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A NEW SPECIES OF *CAROLLIA* (CHIROPTERA: PHYLLOSTOMIDAE) FROM THE ANDES OF PERU AND BOLIVIA

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ABSTRACT

Carollia is a genus of relatively common phyllostomid bats. Six species are recognized: *brevicauda*, *castanea*, *colombiana*, *perspicillata*, *sowellii*, and *subrufa*. In this paper, we describe and name a new species from the montane forests of Peru and Bolivia. The new taxon was first taken in Puno department, southeastern Peru, more than 50 years ago. Now, a series of 23 specimens documents the

distribution of this species from Cuzco, Madre de Dios, and Puno departments in southeastern Peru to La Paz department, in northern Bolivia, and from 1300 to 2250 m in elevation. The new species has been found to be sympatric with *brevicauda* at several localities, and both are sympatric with *perspicillata* at a single locality in Cuzco. We outline and discuss the distribution of the new species and of others of the genus *Carollia*.

RESUMEN

Carollia es un género de murciélagos filostómidos relativamente comunes. Seis especies son reconocidas en el género: *brevicauda*, *castanea*, *colombiana*, *perspicillata*, *sowellii* y *subrufa*. En este trabajo, describimos una nueva especie de los bosques montanos de Perú y Bolivia. Esta nueva especie fue colectada por primera vez en Puno, en el sureste de Perú, hace mas de 50 años. Actualmente, 23 especímenes documentan la distribución de esta especie

en los departamentos de Cuzco, Madre de Dios, y Puno en el sureste del Perú, y el departamento de La Paz en el norte de Bolivia, de 1300 a 2250 m de elevación. Esta nueva especie es simpátrica con *brevicauda* en varias localidades, mientras que ambas especies son simpátricas con *perspicillata* en una única localidad en Cuzco. Se incluye comentarios sobre la distribución de esta nueva especie y otras del género *Carollia*.

INTRODUCTION

The short-tailed bats of the genus *Carollia* are among the most common and better known bats in the Neotropics (Fleming 1988). Four species were recognized in the most recent summaries of the genus (Koopman 1993, 1994): *Carollia perspicillata* (Linnaeus 1758), *C. brevicauda* (Schinz 1821), *C. castanea* H. Allen 1890, and *C. subrufa* (Hahn 1905); however, two additional species, *C. colombiana* Cuartas et al., 2001, and *C. sowelli* Baker et al. 2002, were recently described. Some species of *Carollia* are extensively distributed in the Neotropics (e.g., *C. brevicauda*, *C. castanea*, and *C. perspicillata*), whereas others have geographic ranges restricted to Middle America (e.g., *C. sowelli* and *C. subrufa*) or to the northern Andes of Colombia (*C. colombiana*) (see Pine 1972; Koopman 1993; Cuartas et al. 2001; Baker et al. 2002). The systematic status of the species in the genus has remained largely unmodified since the last taxonomic revision by Pine (1972). His conclusions were followed in more recent summaries (Honacki et al. 1982; Corbet and Hill 1991; Koopman 1993, 1994), in morphometric analyses (McLellan 1984; Owen et al. 1984), and in phylogenetic analyses (Lim and Engstrom 1998; Wright et al. 1999). Pine (1972) remarked on several specimens he was not able to allocate to any recognized species, either because samples consisted of single individuals or because of imprecise character definition. One of those specimens was a male caught in 1950 by Hilda Hempl Heller from San Juan, Sandia Province, Puno Department, Peru (FMNH 78394). Pine (op cit.: 76) wrote about this specimen:

“This specimen is a good deal larger than individuals of any species of *Carollia* from as far south as the portion of Peru in question. The teeth are large, but the central lower incisors are rather small for *perspicillata*, and the conformation of the skull is reminiscent of both *perspicillata* and *brevicauda*. The legs, feet and forearms are unusually hirsute. The body hair is quite long and manifestly tricolored. The feet are large and the width of the skull at the frontals is unusually great.” However, that specimen was assigned to *C. perspicillata*, based on discriminant analysis of morphometric data, by McLellan (1984).

In 1991, the BIOLAT program of the Smithsonian Institution and the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, carried out an expedition to the Cosñipata Valley, Cuzco, Peru. In the course of this expedition, several specimens of *Carollia* were collected that could not be assigned to any of the then known species (Pacheco et al. 1995). These specimens, along with others recently collected from Cuzco, and two additional specimens housed in museum collections, are similar to the Sandia's specimen, and warrant their recognition as a distinct taxon. The purpose of this work is to describe and name this taxon as a new species, at present known only from Peru and Bolivia, and to discuss some aspects of its systematics and distribution.

MATERIALS AND METHODS

Skin measurements (HF, hind foot length; E, ear length) were taken from field labels. The head plus body length (HBL) was estimated by subtracting the tail length (TL) from the total length. The forearm (FA) and tibia lengths (TbL) were measured on dry skins or alcoholic specimens. All skull dimensions were measured to the nearest 0.01 mm using dial calipers. The following skull measurements were used: greatest skull length (GSL); condyloincisive length (CIL); postorbital width (POW); zygomatic width (ZYGW);

greatest width of braincase (BRW); palatal length (PL); maxillary toothrow length (MXTRL); breadth across the outer edges of the second upper molars (M2M2); breadth across canines (CC); dentary length (DL); and, mandibular toothrow length (MANDL) (Tables 1 and 2). Most of the variables are described in Pacheco and Patterson (1992) or Simmons and Voss (1998). The nomenclature for dental topography follows Phillips (1971).

Specimens of *Carollia* examined are housed at:

AMNH American Museum of Natural History, New York, USA.

FMNH The Field Museum, Chicago, USA.

MUSM Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru.

Nacional Mayor de San Marcos, collected by Víctor Pacheco (original number 1191) on 28 September 1991 at Morro Leguía, Paucartambo-Pillcopata road, km. 134, 2250 m, Paucartambo Province, Cuzco Department, Peru, at approximately 13°11'52" S, 71°34'36" W. The holotype is an alcoholic specimen with the skull removed and, except for missing the right third upper molar, is in good condition. The type locality is situated in the Cultural Zone of the Manu Biosphere Reserve on the headwaters of the Río Cosñipata, tributary of the Río Alto Madre de Dios.

SYSTEMATICS

FAMILY PHYLLOSTOMIDAE

Genus *Carollia* Gray 1838
Carollia manu, new species

Carollia sp.? (3) Pine 1972: 76

Carollia perspicillata: Pacheco et al. 1993: 6 [part]

Carollia sp. Pacheco et al. 1995: 10

Carollia sp. nov. Patterson et al. 1996: 641

Carollia perspicillata: Anderson 1997: 221 [part]

Carollia sp. nov. Solari et al. 2001: 112

Type Material.—The holotype (MUSM 8802) is an adult male deposited at the Departamento de Mastozoología, Museo de Historia Natural, Universidad

Paratypes include nine adult specimens: two males (MUSM 8799, 8800) and one female (MUSM 8801) from Bosque de las Nubes, Paucartambo-Pillcopata road, 1700 m; and three males (MUSM 11786, FMNH 172076, 172077) and three females (MUSM 11784, 11785, FMNH 172078) from San Pedro, Paucartambo-Pillcopata road, 1480 m. Both localities are in the Río Cosñipata drainage, Department of Cuzco, Peru (Pacheco et al. 1993). These nine paratypes and additional specimens of *C. manu* from other localities are listed in the Appendix. Selected measurements of each specimen of the type series are provided in Table 1.

Table 1.—Measurements of the type series of *Carollia manu*. Weight is given in grams; all other measurements are in millimeters.

	Holotype MUSM 8802	Paratype MUSM 8799	Paratype MUSM 8800	Paratype MUSM 8801	Paratype MUSM 11784	Paratype MUSM 11785	Paratype MUSM 11786	Paratype FMNH 172076	Paratype FMNH 172077	Paratype FMNH 172078
Sex	male	male	male	female	female	female	male	male	male	female
Weight	21.0	19.0	17.0	17.5	18.0	21.0	19.0	17.0	20.0	17.5
HBL	63.0	59.0	60.0	66.0	60.0	59.0	66.0	60.0	66.0	66.0
HF	13.0	13.0	15.0	14.0	14.0	13.0	13.0	13.0	13.0	13.0
E	20.0	22.0	22.0	20.0	21.0	21.0	21.0	20.0	21.0	18.0
FA	43.0	43.59	43.11	41.92	43.28	43.18	43.91	41.22	43.69	44.43
TbL	17.84	15.98	16.81	15.35	15.76	15.62	16.24	18.27	18.08	18.39
GSL	23.04	23.26	22.80	22.26	22.49	23.36	23.27	22.55	22.88	23.13
CIL	21.17	21.76	21.09	20.72	20.97	21.40	21.50	20.76	21.09	21.33
POW	6.01	6.14	6.09	5.90	5.89	5.88	5.77	6.17	5.98	5.94
ZYGW	-	10.97	10.68	10.47	10.47	10.65	10.93	10.41	10.60	10.50
BRW	10.48	10.29	10.16	10.18	9.89	10.19	10.13	10.02	10.12	10.11
PL	9.56	9.43	9.49	9.68	9.34	9.75	9.79	9.61	9.79	9.91
MXTRL	7.77	7.88	7.67	7.53	7.49	7.64	7.91	7.53	7.74	7.77
M2M2	8.30	8.60	8.17	8.30	-	8.32	8.50	8.23	8.03	8.30
CC	5.14	5.25	5.31	5.23	4.96	5.29	5.61	5.30	5.29	5.19
DL	15.08	15.58	15.10	14.76	14.93	15.51	15.39	14.78	15.34	15.18
MANDL	8.38	8.86	8.37	8.17	7.93	8.23	8.68	8.19	8.42	8.29

Table 2.- Selected measurements of *Carollia manu*, *C. brevicauda* and *C. perspicillata*. Weight (W) is given in grams, all other measurements are in millimeters. Summary statistics (mean and standard deviation [above], observed range, and sample size [below]) of measurements for each species (see Appendix 1 for a list of the specimens measured).

	<i>Carollia manu</i>	<i>C. brevicauda</i>	<i>C. perspicillata</i>
W	18.7±1.6 17.0-21.0(10)	13.1±1.2 11.0-15.0(10)	16.7±1.9 13.0-19.0(10)
HBL	62.5±3.2 59.0-66.0(10)	54.0±3.6 48.0-59.0(10)	64.9±2.9 59.0-68.0(10)
TL	8.5±1.3 7.0-10.0(10)	9.0±1.6 6.0-12.0(10)	9.1±1.1 8.0-11.0(8)
HF	13.4±0.7 13.0-15.0(10)	12.7±0.8 11.0-14.0(10)	12.6±1.0 11.0-14.0(10)
E	20.6±1.2 18.0-22.0(10)	18.9±1.0 10.0-20.0(10)	19.4±1.6 17.0-22.0(10)
FA	43.1±0.9 41.2-44.4(10)	38.4±0.8 37.4-39.9(10)	42.5±1.1 40.8-44.6(10)
TbL	16.8±1.2 15.4-18.4(10)	14.7±0.5 13.9-15.8(10)	17.7±0.8 16.5-19.2(10)
GSL	22.9±0.4 22.3-23.4(10)	21.2±0.5 20.2-21.8(9)	22.5±0.5 21.7-23.5(10)
CIL	21.2±0.3 20.7-21.8(10)	19.4±0.4 18.6-20.0(9)	21.0±0.3 20.4-21.5(10)
POW	6.0±0.1 5.8-6.2(10)	5.4±0.2 5.1-5.6(9)	5.6±0.3 5.2-6.1(10)
ZYGW	10.6±0.2 10.4-11.0(9)	9.5±0.4 8.8-10.1(9)	9.6±0.4 9.0-10.4(10)
BRW	10.2±0.2 9.9-10.5(10)	9.4±0.1 9.1-9.6(10)	9.7±0.3 9.3-10.4(10)
PL	9.6±0.2 9.3-9.9(7)	8.7±0.3 8.2-9.5(9)	9.6±0.3 9.1-10.0(10)
MXTRL	7.7±0.2 7.5-7.9(10)	6.8±0.2 6.5-7.0(10)	7.7±0.2 7.5-8.0(10)
M2M2	8.3±0.2 8.0-8.6(6)	7.3±0.2 6.9-7.4(10)	7.6±0.4 7.2-8.5(10)
CC	5.3±0.2 5.0-5.6(7)	4.8±0.2 4.3-4.9(10)	5.0±0.2 4.7-5.3(10)
DL	15.2±0.3 14.8-15.6(7)	13.8±0.3 13.1-14.2(10)	15.2±0.4 14.5-15.9(10)
MANDL	8.4±0.3 7.9-8.9(10)	7.4±0.1 7.1-7.5(10)	8.5±0.2 8.1-8.8(10)

Distribution.—*Carollia manu* is known from Departments of Cuzco, Madre de Dios, and Puno, in southeastern Peru; and from the Department of La Paz in northern Bolivia (Fig. 1). The elevational range is from 1300 to 2250 m.

Diagnosis.—*Carollia manu* is a large *Carollia* with long and soft fur; thumb long; tibia relatively short; forearm, tibia and femur conspicuously furred; uropatagium proportionately short, holding a short tail. Rostrum broad; anteorbital region inflated; interorbital

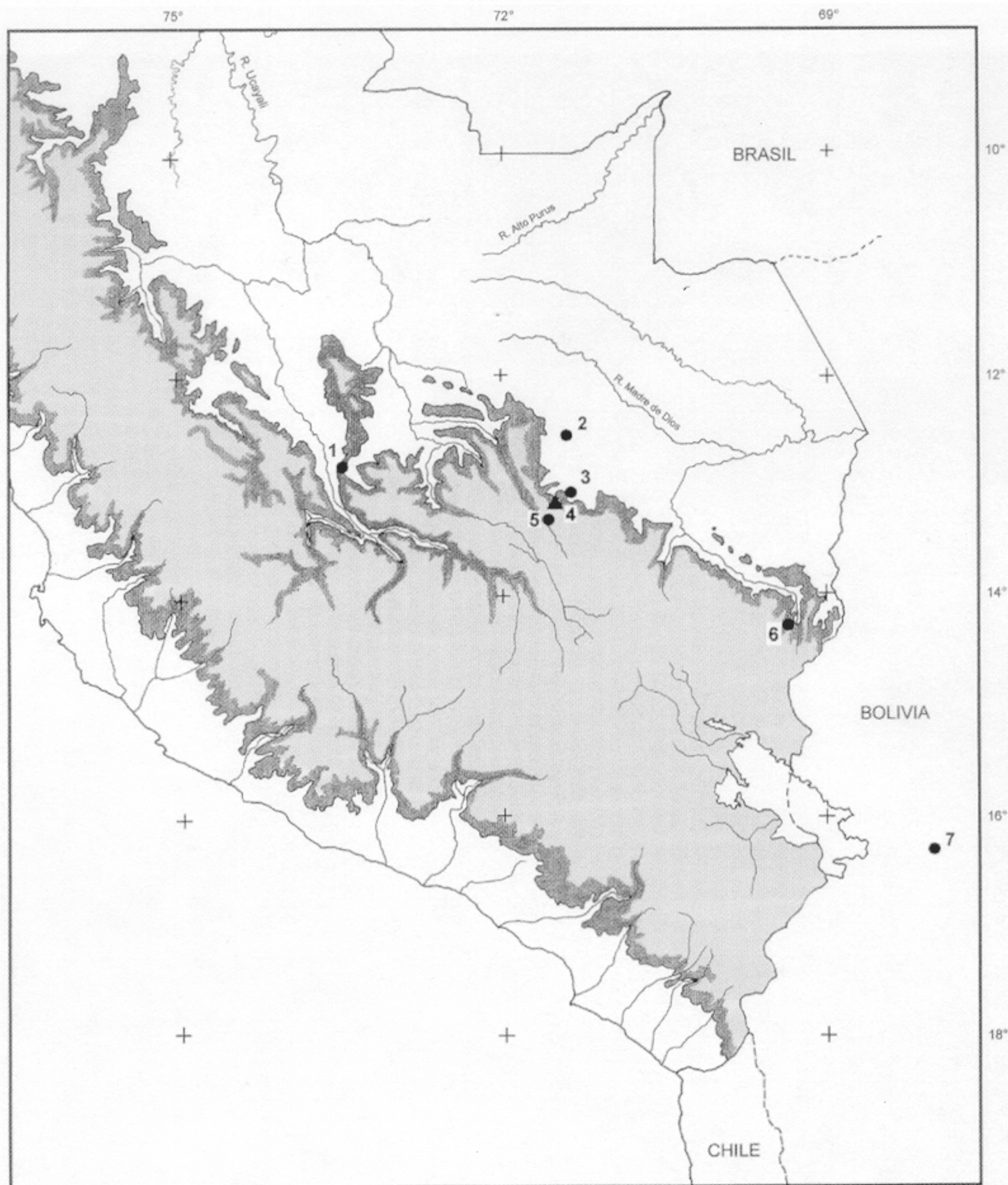


Figure 1. Map of the collecting localities of *Carollia manu* in Peru and Bolivia. Dots correspond to collecting localities (1=Lactahuaman, 2=Cerros de Pantiacolla, 3=San Pedro, 4=Morro Leguia, 5=Bosque de las Nubes, 6=Sandia, 7=Saynani). Type locality is identified by a triangle.

region broad; a distinct and elongated foramen in the dorsal wall of the mesopterygoid fossa, just anterior to the basioccipital pits; paraoccipital processes developed; basioccipital broad with subparallel sides; basioccipital pits moderately deep and separated by a thin vertical septum; petromastoid not overlapping the posterior margin of ectotympanic (Fig. 2). Upper middle incisors short, robust, their anterior surface deeply curved, not projecting forward; premolars and molars

broad and massive; broad contact between upper canine and first upper premolar (P3); anterior cingular style of second upper premolar (P4) developed and overlapping posterior margin of P3, precluding a gap between P3 and P4 (Fig. 3); P3 distinctly higher and larger than P4; P3 medial axis parallels the anteroposterior axis of skull; P4-M3 rows strongly diverging backward; M1 large and placed slightly labial to the P4-M3 axis, shaping a smooth curvature on the

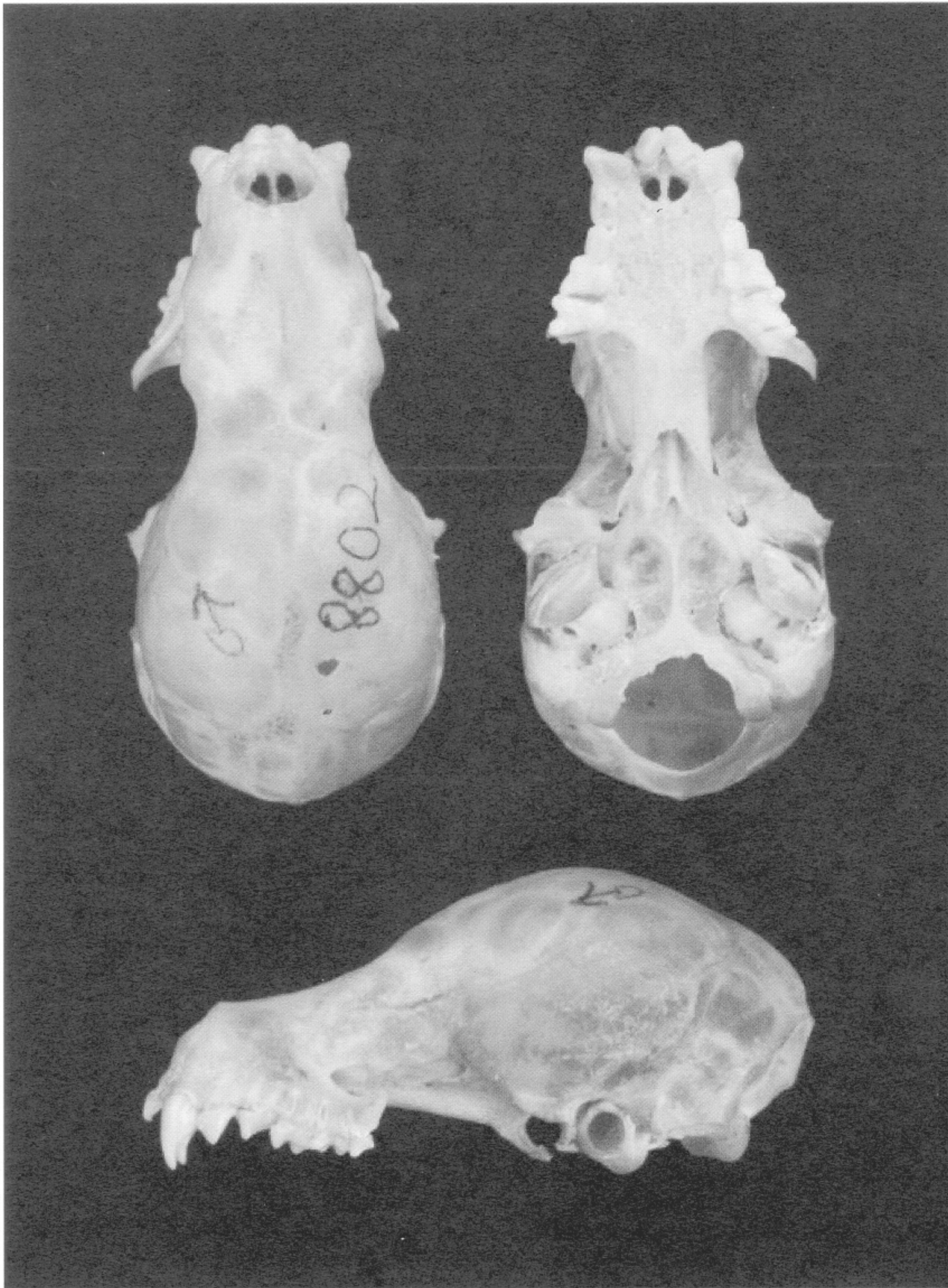


Figure 2. Dorsal, ventral, and lateral views of skull of the holotype of *Carollia manu* (MUSM 8802).

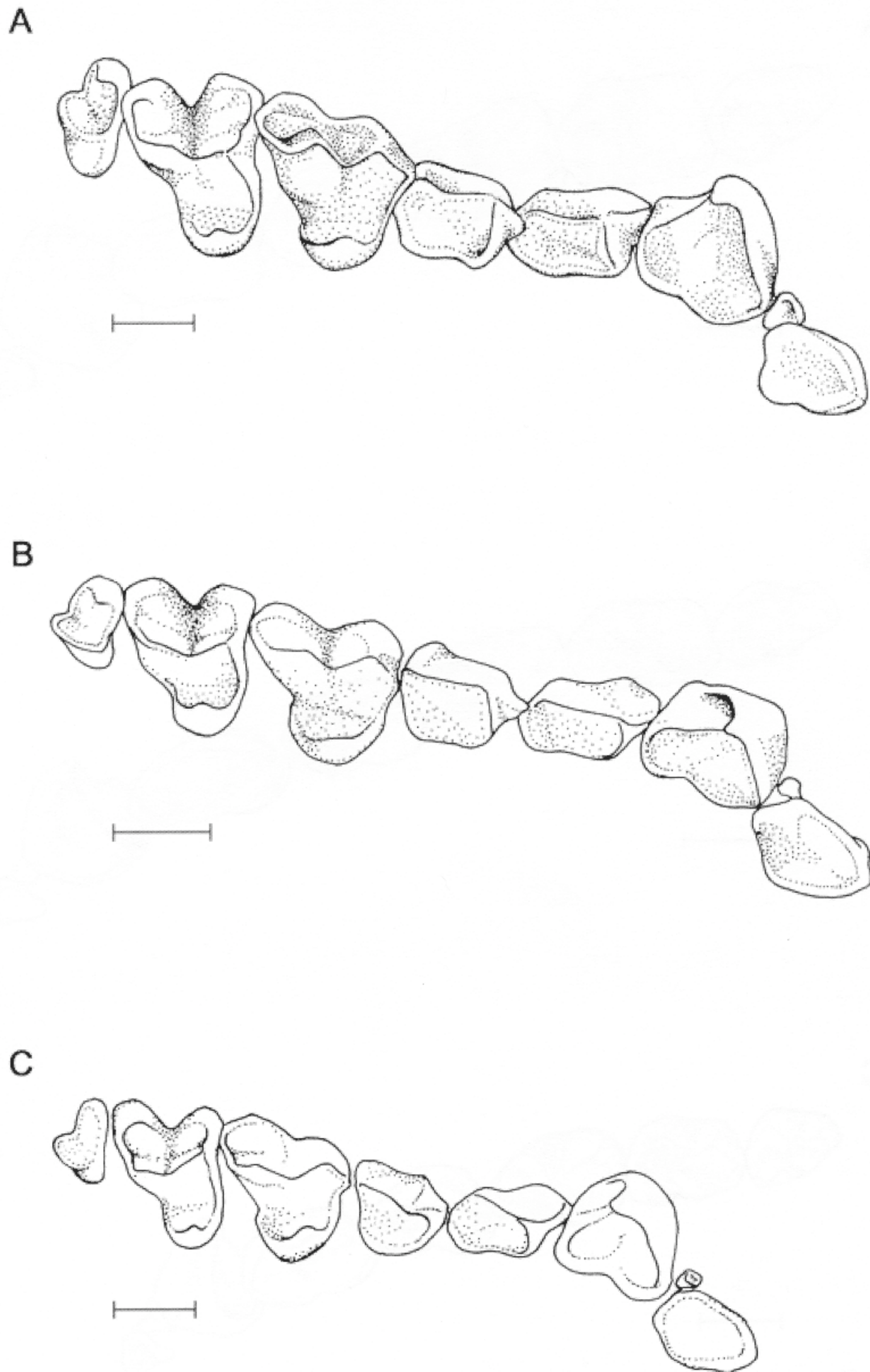


Figure 3. Occlusal view of the upper teeth (right side) of *Carollia* species: **A**, *Carollia manu* (MUSM 8799); **B**, *C. perspicillata* (MUSM 10824); and **C**, *C. brevicauda* (MUSM 8788).

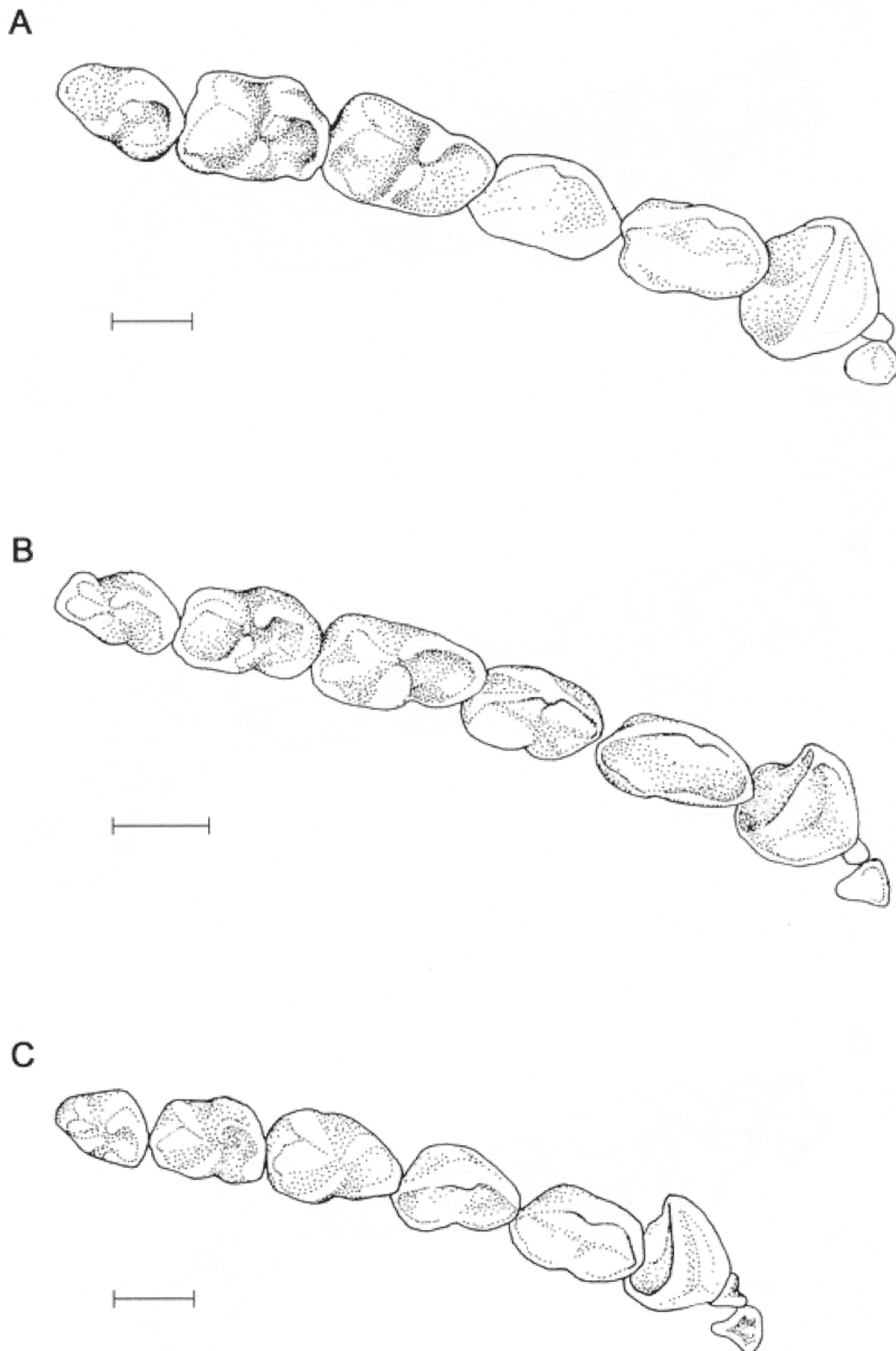


Figure 4. Occlusal view of the lower teeth (left side) of *Carollia* species: A, *Carollia manu* (MUSM 8799); B, *C. perspicillata* (MUSM 10824); and C, *C. brevicauda* (MUSM 8788).

toothrow; coronoid process high, with acute tips and a distinctly triangular shape; lower premolars and molars broad and robust (Fig. 4).

Description.—A large species of *Carollia*, with long, dense, and fluffy fur on back. Dorsal pelage with hairs tricolor, which exhibits a grayish-brown band at the base, followed by a buff-to-whitish brown band, and then a brown band at the tip; ventral pelage with short brown-tipped hairs, tricolored on the pectoral region and bicolored on the abdominal and inguinal regions. Dorsal and ventral pelage not countershaded, appearing brown overall. Forearm long and heavily furred. First and second phalanges of digit IV subequal in length. The uropatagium presents a deep notch; a short tail is evident. Pinna relatively large and broad.

Rostrum comparatively short and wide; anteorbital region inflated; maxillary roots of zygoma robust, usually presenting a square labial margin; posterior palate that extends into the interpterygoid space shorter than anterior palate; anterior margins of mesopterygoid fossa convergent; zygomatic arches incomplete with maxillary roots oriented dorsally; anterior process of ectotympanic short and pointed; upper middle incisors short and robust, oriented downward and not projecting forward, and apex usually pointed; upper canines large and divergent; P3 distinctly higher than P4; axis of P4 diverging laterally with respect to P3's axis; upper and lower molars broad and massive; M1 higher than M2 and subequal or higher than P4; M3 moderately reduced; medial lower incisors larger than the lateral ones; no gaps between lower premolars; mid-internal cusp of m3 (presumably the metaconid) distinct; mandibular rami and toothrows distinctly bowed; and symphysis of mandibular rami with a small keel.

Comparisons.—McLellan (1984) reported significant differences in several skull length variables between northern and southern populations of *C. brevicauda*. However, Brazilian, Peruvian, and Bolivian populations were not included in her phenetic analyses, suggesting that much of the morphological variability among southern populations remains to be explored. On the other hand, she found little morphological differentiation among populations of *C. perspicillata*, although her South American samples

were limited. We provide comparisons of *Carollia manu* with population samples of *Carollia brevicauda* and *C. perspicillata* from the region where sympatry has been documented, assuming that these populations are adequate representatives of these species, acknowledging we still lack an accurate understanding of the degree of differentiation of these from other conspecific populations, including those from the type localities. However, such understanding is beyond the objectives of the present study.

Using size alone, *C. manu* is readily separable from the smaller species *C. castanea* and *C. subrufa*; it is also separable by means of several pelage and cranio-dental features (see Pine 1972). In addition, *C. subrufa* is distributed only in Middle America.

We have not examined specimens referable to *Carollia colombiana*, however several traits described by Cuartas et al. (2001) provide adequate basis for comparisons. This species is characterized by a medium-sized forearm (37.5-39.8), whereas *C. manu* exhibits a larger forearm (41.2-44.4); dorsal hairs are tetracolored in *C. colombiana*, but tricolored in *C. manu*; a sulcus is said to be present between the rostrum and the orbital region in *C. colombiana*, which is absent in *C. manu*; and a gap between P3 and P4 is found in *C. colombiana*, but it is absent in *C. manu*.

Based on our own observations and on the characters described by Baker et al. (2002), *Carollia sowellii* may be distinguished from *C. manu* by its less heavily furred forearm, the presence of a gap between P3 and P4, a conspicuous lateral projection of the mastoid process, and less robust teeth. In addition, *C. sowellii* apparently occurs only in Middle America.

Compared to *Carollia perspicillata*, *C. manu* may be distinguished externally by its longer pelage, with broad and contrasting dark bases; forearm, femur and tibia being heavily furred; tibia shorter; and uropatagium less extensive, with a deeper notch. *Carollia manu* is also distinguished from *C. perspicillata* in cranio-dental characteristics, by having a broader anteorbital and interorbital region, and relatively shallower basioccipital pits with a less developed vertical septum. Premolars and molars (both upper and lower) are more massive and broader in *C. manu* but narrower in *C. perspicillata*. The first upper premolar (P3) in *C. manu*

usually has a broad contact with the canine, contact which is reduced in *C. perspicillata*. A well developed anterior cingular style of the second upper premolar (P4) overlaps the posterior margin of P3 in *C. manu*, whereas a less developed cingular style of P4 does not overlap P3 in *C. perspicillata*. In *C. manu*, P3 is distinctly higher than P4 but is subequal in height in *C. perspicillata*. Middle lower incisors are larger than the outer ones and slightly projected forward in *C. perspicillata*, whereas the lower incisors are subequal in size and not projected in *C. manu*. In *C. manu*, p3 is distinctly higher than p4 but they are subequal in height in *C. perspicillata*. In *C. manu*, m3 is strongly oriented inward but it is more in line with the other molars in *C. perspicillata*. The mandibular rami and tooththrows are markedly bowed in *C. manu*, but almost straight in *C. perspicillata*. No external measurement is sufficient to discriminate the two species (see Table 2), although *t* tests show five cranial measurements (POW, ZYGW, BRW, M2M2, CC) with significant differences ($P < 0.05$).

Carollia manu is more similar in external appearance to the smaller *C. brevicauda*. Both species have brown pelage, long fur, and conspicuously hairy forearms, but *C. manu* is readily distinguished by its larger size (mean FA 43.1 vs. 38.4); longer fur; longer and more furry tibia (in contrast to a shorter and naked tibia in *C. brevicauda*). The basioccipital pits are deep and separated by a conspicuous septum in *C. brevicauda* whereas the basioccipital pits are shallow and separated by a less developed septum in *C. manu*. The basioccipital is narrow and with rounded borders in *C. brevicauda*, but there is a broad basioccipital with parallel sides in *C. manu*. Also, paraoccipital processes are well developed in *C. manu* but shallow in *C. brevicauda*. Anterior margins of mesopterygoid fossa are more or less straight in *C. manu*, but it is more curved in *C. brevicauda*. First upper premolar (P3) is broadly in contact with upper canine in *C. manu*, but the contact is reduced in *C. brevicauda*. Anterior cingular style of second upper premolar (P4) is well developed and overlaps the posterior margin of P3 in *C. manu*, but cingular style of P4 is reduced and rarely overlaps P3 in *C. brevicauda*. Lingual margins of p4, and usually p3, are in line in *C. manu* but form an inward angle in *C. brevicauda*. Middle lower incisors are slightly projected in *C. brevicauda*, but not projected forward in *C. manu*. Cranial and dental mea-

surements are markedly larger in *C. manu* than in *C. brevicauda* (Table 2).

Habitat.—*Carollia manu* was collected in habitats that correspond to the “tropical montane forests” of Frahm and Gradstein (1991) or to the “cloud forest” of Terborgh (1971). The forests from 1500 to 2500 m have been generally referred to as lower montane forests, which typically have abundant epiphytes, hepatics, and pteridophytes (including “tree ferns”); mean annual temperature from 15 to 19°C, and an average annual precipitation of 1500 to 3000 mm (Young and León 1999).

At San Pedro, Río Cosñipata Valley, 1480 m, bats were collected near an ecotourism base camp with large areas dominated by secondary forest, the slope was moderate from 20°-30°, and several small creeks fed into a large stream flowing eastward. The landscape was dominated by climbing bamboo thickets (*Chusquea* sp.) on both sides of the road, and by trees sparsely covered by epiphytes. The understory included areas relatively uncluttered. In Lactahuamán, in the Río Apurimac Valley, 1710 m, the slope was generally about 40°, but steeper in some areas. This locality is a lower montane forest, with high epiphyte loading. The common highland bamboo (*Chusquea* sp.) was dominant in the understory (Solari et al. 2001), but patches of the larger bamboo (*Guadua* sp.) were also present in some areas. Two small streams, which empty into the Río Apurimac, passed near the camp.

Etymology.—The specific epithet *manu* is a noun in apposition, referring to the Manu Biosphere Reserve (MBR), where the largest series for this species was collected. The MBR, with an area of 18,812 sq km, is located in the departments of Cuzco and Madre de Dios, Peru, and protects one of the richest mammal fauna in the world, with more than 215 recorded species (Solari et al. in prep.).

Remarks.—*Carollia manu* inhabits lower montane forests from 1300-2250 m in MBR, Peru, and at a single locality at 2163 m in Bolivia. In MBR, *C. brevicauda* is found from 320 to 1700 m, and sympatry with *C. manu* is documented from Cerros de Pantiacolla (1300 m) in department Madre de Dios; and San Pedro (1480 m) and Bosque de las Nubes (1700 m) in department Cuzco. Sympatry of *C.*

brevicauda, *C. perspicillata*, and *C. manu* was recorded at a single locality in Llactahuamán, Cordillera de Vilcabamba, at 1700 m (Solari et al. 2001). Anderson (1997) reported sympatry of *C. brevicauda* with *C. manu* (identified as *C. perspicillata*) from 0.5 km E of Saynani, in La Paz, Bolivia.

The altitudinal distribution of *C. perspicillata* in MBR is herein reported from 330 to 1100 m, correcting previous reports. Pacheco et al. (1993) reported *C. perspicillata* in MBR from 350 to 2250 m, but the highest record, at 2250 m, included misidentified specimens of *C. manu*. Patterson et al. (1996) gave the upper limit of *C. perspicillata* as 1300 m but this was also erroneous because their highest record (FMNH 139135) also proved to be a specimen of *C. manu*. At

present, sympatry of *C. manu* with *C. perspicillata* has not been recorded in MBR, but sympatry is likely there because both species have been recorded at Llactahuamán, Cuzco (Solari et al. 2001).

Other records of *Carollia perspicillata* from high elevations were not examined in this report, but Koopman (1978) reported *C. perspicillata* up to 1550 m on the west side of the Cordillera Vilcabamba, department Cuzco; and Graham (1983) extended the upper range to 1700 m. *Carollia manu* is unknown north of Cuzco department, but records of *C. brevicauda* and *C. perspicillata* from other higher elevations should be reexamined because they might be based on misidentified specimens of *C. manu*.

DISCUSSION

Previous taxonomic accounts recognized a maximum of only four species within *Carollia* (Koopman 1993), but the study of appropriate series from remote areas of its distribution, along the Andes of Colombia and Peru, has resulted in the discovery of two new species: *C. colombiana* and *C. manu*. On the other hand, high levels of sequence divergence in the mitochondrial cytochrome-*b* gene provided the first indication of paraphyly within *C. brevicauda* (Baker et al. 2002). Thus, the combined application of morphological and molecular data to studies on *Carollia* have brought about a better understanding of the diversity of these short-tailed bats, which now consists of seven species. Recent molecular analysis suggests the real diversity in the genus is still underestimated (Hoffmann and Baker 2003).

A hypothesis of relationships among these seven species has not been yet accomplished. Development of such a hypothesis should enable us to understand the patterns of distribution in this genus. At present,

only *Carollia colombiana* and *C. manu* appear to be restricted to lower montane forests. *Carollia manu* appears to replace *C. perspicillata* at higher elevations in most of the range of the last species. The distributional range of *C. manu* mirrors the distribution of other montane taxa from southeastern Peru and Bolivia, for example the caenolestid *Lestoros inca*, the didelphids *Monodelphis osgoodi* and *Gracilinanus aceramarcae*, and the murids *Thomasomys daphne*, *T. oreas*, and *Lenoxus apicalis*. Thus, the distribution of *Carollia* suggests that the Andes have played an important role on the evolutionary history of the genus. Studies of other diverse genera of Neotropical bats, such as *Artibeus* (Patterson et al. 1992) and *Sturnira* (Pacheco and Patterson 1992) have also remarked the role of the Andes in their diversification. Nonetheless, additional surveys along the Andes are required to test whether the apparently restricted distributions of *C. colombiana*, *C. manu*, and *C. sowellii* are real or are artifacts of sampling.

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APPENDIX

Specimens Examined

We examined 78 specimens. Asterisks (*) indicate specimens for which measurements were used in Tables 1 and 2. Specific localities as given in the collector's labels.

Carollia brevicauda: **Peru**: *Amazonas*, La Peca, 12 km E (MUSM 122, 157, 158); La Peca, 20 km E (MUSM 121, 193--195). *Cajamarca*, San Ignacio, 4 km W El Chaupe (MUSM 10645). *Cuzco*, 40 road km E Quincemil on Río Marcapata (MUSM 1409); Amaybamba (MUSM 1467, 1468); La Convención, Kimbiri, Llactahuamán (MUSM 14521, 14525*, 14529*); Paucartambo, carretera Paucartambo-Pillcopata, km 135, Bosque de las Nubes (MUSM 8788*); Paucartambo, Queros (Pillcopata) (MUSM 8553); Paucartambo, Quitacalzón (MUSM 8788*); Paucartambo, carretera Paucartambo-Pillcopata, km 154, San Pedro (MUSM 8793*, 11774*, 11776*, 11778, 11779*, 11781*). *Huánuco*, 35 km E Tingo María, Carpish (MUSM 1410, 1411). *Madre de Dios*, 15 km NE Pto. Maldonado, Reserva de Cuzco Amazónico (MUSM 6116-6120); Manu, Pakitza (MUSM 6844-6848). *Pasco*, Oxapampa, límite E Parque Nacional Yanachaga Chemillén (MUSM 14917, 14918). Total, 36.

Carollia manu: **Bolivia**: *La Paz*, 0.5 km E Saynani (AMNH 264995). **Peru**: *Cuzco*, La Convención, Kimbiri, Llactahuamán (MUSM 14535); Paucartambo, carretera Paucartambo-Pillcopata, km 135, Bosque de las Nubes (MUSM 8799-8801*); Paucartambo, carretera Paucartambo-Pillcopata, km 135, Morro Leguía (MUSM 8802*, *holotype*); Paucartambo, carretera Paucartambo-Pillcopata, km 154, San Pedro (FMNH 172063, 172068-172075, 172076-172078*; MUSM 11784-11786*). *Madre de Dios*, Cerro de Pantiacolla, above Río Palotoa (FMNH 139135). *Puno*, Sandia, San Juan (FMNH 78394). Total, 23.

Carollia perspicillata: **Peru**: *Amazonas*, Condorcanqui, Puesto de Vigilancia 22, Falso Paquisha, Cordillera el Condor (MUSM 316, 317, 339); Balsas, 19 km by road E (MUSM 4857). *Cuzco*, La Convención, Kimbiri, Llactahuamán (MUSM 14536*); La Convención, Camisea, Armihuari (MUSM 13579, 13583, 13585, 13591-13593*). *Madre de Dios*, Hda. Erika, Río Alto Madre de Dios opposite Salvación (MUSM 1479-1481*, 1483, 1484*). *Pasco*, Oxapampa, Pozuzo, Palmira (MUSM 10850); Oxapampa, Pozuzo, Río Negro (MUSM 10824, 10826). Total, 19.

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