (1950) grouped *Centronycteris* with *Cormura* based on premolar morphology and presence of a median septum dividing the basisphenoid pits. However, placement in a key cannot be assumed to represent a hypothesis of relationships, and it was not until the 1970s that the phylogenetic

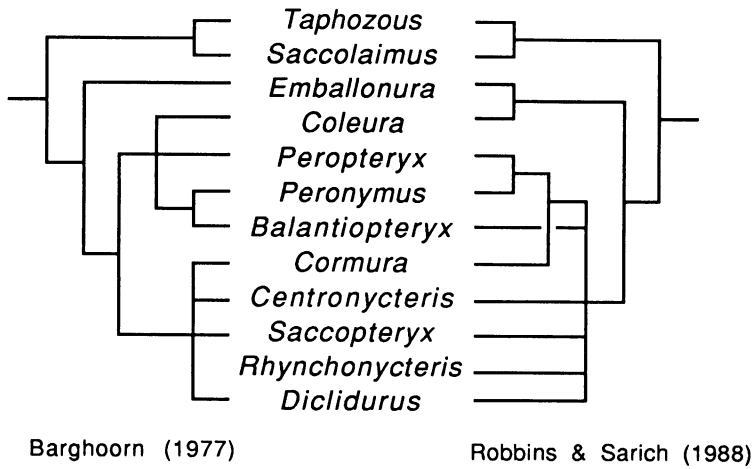


Fig. 8. Two phylogenies illustrating the possible relationships of *Centronycteris* and other emballonurids. The phylogeny of Barghoorn (1977) was based on craniodental characters; that of Robbins and Sarich (1988) was based on immunological and allozyme data.

relationships of *Centronycteris* were explicitly addressed.

The first phylogenetic analysis including *Centronycteris* was that of Barghoorn (1977), who considered only craniodental features. In a manual cladistic analysis of 23 characters scored in 13 taxa, he found that *Centronycteris* fell in an unresolved clade containing *Cormura*, *Saccopteryx*, and *Diclidurinae* (*Cyttarops* + *Diclidurus*; fig. 8). The sister-group to this clade was another large clade including *Balantiopteryx*, *Peropteryx*, *Peronymus*, and *Coleura*. A survey of the derived characters linking *Centronycteris* with other taxa reveals that, as far as Barghoorn's data are concerned, *Centronycteris* is identical to *Cormura* and falls within the range of variation seen in *Saccopteryx*. *Rhynchonycteris* was not included in Barghoorn's (1977) study.

Robbins and Sarich (1988) included *Centronycteris* in an analysis of emballonurid relationships based on allozymes and immunological distance data. A manual locus-by-locus cladistic analysis of the allozyme data placed *Centronycteris* in a clade with *Saccopteryx*, *Balantiopteryx*, *Rhynchonycteris*, and *Diclidurus* (Robbins and Sarich, 1988). Alternatively, they placed *Centronycteris* in a large, unresolved group with *Emballonura*, *Coleura*, *Balantiopteryx*, *Diclidurus*, *Cormura*, *Peropteryx*, *Peronymus*, *Rhynchonyc-*

*teris*, and *Saccopteryx* based on analysis of albumin and transferrin immunological distances. The distance data reported by Robbins and Sarich (1988: table 3) suggest that *Centronycteris* is most similar immunologically to *Cormura* and *Rhynchonycteris*. However, it is not clear if this similarity is relatively primitive (symplesiomorphic) or derived (synapomorphic).

At the conclusion of their study, Robbins and Sarich (1988: fig. 4) summarized the results of their allozyme and immunological studies in a single tree shown in figure 8. This phylogenetic tree indicated that Neotropical emballonurids form a monophyletic group, but did not provide resolution of most relationships within that clade.

Results of the studies discussed above suggests that *Centronycteris* is probably closely related to *Cormura* (with which it shares immunological similarities and derived craniodental features), *Rhynchonycteris* (with which it shares immunological similarities and derived isozymes), *Saccopteryx* (with which it shares derived craniodental features and isozymes), and/or *Balantiopteryx* (with which it shares derived isozymes). Lack of a wing sac in *Rhynchonycteris* and *Centronycteris*, which we interpret as a plesiomorphic character, leads us to suspect that these taxa may lie near the base of the Neotropical emballonurid clade, outside the clade that in-



cludes *Cormura*, *Saccopteryx* and *Balantiopteryx* (taxa that have wing sacs). A formal phylogenetic analysis of relationships among Neotropical emballonurids (including both species of *Centronycteris*) will be presented elsewhere.

### NATURAL HISTORY

Little is known about the natural history of *Centronycteris*. Habitat preferences are poorly understood, although some patterns emerge from a review of collection records. Several specimens have been shot on the wing, presumably while foraging or commuting from one location to another (e.g., AMNH 74820; FMNH 41558; KU 32088, 156014). Others have been shot while roosting (AMNH 267397), caught in hand nets (e.g., USNM 304864; UWZM-NEP 291170-07), or captured in harp traps set along trails (e.g., KU 127971). Several specimens have been recovered from ground-level mist nets (e.g., TTU 30670; USNM 503827, 514956, 535021) or nets 6 to 10 m above the ground (e.g., ROM 107081, 107082; TTU 13419). Recent advances in acoustic monitoring techniques now make it possible to identify *Centronycteris* by its echolocation calls (B. Miller, personal commun.; E. Kalko, personal commun.), but ecological studies using these methods have not yet been completed. Collection records thus form the basis of our limited understanding of the ecology of *Centronycteris*.

Most known specimens of *Centronycteris* have been collected in lowland forest at elevations between sea level and 300 meters, but *C. centralis* is also known from localities between 1160 and 1450 m in Panama, Ecuador, and Peru (see Gazetteer). Peters (1872) described an individual reputedly from the "high plains" of Peru, but this specimen appears to have been subsequently lost and no detailed locality information is available (see discussion in Tuttle [1970] and Koopman [1978]).

Starrett and Casebeer (1968: 4) offered the following observations about habitat requirements of *Centronycteris* based on their experiences with *C. centralis* in Costa Rica:

that it requires relatively heavy forest (possibly virgin stands) in which to live. The very slow and highly maneuverable, floppy flight of this species makes it well-adapted to hunting insects among trees and along natural (and now man-made) pathways and clearings. The three specimens reported here were all collected in just such situations.

These observations are in agreement with many but not all collection records for *Centronycteris*. Most collection localities for *C. centralis* and *C. maximiliani* are apparently dominated by primary evergreen rainforest (e.g., Dalquest et al., 1950; Starrett and Casebeer, 1968; La Val, 1977; Greenbaum and Jones, 1978; Albuja, 1982; Williams et al., 1983; Reis and Peracchi, 1987; personal obs.). Degree of development of forest growth at these localities has been described as ranging from "dense" (e.g., Dalquest et al., 1950: 431; Reis and Peracchi, 1987: 167) to "dense . . . with moderately developed understory" (Williams et al., 1983). In Guyana, specimens of *C. maximiliani* were collected in poorly drained lowland forest dominated by *Mora*, *Pentaclethra*, and *Licania* trees (Pakatau Falls; see Gazetteer) but also nearby in well-drained forest dominated by *Chlorocardium*, *Eperua*, and *Escheweilera* (Burro Burro River; B. Lim, personal commun.). In addition to lowland rainforest habitats, one specimen of *C. maximiliani* from Venezuela was collected in a region dominated by "sclerophile evergreen forest" (McCarthy and Ochoa, 1991), another specimen from Surinam was collected in "savanna forest" (Husson, 1962, 1978), and a specimen of *C. centralis* was taken in ridgetop cloud forest in Panama (USNM 339021). These records suggest some degree of flexibility in habitat requirements. *Centronycteris centralis* has been recorded several times in disturbed forest, including (1) in secondary forest in Colombia (UMZM-NEP 291170-07), (2) on trails through secondary forest in central Panama (USNM 503927, 514956, 535021) and Costa Rica (see fig. 7), and (3) in Nicaragua in a telegraph right-of-way through second growth forest in which logging was underway (Baker and Jones, 1975). In the latter instance, several individuals were sighted "traveling extremely slowly and in a straight path along the right of way" (Baker and Jones 1975: 1).

The rarity of specimens of *Centronycteris* . . . , in the light of our limited experience with this bat, suggests



Little is known about the roosting requirements of *Centronycteris* species. Female *C. centralis* have been collected from tree holes in Ecuador (FMNH 41431; Sanborn, 1936) and Belize (FMNH 63949; Sanborn, 1941), suggesting that these bats may roost in tree holes during the day. However, one of us (COH; 17 February 1991) found a *C. centralis* of unknown sex hanging at midday 5 m above the ground under a large *Philodendron* leaf in the subcanopy in tall secondary forest in Panama. When disturbed, the bat flew to another *Philodendron* leaf on another tree in the subcanopy. This sighting is similar to that reported for a male *C. maximiliani* (AMNH 267397), which was "shot at 4 PM while hanging from underside of large Melastamaceae leaf, about 3 m above ground in well-drained primary forest" in French Guiana (R. Voss, field notes for 31 August 1993). It is not clear whether this was the day roost of this bat, or an interim roost used prior to the start of foraging.

Several reports of *Centronycteris* have noted that they may be active before dark. The specimen of *C. centralis* collected by Dalquest in Mexico (KU 32088) was shot while flying in the late afternoon (Dalquest et al., 1950). Another specimen captured on Barro Colorado Island by C. B. Koford (USNM 304864) was caught with a hand net in the "evening," possibly before it was fully dark. The individual shown in figure 7 was captured in a net while flying along a trail in Costa Rica at 18:05 h. At Burro Burro River in Guyana, a specimen of *C. maximiliani* (KU 156014) was shot while it was flying in the forest at 1700 h.

As with other aspects of natural history, little is known about reproduction in *Centronycteris*. Two pregnant female *C. centralis* were captured in mid-May in Costa Rica, each with a single, large fetus (length 19 mm in specimen collected; La Val, 1977). Similarly, a pregnant *C. centralis* was captured in late May in Nicaragua (Greenbaum and Jones, 1978). In Ecuador, a female *C. centralis* pregnant with a 9 mm fetus was collected in March (Albuja, 1982). A female *Centronycteris maximiliani* collected in central Brazil (INPA 2495) was lactating at the

time of her capture in mid-February. Nothing else is known about reproduction in these species.

#### ACKNOWLEDGMENTS

We give special thanks to E. Sampaio and E. Bernard for kindly allowing us to study the specimens of *Centronycteris* that they collected near Manaus, to B. Miller for providing the specimens from Gallon Jug, Belize, and to M. Engstrom, B. Lim, and R. Timm for permission to study their specimens from Guyana. A. Ditchfield and R. Voss examined specimens for us in the BMNH and ZMB, for which we thank them. T. Conway, A. Ditchfield, J. Dunlop, A. Gardner, and T. Griffiths provided helpful reviews of earlier versions of this manuscript, and we thank them for their comments and suggestions. We also sincerely thank R. Angermann (ZMB), R. Baker and R. Monk (TTU), M. Engstrom and B. Lim (ROM), M. Hafner (LSU), P. Jenkins (BMNH), V. Pacheco (MUSM), B. Patterson, L. Heaney, and W. Stanley (FMNH), J. Patton and B. Stein (MVZ), M. Rutzmoser (MCZ), and R. Timm and T. Holmes (KU) for permitting us to study specimens in their care. T. Conway organized the gazetteer and plotted localities for figures 2 and 3, and P. Brunaeur was responsible for locating most of the references cited in this study. We thank them both for their efforts and patience. P. Wynne worked her customary magic with the line illustrations, for which we are grateful. Special thanks also to B. Fenton for permission to use the photograph reproduced in figure 7, and to J. Dunlop for providing the capture data for the specimen shown in that photograph. The collection of a *Centronycteris* at Paracou, French Guiana, stimulated this study, and we thank the National Geographic Society (grant number 4991-93) and the American Museum of Natural History Taxonomic Mammalogy Fund for support of that project. Studies of *Centronycteris* in Panama were made possible by the Environmental Sciences Program and Research Opportunities Fund of the Smithsonian Institution, and by a gift from James and Paula Nelson, Hillsboro, Oregon.

## REFERENCES

- Albuja, V. L.  
1982. Murciélagos del Ecuador. Quito, Ecuador: Esc. Politécnica Nac., Depto. Cienc. Biol., 285 pp.
- Allen, G. M., and T. Barbour  
1923. Mammals from Darien. Bull. Mus. Comp. Zool. Harvard 65: 259–274.
- Baker, R. J., and J. K. Jones  
1975. Additional records of bats from Nicaragua, with a revised checklist of Chiroptera. Occas. Pap. Mus. Texas Tech Univ. 32: 13 pp.
- Barghoorn, S. F.  
1977. New material of *Vespertiliavus* Schlosser (Mammalia, Chiroptera) and suggested relationships of emballonurid bats based on cranial morphology. Am. Mus. Novitates 2618: 29 pp.
- Carter, D. C., and P. G. Dolan  
1978. Catalogue of type specimens of Neotropical bats in selected European museums. Spec. Publ. Mus. Texas Tech Univ. 15: 136 pp.
- Dalquest, W. W., W. G. Frum, and E. R. Hall  
1950. A northern record for *Centronycteris maximiliani centralis* with a key to the skulls of North American emballonurine bats. Ann. Inst. Biol. Mex. 21: 431–433.
- Dobson, G. E.  
1878. Catalogue of the Chiroptera in the collection of the British Museum. London: British Museum (Natural History). 567 pp.
- Fischer, J. B.  
1829. Synopsis Mammalium. Stuttgart: J. G. Cotta. 752 pp.
- Gervais, P.  
1856. Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para; exécutée par ordre du Gouvernement Français pendant les années 1843 à 1847, sous la direction du Comte Francis de Castelnau. Paris: P. Bertrand. 1(2): 116 pp. [Dated 1855 but published in 1856; see Sherborn and Woodward, 1901, Ann. Mag. Nat. Hist. Ser. 7, 8: 161–164, 333–336, and 491–494 for dates of publication].
- Goldman, E. A.  
1920. Mammals of Panama. Smithsonian Misc. Collect. 69: 309 pp.
- Goodwin, G. G.  
1947. Mammals of Costa Rica. Bull. Am. Mus. Nat. Hist. 87: 271–474.
- Gray, J. E.  
1838. A revision of the genera of bats (Vespertilionidae), and the description of some new genera and species. Mag. Zool. Bot. 2: 483–505.
1843. Mammalia. In R. B. Hinds (ed.), The zoology of the voyage of H. M. S. Sulphur: under the command of Captain Sir Edward Belcher during the years 1836–42. London: Smith, 1: 9–36.
- Greenbaum, I. F., and J. K. Jones  
1978. Noteworthy records of bats from El Salvador, Honduras, and Nicaragua. Occas. Pap. Mus. Texas Tech Univ. 55: 7 pp.
- Griffiths, T. A., and A. L. Smith  
1991. Systematics of emballonuroid bats (Chiroptera: Emballonuridae and Rhinopomatidae) based on hyoid morphology. Bull. Am. Mus. Nat. Hist. 206: 62–83.
- Hall, E. R.  
1981. Mammals of North America. 2nd ed. New York: Wiley.
- Handley, C. O., Jr.  
1959. A revision of American bats of the genera *Euderma* and *Plecotus*. Proc. U.S. Natl. Mus. 110: 95–246.
1966. Checklist of the mammals of Panama. In R. L. Wenzel and V. J. Tipton (eds.), Ectoparasites of Panama: 753–795. Chicago: Field Museum.
- Husson, A. M.  
1962. The bats of Suriname. Leiden, J. Brill. 282 pp.
1978. The mammals of Suriname. Zoöl. Monogr. Rijksmus. Nat. Hist. 2: 569 pp.
- Koopman, K. F.  
1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. Am. Mus. Novitates 2651: 33 pp.
1993. Order Chiroptera. In D. E. Wilson and D. M. Reeder (eds.), Mammal species of the world, a taxonomic and geographic reference, 2nd ed.: 137–241. Washington, D. C.: Smithsonian Institution Press.
1994. Chiroptera: Systematics. Handbook of zoology, vol. 8, pt. 60, Mammalia. 217 pp. Berlin: Walter de Gruyter.
- LaVal, R. K.  
1977. Notes on some Costa Rican bats. Brevnesia 10/11: 77–83.

- Lemke, T. O., A. Cadena, R. H. Pine, and J. Hernandez-Camacho  
 1982. Notes on opossums, bats, and rodents new to the fauna of Colombia. *Mammalia* 46: 225–234.
- Matschie, P.  
 1899. Die Fledermäuse des Berliner Museums für Naturkunde. 1. Lieferung. Die Megachiroptera des Berliner Museums für Naturkunde. Berlin: Georg Reimer. 103 pp.
- McCarthy, T. J., and J. O. Ochoa  
 1991. The presence of *Centronycteris maxilliani* and *Micronycteris daviesi* (Chiroptera) in Venezuela. *Texas J. Sci.* 43: 332–334.
- McKenna, M. C., and S. K. Bell  
 1997. Classification of mammals above the species level. New York: Columbia Univ. Press.
- Miller, G. S.  
 1907. The families and genera of bats. U.S. Natl. Mus. Bull. 57: 282 pp.
- Palmer, T. S.  
 1898. Random notes on the nomenclature of the Chiroptera. *Proc. Biol. Soc. Washington*. 12: 109–114.  
 1904. Index generum mammalium: a list of the genera and families of mammals. *N. Am. Fauna* 23: 1–984.
- Paynter, R. A.  
 1982. Ornithological gazetteer of Venezuela. Cambridge, MA: Museum of Comparative Zoology.
- Peters, W.  
 1867. Über die zu den Gattungen *Mimon* und *Saccopteryx* gehörigen Flederthiere. *Monatsber. K. Preuss. Akad. Wiss. Berlin* 1867: 469–481.  
 1872. Über den *Vespertilio calcaratus* Prinz zu Wied und eine neue Gattung der Flederthiere, *Tylonycteris*. *Monatsber. K. Preuss. Akad. Wiss. Berlin* 1872: 699–706.
- Rafinesque, C. S.  
 1818. Further discoveries in natural history made during a journey through the western region of the United States. *Am. Mon. Mag. Crit. Rev.* 3: 445–447.
- Reis, N. R., and A. L. Peracchi  
 1987. Quirôpteros da região de Manaus, Amazonas, Brasil (Mammalia, Chiroptera). *Bull. Mus. Emilio Goeldi, Ser. Zool.* 3: 161–182.
- Robbins, L. W., and V. M. Sarich  
 1988. Evolutionary relationships in the family Emballonuridae (Chiroptera). *J. Mammal.* 69: 1–13.
- Sanborn, C. C.  
 1936. Records and measurements of Neotropical bats. *Field Mus. Nat. Hist. Publ. Zool. Ser.* 10: 93–106.  
 1937. American bats of the subfamily Emballonurinae. *Field Mus. Nat. Hist. Publ. Zool. Ser.* 20: 321–354.  
 1941. Descriptions and records of Neotropical bats. *Field Mus. Nat. Hist. Publ. Zool. Ser.* 27: 371–387.
- Schinz, H. R.  
 1821. Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Vol. 1, 894 pp. J. S. Cottaschen. [German translation of Cuvier. Includes original description of *Vesp.[ertilio] calcaratus*, which was collected by Wied-Neuwied. Schinz, not Cuvier or Wied-Neuwied, is the author of this name].
- Slaughter, B. H.  
 1970. Evolutionary trends of chiropteran dentitions. In: B. H. Slaughter and W. D. Walton (eds.), *About bats*, *Fondren Sci. Ser.* 11: 51–83. Dallas: Southern Methodist Univ. Press.
- Starrett, A., and R. S. Casebeer  
 1968. Records of bats from Costa Rica. *Los Angeles Co. Mus. Contrib. Sci.* 148: 21 pp.
- Temminck, C. J.  
 1841. Monographies de mammalogie, ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différens musées de l'Europe. Tome 2. Leiden: C. Van der Hoek.
- Thomas, O.  
 1908. The missing premolar of the Chiroptera. *Ann. Mag. Nat. Hist. Ser.* 8, 1: 346–348.  
 1909. Notes on some South-American mammals, with descriptions of new species. *Ann. Mag. Nat. Hist. Ser.* 8, 4: 230–242.  
 1912. New *Centronycteris* and *Ctenomys* from S. America. *Ann. Mag. Nat. Hist. Ser.* 8, 10: 638–640.  
 1913. On some rare Amazonian mammals from the collection of the Pará Museum. *Ann. Mag. Nat. Hist. Ser.* 8, 11: 130–136.
- Trouessart, E.-L.  
 1897. *Catalogus mammalium tam viventium quam fossilium*. Nova editio (primo completa). Fasc. 1. Primates, Prosimiae, Chiroptera, Insectivora. Berlin: R. Friedländer, 218 pp.

1904. *Catalogus mammalium tam viventium quam fossilium. Quinquennale supplementum, anno 1904, Fasc. 1, pp. 1–288.* Berlin: R. Friedländer, 929 pp.
- Tuttle, M. D.  
1970. Distribution and zoogeography of Peruvian bats, with comments on natural history. *Univ. Kansas Sci. Bull.* 49: 45–86.
- Wied-Neuwied, Maximilian Prinz zu  
1822–31. *Abbildungen zur Naturgeschichte Brasiliens. Recueil de planches coloriées d'animaux du Brésil.* Weimar. (For dates of publication see *Cat. Libr. Brit. Mus. [Nat. Hist.]*, 1915, vol. 5, p. 2315).
1826. *Beiträge zur Naturgeschichte von Brasilien. Verzeichniss der Amphibien, Säugethiere und Vögel, welche auf einer Reise zwischen dem 13ten und dem 23sten Grade südlicher Breite im östlichen Brasilien beobachtet wurden. II. Abt. Mammalia. Säugethiere. 2: 620 pp.* Weimar.
- Williams, S. L., H. H. Genoways, and J. A. Groen  
1983. Results of the Alcoa Foundation-Suriname Expeditions. VII. Records of mammals from central and southern Suriname. *Ann. Carnegie Mus.* 52: 329–336.

### Appendix: Specimens Examined

The following list includes all specimens examined in this study. See "Gazetteer" for institutional abbreviations and detailed locality and specimen information for *Centronycteris*.

***Centronycteris*:** *Centronycteris centralis*: **Mexico:** KU 32088; **Belize:** AMNH 269847, 269848; FMNH 63949; **Guatemala:** FMNH 41558; **Nicaragua:** TTU 30670; **Costa Rica:** KU 127971; LSU 9338; MCZ 7092; **Panama:** BMNH 0.7.11.3 (holotype); MVZ 108943; USNM 304864, 311571, 339021, 503827, 514956, 535021; **Colombia:** FMNH 98230; KU 135138; UWZM-NEP 291170-07; **Ecuador:** AMNH 63663; FMNH 41431, 53421; USNM 548065; **Peru:** MUSM 1078; *Centronycteris maximiliani*: **Venezuela:** AMNH 74820; **Guyana:** KU 156014; ROM 107081–107082; **French Guiana:** AMNH 267397; **Brazil:** AMNH 78858; INPA 2495, 2502, 2541; BMNH 12.22.4.3; 44.6.9.9; ZMB 54654 (holotype).

**Other Emballonuridae:** *Balantiopteryx io* (AMNH 185765, 214401–214403); *Balantiopteryx plicata* (AMNH 175388–175389, 189577–189578); *Cormura brevirostris* (AMNH 74103, 265994,

266001–266004, 266008–266009, 267069–267070, 267072–267075, 267077–267079, 267394, 267819–267831); *Cyttarops alecto* (USNM 566432–566434); *Diclidurus albus* (AMNH 99310, 149167, 214183; USNM 120577, 407097–404099, 534417); *Diclidurus ingens* (USNM 407091–407092); *Diclidurus isabellus* (USNM 388542–388544); *Diclidurus scutatus* (AMNH 95779, 99309, 142908, 267832; USNM 407102–407103); *Peropteryx leucoptera* (AMNH 266011–266014, 267087–267088, 267280); *Peropteryx macrotis* (AMNH 209227, 210518, 266006–266007); *Peropteryx kappleri* (AMNH 61486–61494, 239068, 265989–265990); *Peropteryx trinitatus* (AMNH 7493–7495, 17556, 175558–175559); *Rhynchonycteris naso* (AMNH 209190–209191, 209205, 209213–209215, 210455, 248745, 265981, 265986, 265988); *Saccopteryx bilineata* (AMNH 210461, 265962–265965, 267059, 267061–267063, 267374–267378); *Saccopteryx canescens* (AMNH 94366, 164753; USNM 392995); *Saccopteryx gymnura* (AMNH 93519–93520, 265967, 267843; USNM 392995, 460080); *Saccopteryx leptura* (AMNH 265968–265973, 267065–267066, 267380–267386, 267844–267849).

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site <http://nimidi.amnh.org>. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: [scipubs@amnh.org](mailto:scipubs@amnh.org)