

MITOCHONDRIAL DNA SEQUENCE, KARYOTYPIC, AND MORPHOLOGICAL VARIATION IN THE *CAROLLIA CASTANEA* SPECIES COMPLEX (CHIROPTERA: PHYLLOSTOMIDAE) WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT

Use of mitochondrial cytochrome-*b* (cyt-*b*) gene sequences to address problems in bat systematics has increased significantly in recent years. In the phyllostomid genus *Carollia*, it has resulted in a more accurate taxonomy and a better understanding of genealogical relationships. Thus far, eight species have been recognized, four of them described in the last five years by using either morphology or a combination of morphology and DNA sequence data. Here, we name and describe another new species, using a combination of cyt-*b* sequences, karyotypic data, and discrete morphological characters. The new species is a member of the *C. castanea* species complex, and until now it was included under that name. However, it possesses a distinctive karyotype ($2N=22$, as opposed to $2N=20/21$ in other species), its cyt-*b* sequence diverges by almost 8.1% from that of *C. castanea*, it shows subtle but consistent differences in the upper teeth, and it is smaller than *C. castanea*. Geographically, the new species is restricted to Peru, Bolivia, and Brazil, south of the Amazon River, at elevations ranging from 200 to 1100 m. We discuss the value of multiple datasets when recognition of a new species may be subject to debate.

Key words: *Carollia castanea*, cytochrome-*b*, genetic species concept, karyotypes, morphology, new species, systematics

RESUMEN

El uso de secuencias moleculares del gen citocromo-*b* para resolver problemas en sistemática de murciélagos se ha incrementado significativamente en los últimos años. En el género de filostómido *Carollia*, esto ha permitido tener una taxonomía más precisa y un mejor entendimiento de las relaciones entre especies. Al presente, ocho especies han sido reconocidas, cuatro de ellas en los últimos cinco años, usando solamente morfología o combinando morfología y análisis de datos moleculares. Nosotros describimos una nueva especie en base a secuencias del citocromo-*b*, datos cariotípicos, y caracteres morfológicos discretos. Esta nueva especie pertenece al complejo de especies de *C. castanea*, y hasta ahora había sido incluida bajo ese nombre; sin embargo, ésta posee un cariotipo único ($2N=22$, versus $2N=20/21$ en otras especies), su secuencia del citocromo-*b* diverge por casi 8.1% de *C. castanea*, muestra pequeñas pero consistentes diferencias en la dentición superior, y es comparativamente más pequeña que *C. castanea*. La nueva especie se encuentra en Perú, Bolivia, y Brasil, al sur del Río Amazonas, y su rango altitudinal es entre 200 y 1100 m. Finalmente, discutimos el valor de múltiples conjuntos de datos cuando el reconocimiento de una nueva especie puede ser discutible.

INTRODUCTION

Research on systematic relationships among Neotropical bats has been augmented in recent years by the availability of modern methods. One method which has shown utility in resolving phylogeographic questions is DNA sequencing, with the mitochondrial cytochrome-*b* gene providing the most resolution thus far (Avice 2000). The use of this approach for bats of the genus *Carollia* (Phyllostomidae) has provided a more accurate taxonomy (Baker et al. 2002) as well as clarified phylogenetic relationships among populations (Hoffmann and Baker 2003).

Although only four species (*brevicauda*, *castanea*, *perspicillata*, and *subrufa*) were included in the last account of *Carollia* (Koopman 1993), eight species are currently recognized, including *colombiana* Cuartas et al. 2001, *sowelli* Baker et al. 2002, *manu* Pacheco et al. 2004, and *monohernandezi* Muñoz et al. 2004. *Carollia sowelli* was first identified as a consistent and divergent clade in an analysis of molecular (mitochondrial DNA) sequences (Wright et al. 1999). It is unlikely that *C. sowelli* could have been distinguished from *C. brevicauda* otherwise, because no significant morphological features were recognized to set them apart (Pine 1972; Owen et al. 1984), although McLellan (1984) found consistent size differences between northern and southern populations of what was then regarded as *C. brevicauda*. Further analyses and increased sampling justified the description of *C. sowelli* (Baker et al. 2002).

Molecular phylogeography was also used to further study geographic variation among populations of *C. castanea*. Previously, Patton and Gardner (1971) had identified a karyotypic race ($2N=22$) in specimens from southeastern Peru, which departed from the $2N=20[\text{♀}]/21[\text{♂}]$ found in populations of Costa Rica and Colombia (Baker and Bleier 1971), and eastern Ecuador (Lim and Engstrom 1998). Using morphometric variation, McLellan (1984) suggested a size cline in this species too, with smaller individuals in the southern part of the range (central Peru) as compared to individuals from Central America. The phylogeographic analyses by Hoffmann and Baker (2003) supported the hypothesis that geographic groups in *C. castanea* might represent more than one evolutionary lineage, by showing them as clades divergent from each other by $>7\%$ (Kimura-2 parameter; Kimura 1980).

Although no morphological distinction had been previously recognized in *C. castanea*, the situation was similar to that in other pairs of cryptic species, such as *C. brevicauda* and *C. sowelli* (Baker et al. 2002), *Rhogeessa tumida* and *R. genowaysi* (Baker 1984), or *Notiosorex crawfordi* and *N. cockrumi* (Baker et al. 2003). Given this level of genetic and karyotypic variation and their implications for species boundaries, we describe a new species based primarily on chromosomal and DNA sequence evidence. We provide a morphological diagnosis for the species of bats previously recognized as *C. castanea* and assess the observed morphological variation in the context of molecular and karyotypic variation.

MATERIALS AND METHODS

We examined morphological and morphometric traits of the geographic populations used in the molecular analyses by Hoffmann and Baker (2003). To determine the extent of variation in these traits, we enhanced the taxonomic and geographic sampling by including specimens from other museum collections. However, this study does not represent a complete revision of this group of species. We also included four specimens used in the original report of the $2N=22$ karyotype, to make sure they correspond with

our taxonomic decisions. Only adult animals (based on fusion of epiphyses of metacarpals and phalanges; Pine 1972) were used in taking measurements and ascertaining diagnostic characters. Specimens examined are listed in the Appendix.

Five geographic units were defined based on the phylogenetic analyses presented by Hoffmann and Baker (2003). Two units correspond to the groups 1 (eastern Ecuador) and 2 (Peru and Bolivia), two are

formed from group 3 (western Ecuador, and Costa Rica plus Honduras and Panama), and the final one (Colombia and Venezuela) was not represented in the tree of Hoffmann and Baker (2003). External and cranial discrete characters used in previous studies (Hahn 1907; Pine 1972; Owen et al. 1984; Pacheco et al. 2004) were recorded for each geographic unit.

External measurements were taken from skin tags. Forearm length (FA) was measured on dry skins or fluid-preserved specimens. In addition, the following skull dimensions (to the nearest 0.01 mm) were taken: greatest skull length (GSL); condyloincisive length (CIL); postorbital width (POW); greatest width of braincase (BRW); palatal length (PL); breadth across canines (CC); maxillary toothrow length (MXTR); breadth across the outer edges of the second upper molars (M2M2); dentary length (DL); and, mandibular toothrow length (MDTR) (Table 1). Measurements were subjected to a multivariate analysis (MANOVA) to test the null hypothesis that no significant differences exist among the vector of means for geographic and taxonomic groups. Differences were considered significant for $P < 0.05$.

TAXONOMIC HISTORY

Although no synonyms are known for *Carollia castanea*, the distribution attributed to the species increased as animals similar to the Central American ones were discovered in South America (see below). The current known distribution of *C. castanea* (sensu lato) extends from Honduras into Peru, Bolivia, western Brazil, and Venezuela (Koopman 1993). Allen (1890) described the species from a single specimen with type locality in Costa Rica; its distribution was extended to Panama (Goldman 1920), Ecuador and Peru (Thomas 1920), and then to Honduras and Guyana (Goodwin 1942). Hershkovitz (1949) recorded *castanea* from northern Colombia, Cabrera (1958) listed it as present in Guyana, Colombia, Ecuador and Peru, and Husson (1962) recorded it from Suriname. In French Guiana, Brosset and Dubost (1967) also assigned some bats to *castanea*. Shortly later, Pine (1972) updated the distribution for all the known species in the genus, including records of *C. castanea* from Bolivia.

Molecular data were obtained following Hoffmann and Baker (2003). We sequenced the cytochrome-*b* gene of four additional individuals from Peru (see Appendix); these sequences were compared with others available at GenBank or produced by our lab, including those of the outgroups (*Glyphoncteris sylvestris* and *Trinycteris nicefori*; see Baker et al. 2003) and representatives of other recognized species. Phylogenetic relationships were estimated using the neighbor-joining algorithm (Saitou and Nei 1987), using Kimura-2 parameter distances (Kimura 1980) as implemented in PAUP 4.0 b10 (Swofford 1999).

Shorter sequences (100–200 bp) were obtained from skin clips for four specimens (MVZ 136460, 136462–4) with karyotypic data but no tissue samples, to verify they matched the longer sequences of other specimens representing the new species. A specific protocol and designed primers were developed to obtain these sequences (M. C. Knapp and K. Nelson, in prep.).

Compounding the problem, the name *castanea* was employed for the smaller species of *Carollia* in South America, sometimes including what is now called *brevicauda*, but also used as conspecific with *subrufa* in Middle America (Felten 1956; Hall and Kelson 1959). Records from Ecuador and Peru (Thomas 1920) were later re-identified as *C. brevicauda* by Tuttle (1970) and Pine (1972). Although Hershkovitz (1949) discussed the taxonomy of most other bats in northern Colombia, he provided no further information on *castanea*. Judging from the data presented by Husson (1962) from Suriname, his *castanea* appears to be *brevicauda* (Genoways and Williams 1979). Pine (1972) confirmed the separation of *C. castanea* from *C. brevicauda*, and stated that the specimen from Guyana (in Goodwin 1942) was similar to but not conspecific with *C. castanea*, calling it *Carollia* sp.? (1). Records from French Guiana were re-identified as *C. brevicauda* by Brosset and Charles-Dominique (1990).

The first indication of genetic variation within *Carollia* was reported by Patton and Gardner (1971); karyotypes of Peruvian *C. castanea* (sensu lato) were shown to be distinct from those of other *Carollia* species, which have, typically, a sex-chromosome system with diploid numbers of 20 in females (XX) and 21 in males (XY₁Y₂; Hsu et al. 1968). Patton and Gardner (1971) regarded that karyotype as the ancestral condition for *Carollia*, because it showed the basic sex-chromosome system, with 2N=22 for both males and females. The typical system (2N=20-21) has been found in specimens of *C. castanea* (sensu lato) from Costa Rica and Colombia (Baker and Bleier 1971) and eastern Ecuador (Lim and Engstrom 1998; D. Parish, unpubl. data). Hsu et al. (1968) showed that the small Y₁ attaches end-to-end to the short arm of the X chromosome, and the long acrocentric Y₂ synapses with

the long arm of the X. Thus, the long arm of the X is homologous to Y₂. Based on G-banding patterns, Stock (1975) confirmed the X-autosome relationship proposed by Hsu et al. (1968) of the extra sex-chromosomes in specimens from Costa Rica and Colombia and that the extra Y was an autosome translocated without a sex-determining role. *Carollia* is a classical example of an X-autosome translocation.

Following, we provide a morphological diagnosis for the *Carollia castanea* clade of Fig. 3 of Hoffmann and Baker (2003), and describe a new species based on specimens from eastern Peru and Bolivia. We compare this new species with populations from Middle America, which would bear the name *C. castanea* in its restricted sense.

RESULTS

Morphological diagnosis of *Carollia castanea* (sensu lato)

Carollia castanea (sensu lato) includes the smallest and the most divergent members of the genus. Several external, cranial, and dental traits are common to all: fur color usually chestnut, but varying from dull, dark gray-brown to pale tan; banding ill-defined, but darkest at tips; forearm short and naked, its length usually less than 38 mm; uropatagial notch shallow; skull small and delicate; greatest skull length (GSL) ≤ 21 mm; maxillary toothrow (MXTR) ≤ 6.9 mm; braincase globular with well-developed anteorbital processes and low sagittal crest; second upper premolar (P4) considerably lingual to the labial edge of the first upper molar, creating a prominent notch in the outline of the toothrow (Pine 1972); upper canines slender and elongated; upper external incisors greatly reduced, peg-like or spicule-like; anterior cingular style of P4 greatly reduced or short and never in contact with P3; anterior portion of the bony palate concave, the posterior projection long and narrow, and the mesopterygoid fossa is v-shaped; outer lower incisors rather reduced but not concealed dorsally by cingula of canines (Pine 1972; Koopman 1994); first lower premolar (p2) noticeably lower than the second (Pine 1972); crown of first lower

molar (m1) extremely low; mid-internal (metaconid) cusp of the third lower molar reduced to undeveloped; and coronoid process of the mandible low, relative to the canine height.

Emended diagnosis of *Carollia castanea* H. Allen 1890

The following synonymy includes most of the relevant taxonomic and distributional works, but it does not constitute a full synonymy.

Carollia castanea H. Allen 1890: 19. Type locality: [Angostura,] Costa Rica

[*Hemiderma*] *castaneum*: Elliot 1904: 670. Name combination.

Hemiderma castaneum: Hahn 1907: 116

Carollia castanea: Miller 1924: 54

C.[arollia] castanea: Felten 1956: 199 (part)

Carollia castanea castanea: Hall and Kelson 1959: 125 (part)

Carollia castanea: Pine 1972: 17 (part)

Carollia castanea: Koopman 1993: 186 (part)

From the examination of the holotype of *Carollia castanea* (USNM 36384) and other specimens from Costa Rica and Honduras, this is clearly one of the most

divergent species of the genus. The following traits can be considered diagnostic for this species. Dorsal color varying from dull, dark gray-brown or chestnut to pale tan; tricolor fur banding not well-defined. Forearm and legs appearing naked, with only sparse small hairs. Skull small and delicate with well-developed anteorbital processes. Narrow contact between the cingula of the upper canine and first premolar. The second upper premolar (P4) is displaced lingually with respect to the first upper molar. There is a short and blunt anterior projection of the cingulum of P4 toward P3; P4 in close contact with M1, through a short anterior projection of the cingulum of M1 that contacts P4. Lower premolars graded, the first being smaller rather than subequal; there is an evident gap between these teeth. Measurements of the holotype (from Costa Rica), and Central and South American specimens are presented in Table 1.

Diploid chromosome number (2N) = 20-21, fundamental number (FN) = 36, with an autosome translocated to the subtelocentric X chromosome (Baker and Bleier 1971; Stock 1975), which shows a marked secondary constriction on the longer arms.

As restricted here, this species is distributed from Honduras (Goodwin 1942) to Panama (Goldman 1920) in Central America, and in northern South America from southwestern Venezuela (Handley 1976) into Colombia (Hershkovitz 1949) and western Ecuador (Albuja 1999).

Although the need for recognition of additional entities at the species level may be open to question, we consider that under both a phylogenetic (Cracraft 1983) and a genetic species concept (Dobzhansky 1950), each of the clades in the cytochrome-*b* gene tree is sufficiently divergent to be considered valid species (see Bradley and Baker 2001). In addition, there are cranial and dental characteristics allowing these groups to be recognizable morphologically. Thus far, we have no evidence of sympatry; however, we do not expect distributional overlap given that the distributions are probably delimited by major geographic features, such as the Andes or the Amazon River (Hoffmann and Baker 2003; Pacheco et al. 2004).

A new species of *Carollia* Gray 1838

Carollia benkeithi, new species

Carollia castanea: Pine 1972 (part)

Carollia castanea: Koopman 1978 (part)

Carollia castanea: Koopman 1993 (part)

Carollia castanea: Pacheco et al. 1995 (part)

Carollia castanea: Fonseca et al. 1996

Carollia castanea: Anderson 1997

Holotype.—An adult female deposited at the Natural Science Research Laboratory (NSRL) of the Museum of Texas Tech University (TTU 46187), caught by a field team including Robert J. Baker, Jane A. Groen (field number JAG 3549), Robert D. Owen, Michael J. Smolen, and Priscilla K. Tucker, on 13 October 1983 at 2 km S of Tingo María, Province of Leoncio Prado, Department of Huánuco, Peru, at approximately 9°18'S, 75°59'W (Stephens and Traylor 1983). The holotype consists of a skin and skull, both in good condition, plus frozen tissues (TK 22892). External measurements (in millimeters): total length 65; tail length 12; hind foot 11; ear 17; forearm (dry) 33.68. Weight was not recorded. Cranial measurements (in millimeters): greatest length of the skull 18.99; condyloincisive length 17.44; postorbital width 5.46; greatest width of braincase 9.09; palatal length 8.01; breadth across canines 4.29; maxillary tooththrow length 6.05; breadth across outer edges of second upper molars 6.66; dentary length 12.48; mandibular tooththrow length 6.56 (Table 1).

Distribution.—We have examined voucher specimens of *Carollia benkeithi* from the lowland forests of eastern Peru (Departments of Cusco, Huánuco, Junin, Madre de Dios, and Ucayali), and northwestern Bolivia (Departments of Beni and La Paz) (see Appendix). Additional reports, under the name *C. castanea*, have been provided by Anderson (1997), Ascorra et al. (1993), Eisenberg and Redford (1998), Koopman (1978), Pacheco et al. (1993), Patterson (1992), Pine (1972), Tuttle (1970), and Uieda (1980). All of these records reveal the range illustrated in Figure 1, with the elevational range from 200 to 1100 m (Patterson et al. 1996). However, the true extent of the species' range is not known at present, even with the large existing collections from South America.

Table 1. Selected measurements (as defined in the text) of *Carollia benkeithi* and *C. castanea*, including the holotypes (TTU 46187 and USNM 36384, respectively). All measurements are in millimeters. Summary statistics (mean \pm standard deviation [above], observed range, and sample size [below]) are provided.

	Holotype TTU 46187	<i>C. benkeithi</i>	Holotype USNM 36384	<i>C. castanea</i>
HBL	65	60.85 \pm 4.32 52.0-68.0 (27)	—	60.94 \pm 4.31 51.0-67.0 (39)
TL	12	9.26 \pm 2.18 5.0-14.0 (27)	8	8.94 \pm 2.07 5.0-14.0 (38)
HF	11	10.67 \pm 1.30 8.0-14.0 (27)	10	11.19 \pm 1.24 8.0-14.0 (40)
E	17	16.93 \pm 1.82 11.0-20.0 (27)	15	17.35 \pm 1.23 15.0-20.0 (38)
FA	33.68	35.70 \pm 0.70 33.68-37.21 (29)	—	35.670 \pm 0.92 34.24-37.13 (31)
GSL	18.99	19.27 \pm 0.30 18.70-19.94 (31)	19.98	19.60 \pm 0.44 18.98-20.94 (48)
CIL	17.44	17.45 \pm 0.28 16.89-18.01 (30)	17.72	17.71 \pm 0.42 16.70-18.76 (48)
POW	5.46	5.33 \pm 0.17 5.06-5.79 (31)	5.10	5.43 \pm 0.17 5.10-5.83 (48)
BRW	9.09	8.84 \pm 0.18 8.39-9.24 (31)	8.94	8.96 \pm 0.21 8.47-9.33 (48)
PL	8.01	8.02 \pm 0.18 7.62-8.35 (31)	8.03	8.27 \pm 0.38 7.07-9.14 (48)
MXTR	6.05	6.07 \pm 0.12 5.74-6.29 (31)	6.28	6.25 \pm 0.22 5.82-6.91 (48)
M2M2	6.66	6.78 \pm 0.20 6.38-7.08 (31)	6.53	6.73 \pm 0.21 6.27-7.14 (48)
CC	4.29	4.34 \pm 0.14 4.06-4.59 (29)	4.19	4.35 \pm 0.16 3.94-4.74 (46)
DL	12.48	12.57 \pm 0.23 11.97-13.06 (31)	12.97	12.82 \pm 0.39 12.43-13.89 (48)
MDTR	6.56	6.65 \pm 0.15 6.41-6.93 (31)	6.20	6.81 \pm 0.23 6.39-7.36 (47)

Morphological diagnosis.—*Carollia benkeithi* is a small *Carollia* with chestnut to dull-gray brown dorsal fur; short and naked forearm, a tuft of hairs at the base of thumb; legs short and apparently naked; uropatagium wide, with shallow distal notch. Skull relatively broad; a low sagittal crest in some individuals; rostrum slender; high forehead; interorbital constriction well-defined, making the anteorbital region appear inflated; braincase globular (Fig. 2). Second upper premolar (P4) displaced toward the lingual side of the toothrow, making a break in the lateral outline of the toothrow; however, this tooth is not in close contact with the first molar

(M1) and there is no projection of the cingulum of M1 toward P4. A robust anterior projection of the cingulum of P4 extends toward P3 (Fig. 2). A small, reduced gap is between the bases of the lower canine and first premolar. The space between the lower premolars is reduced, but they are never in close contact. Cusps of the first lower molar reduced, almost inconspicuous in side view. A small accessory cusp on the postero-lingual side of the third lower molar (m3) is always present. The angular process of the mandible is short and stout. Measurements of additional specimens of *C. benkeithi* are included in Table 1; their localities are listed in the Appendix.



Figure 1. Distribution of the three species of the *Carollia castanea* species complex. Localities for *C. benkeithi*, new species, as determined by specimens examined and literature references. The stars represent type localities for *C. benkeithi* and *C. castanea*. Some localities are lumped for purposes of graphic representation.



Figure 2. Ventral view of the skull and mandible of the holotype of *Carollia benkeithi* (TTU 46187) and a specimen of *C. castanea* (TTU 13177) from Honduras.

Karyotypic diagnosis.—Diploid chromosome number ($2N$) = 22 in both males and females, Fundamental number (FN) = 38; there is a single pair of medium-small acrocentrics in the autosomal complement (which are translocated to the X chromosome in other *Carollia* species; Patton and Gardner 1971), and the X chromosome is a small submetacentric (Fig. 3). *Carollia benkeithi* also lacks much of the heterochromatin in comparison to *C. brevicauda* and *C. perspicillata* (Stock 1975).

Molecular diagnosis.—1110 bp of the mitochondrial cytochrome-*b* gene from 4 additional specimens of *Carollia*, assigned to *C. benkeithi*, based on morphology and distribution, were obtained. These have been deposited at GenBank [DQ 177279-177282]. Another 4 sequences available from GenBank (AF 512002-004 [Bolivia], AF187021 [Peru]), also represent *C. benkeithi*. The Neighbor Joining tree using Kimura-2 parameter distances for these and other species of *Carollia* is shown in Fig. 4. The average distance value that separates *C. benkeithi* from *C. castanea* (sensu stricto) is 8.1%, and ranges from 7.3 to 9.1%. Genetic differences within the two clades in *C. benkeithi* averages 1.7%.

A third clade emerging from this tree includes two samples from eastern Ecuador, which diverge from *C. castanea* by 8.3% and from *C. benkeithi* by 8.1%. Presently, we recognize this genetically defined phylogroup as a third unnamed species of the *C. castanea* species complex (the *C. castanea* of Koopman 1993), although we do not provide a name for it. Based on a preliminary revision of voucher specimens, this species has a diploid chromosome number ($2N$) = 20-21 (Lim and Engstrom 1998; D. Parish, unpubl. data), and is distributed in eastern Ecuador (Albuja 1999) and northeastern Peru (Pirlot 1968).

Codon position changes that distinguish *C. benkeithi* from *C. castanea* include 27 fixed changes in 3rd position, one in 2nd position, and one in 1st position, involving 25 transitions and 4 transversions. One transition (position 917; T in *castanea*, C in *benkeithi*) and one transversion (position 925; T/C in *castanea*, A in *benkeithi*) resulted in two fixed amino acid replacements.

Shorter sequences (ranging from 80-150 bp) were obtained from the individuals with karyotypic data (MVZ 136460, 136462-4) and compared to the available sequences using the neighbor-joining algorithm of PAUP. The four sequences clustered together with the specimens representing *C. benkeithi*, thus confirming the observed morphological similarity among the voucher specimens. These sequences are available from the authors on request.

Description.—A small species of *Carollia*, with long, fluffy fur on back. Dorsal pelage without sharply defined banding; a broad buffy-chestnut band at the base, followed by a brown-yellowish band, and then narrow chestnut to dull gray-brown tips. Ventral pelage with short bicolored, brown-tipped hairs throughout. Forearm short (< 38 mm) and apparently naked; short legs, apparently naked. The uropatagium with a shallow and rounded notch.

Skull delicate, but relatively broad; a low sagittal crest sometimes present; rostrum slender, with a high forehead. Interorbital constriction well-defined, making the anteorbital region appear inflated; braincase globular. Posterior extension of the palate shorter than anterior portion. Maxillary roots delicate and usually presenting a pointed labial margin, oriented dorsally. One or two small spines on the antero-internal wall of the bullae; when two spines are present, they are connected by a low ridge at their bases. Angular process of the mandible are short and stout. Elongated and slender upper canines, slightly projected forward. Outer upper incisors spicule-like, much smaller than the middle ones. Second upper premolar (P4) displaced toward the lingual side of the toothrow, producing a break in the lateral outline of the toothrow, and with a robust anterior projection toward P3. Anterior cingulum of the first upper molar (M1) does not project toward P4. Lower incisors subequal in size, their occlusal outline slightly convex. A small, reduced gap between the bases of the lower canine and first premolar (p2). Second lower premolar (p3) almost twice as high as the first lower molar (m1), the cusps of which are reduced and inconspicuous in side view. Third lower molar (m3) proportionally small, with a small accessory cusp on the postero-lingual side. Mandibular rami and toothrows almost straight.

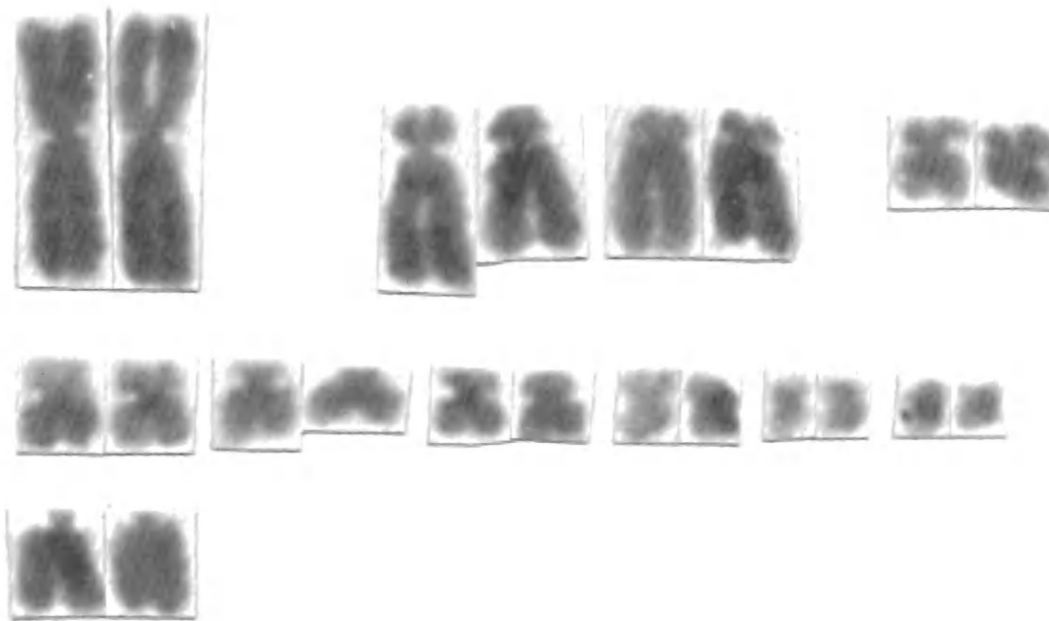


Figure 3. Karyotype of a female specimen of *Carollia benkeithi*, MVZ 136462 (courtesy of James L. Patton).

Comparisons.—We provide comparisons of *Carollia benkeithi* with samples of *C. castanea*, within which it usually has been included (Pine 1972; Koopman 1993). In the absence of a more accurate understanding of the degree of variation within and among populations of *C. castanea*, we assume that populations from Costa Rica, where the type locality is located, are representatives of that species. However, a full review of the variation in this group of species is beyond the objectives of this study. When more voucher specimens are accompanied by sequence and chromosomal data, such analysis will provide the most powerful resolution.

Using size alone, *Carollia benkeithi* is readily separable from the larger species of the genus, as well as by means of several pelage and cranio-dental features (Pine 1972; Pacheco et al. 2004). *Carollia benkeithi* is most similar in all respects to *C. castanea*; both species have variations of chestnut or pale brown pelage, apparently naked forearms, and a shallow notch in the edge of the uropatagium. In fact, *C. benkeithi* is hardly distinguishable by external characters from *C. castanea*, and their cranio-dental characters are also similar. A few dental characters are useful in differentiating *C. benkeithi* from *C. castanea*, including

the following: (a) a robust projection of the anterior cingulum of P4 toward P3 in *benkeithi* (Fig. 2), which is reduced to a short and blunt projection in *castanea*; (b) P4 not in contact with M1 in *benkeithi* (Fig. 2), or if so then there is no development of a projection of the anterior cingulum of M1; in *castanea*, an anterior cingular projection of M1 makes contact with P4; and (c) a small cusp on the postero-lingual side of m3 in *benkeithi* (Fig 2), which is rarely present in *castanea*.

McLellan's (1984) analyses provided early evidence of geographic differences within *Carollia castanea* (*sensu lato*). Although all of her 22 variables showed the lowest means for *C. castanea* as opposed to other species of *Carollia*, she found that locality variation within *castanea* accounted for 29.25% of the total variation. Five measurements showed overall variation over 40%; three of these were related to skull length, and two to skull width. This variation corresponded with latitude, because her samples from Peru (which came from close to the type locality of *C. benkeithi*) had the smallest values in all but two measurements, and five of them showed significant differences between what we recognize as *C. benkeithi* and *C. castanea*.

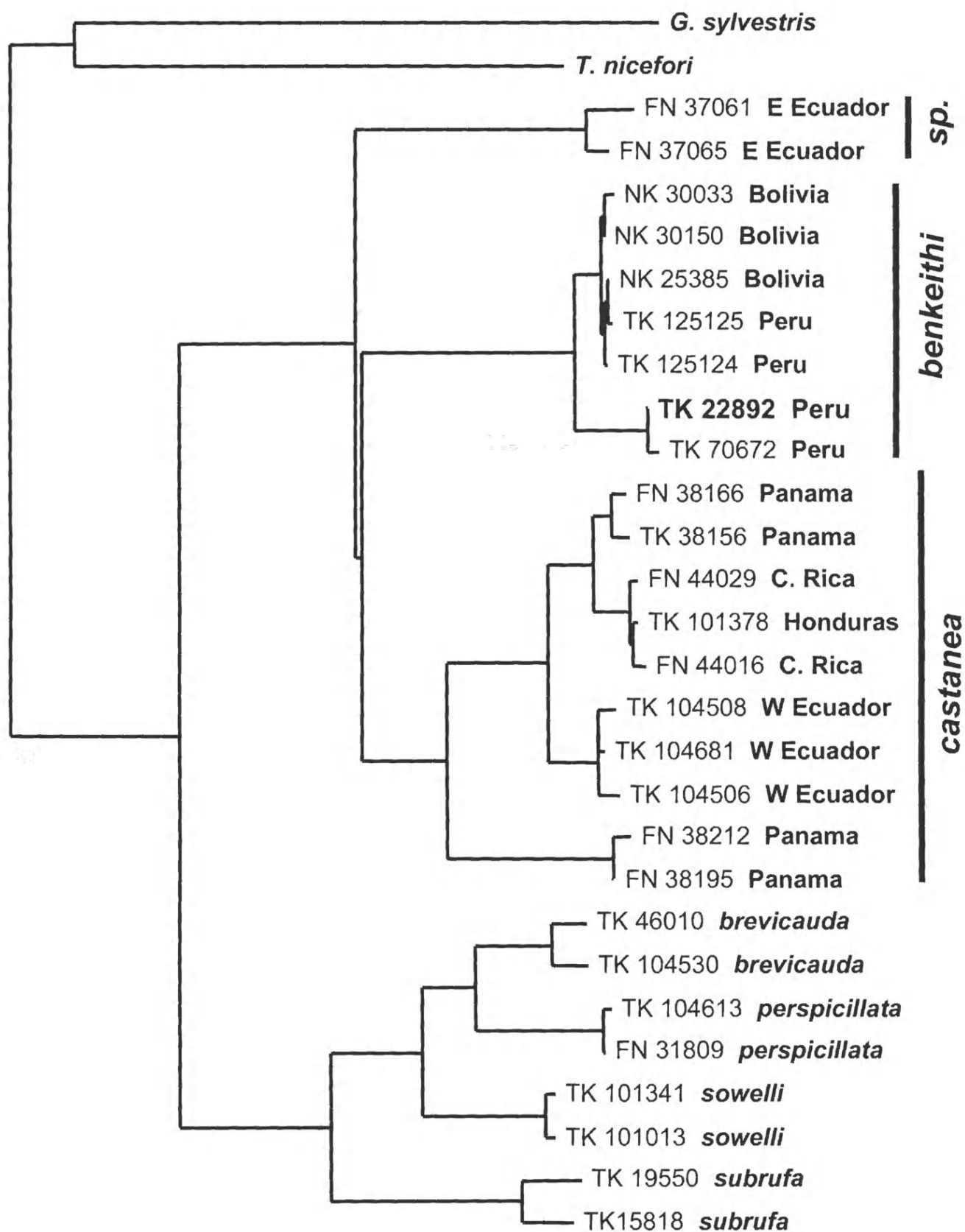


Figure 4. Phylogenetic relationships among seven species of *Carollia* as indicated by the neighbor joining tree based on Kimura-2 parameter distances. Outgroups are *Glyphonyceris sylvestris* and *Trinycteris nicefori*.

Our data also show significant differences in most of the craniodontal measurements in both MANOVA tests. When the five geographic groups were compared, the differences among the vectors of means were statistically significant (Wilks' Lambda = 0.177; $df = 50, 290.7$; $P < 0.001$), and all but one variable (M2M2) showed significant differences. A second MANOVA test including only two taxonomic entities (*C. castanea* and *C. benkeithi*) also found significant differences (Wilks' Lambda = 0.623; $df = 10, 59$; $P < 0.002$), but in this case two measurements (CC and M2M2) showed no differences between the groups.

Remarks.—The genus *Carollia* includes species that are common to abundant almost everywhere in the Neotropics (Pine 1972), and *C. benkeithi* is not an exception. Based on our records and several others (as *C. castanea*), this species is typically found in tropical evergreen forests at lower elevations, mostly below 1000 m. Based on their overall resemblance, the ecological and reproductive habits of *C. benkeithi* should be similar to those of *C. castanea*.

Etymology.—The specific epithet *benkeithi* is a modified Latin genitive after Mr. Ben E. Keith, a long-time benefactor of the Natural Science Research Laboratory (NSRL) of the Museum of Texas Tech University. Species such as *Carollia* are not only hard to tell apart, but often deemed too common to merit specific focus of systematic studies. Funding of research institutions has a direct impact on our work and allows for significant effort on many poorly understood taxa. A recent grant by Mr. Keith and his family has resulted in a new wing that more than doubled the size of the NSRL and greatly improved the available facilities. We acknowledge his commitment to the study of natural science collections by naming this new species after him. Date of publication of this new name was chosen to coincide with the day the first catalogued mammal specimens were transferred to the museum wing constructed through Mr. Ben Keith's generosity.

DISCUSSION

An inability to discriminate between cryptic species may lead to serious underestimation of biodiversity, the perception of misleading biogeographic patterns, and misinterpretation of ecological data (Dorbigny et al. 2003). These misperceptions may be critical in the case of health-related issues, such as rabies, Bolivian hemorrhagic fever, etc., where proper recognition of host species is vital. However, access to sufficient biological information that would allow indisputable recognition between congeneric species is frequently unavailable. Rather, we depend on particular sets of characters to shape a useful and convincing species concept (Bradley and Baker 2001).

Evidence from nucleotide variation of the cytochrome-*b* gene (Hoffmann and Baker 2003) and the karyotypic polymorphism involving sex-chromosomes (Baker and Bleier 1971; Patton and Gardner 1971) concerning what was previously recognized as a single species *C. castanea* (Koopman 1993) has convinced us that the proper action was to recognize this taxon as a species complex. Molecular sequence divergence among phyllostomid bats is indicative of specific distinction at values between 5-7% (Bradley

and Baker 2001). In the order Chiroptera there are few chromosomal races or chromosomal polymorphisms (Baker 1979). The sex chromosome translocation discussed in this paper is most parsimoniously regarded as occurring at the base of the radiation of *Carollia* and may be a synapomorphy for the remainder of the genus after *C. benkeithi* diverged from the common ancestor for the genus. Cytochrome-*b* data (Hoffmann and Baker 2003) suggest that either *C. castanea* (sensu lato) is paraphyletic and the translocation to the X has occurred twice or, alternatively, there has been a reversal to the primitive character state in *C. benkeithi* (see also Lim and Engstrom 1998).

Pine (1972) discussed the diversification of *Carollia*, concluding that *castanea* (sensu lato) would be the most distinctive species in the genus; and McLellan (1984) stated that *C. castanea* was the most morphologically distinct species in the genus. The same conclusion has been reached using molecular data (Lim and Engstrom 1998; Wright et al. 1999; Hoffmann and Baker 2003), but phylogenies based on morphological characters are missing.

The morphological and morphometric information provided by the analyses of representative samples of *C. castanea* (sensu lato) has allowed us to support the results of Hoffmann and Baker (2003) regarding the recognition of unidentified species of *Carollia*. A similar approach has proven useful previously (Baker et al. 2002) and we hope to complement the morphological description of *C. manu* (Pacheco et al. 2004) with karyotypic information and mtDNA sequences. Thus,

we could refine our current hypotheses on the origin and diversification of this widespread genus, that now includes 10 species: *C. perspicillata* (Linnaeus 1758), *C. brevicauda* (Schinz 1821), *C. castanea* H. Allen 1890, *C. subrufa* (Hahn 1905), *C. colombiana* Cuartas et al. 2001, *C. sownelli* Baker et al. 2002, *C. manu* Pacheco et al. 2004, *C. monohernandezii* Muñoz et al. 2004, *C. benkeithi* Solari and Baker 2005, and one unnamed from eastern Ecuador and Peru.

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APPENDIX

List of specimens examined and their geographic localities. Specific localities are abbreviated to the major geographic reference, based on the collectors' labels. When two numbers identify a specimen the first one is the museum catalog number, and the second is the tissue number [FN for ROM, NK for MSB, and TK for TTU]. Acronyms for museums and institutions follow Hafner et al. (1997).

Carollia castanea (Total: 51). HONDURAS: *Atlantida*, Lancetilla (3: TTU 84037 [TK 101378], TTU 84121 [TK101462], TTU 84386); *Comayagua*, Cueva de Taulabe (1: TTU 84037); *Olancho*, 12.1 mi by road SSW of Dulce Nombre de Culmi (3: TTU 13176-77, TTU 28100). COSTA RICA: *Heredia*, 7.3 mi SE Puerto Viejo (3: TTU 13184-85, TTU 13487), Parque Nacional Braulio Carrillo (1: USNM 562812); *Limón*, Estación Biológica Cano Palma (1: ROM 108303 [FN 44029]), Tortuga Lodge (1: ROM 108291 [FN 44016]); *San José*, Angostura (1, Holotype: USNM 36384). PANAMA: *Chiriqui*, Ojo de Agua (1: ROM 104305 [FN 38156]), Santa Clara (1: ROM 104315 [FN 38166]); *Darién*, Parque Nacional Darién (2: ROM 104341 [FN 38195], ROM 104353 [FN 38212]); *San Blas*, Armila (4: USNM 335199-200, USNM 335204-05); *Veraguas*, Isla Cebaco (2: USNM 360170-71). COLOMBIA: *Antioquia*, Zaragoza (4: USNM 499323-24, USNM 499326-27); *Valle*, Rio Zabaletas (2: USNM 483411-12). VENEZUELA: *Tachira*, 45 km NE San Cristóbal (2: USNM 419508, USNM 419510); *Territorio Federal Amazonas*, 32 km SSE Puerto Ayacucho (4: USNM 407893-95, USNM 407897). ECUADOR: *Esmeraldas*, 7 km N Quininde on Quininde-Esmeraldas highway (1: USNM 522165), San Lorenzo (3: TTU 85278 [TK 104506], TTU 85280 [TK 104508], TTU 85453 [TK 104681]); *Guayas*, Balao, 10 km ESE Huerta Negra (2: USNM 498858, USNM 522164); *Pichincha*, Santo Domingo, Río Palenque Science Center (8: USNM 528503-10).

Carollia benkeithi (Total: 47). PERU: *Cusco*, La Convención, Camisea (11: MUSM 13564, MUSM 13567, MUSM 13573, MUSM 13577, USNM 577783 [TK 70672], USNM 582800, USNM 582805-09); *Huanuco*, Leoncio Prado, Tingo Maria, 2 km S (1, Holotype: TTU 46187 [TK 22892]); *Junin*, 3.2 km N Vitoc, Río Tulumayo (5: USNM 507179-83); *Madre de Dios*, Albergue Maskoitania, Río Alto Madre de Dios (4: FMNH 174603 [TK 125124], FMNH 174605 [TK 125125], FMNH 174607, FMNH 174609 [TK 125127]), Manu, Pakitza (12: MUSM 6837-41,

USNM 564376-78; USNM 566511-14); *Ucayali*, Balta, Río Curanja (4: MVZ 136440, MVZ 136462-4). BOLIVIA: *Beni*, Yacuma (1: MSB 68356 [NK 25385]); *Cochabamba*, Sajta (1: MSB 70297 [NK 30150]), Villa Tunari (1: MSB 70298 [NK 30033]); *La Paz*, 1 mi W Puerto Linares (1: TTU 34814-20).

Carollia unnamed species (Total: 9). ECUADOR: *Napo*, Parque Nacional Yasuni (2: ROM 103979 [FN 37061], ROM 103983 [FN 37065]); *Pastaza*, Amazonas Military Fort (1: TTU 84903), Taculin, below Puyo (2: USNM 548109-10), Tiguino, 130 km S of Coca (2: USNM 574522-23); *Zamora-Chinchipe*, Cumbartza, 3 km NE (1: USNM 513443), Los Encuentros, 4 km ENE (1: USNM 513444). PERU: *Loreto*, Puerto Indiana (Pirlot 1968).

Carollia brevicauda. ECUADOR: *Esmeraldas*, San Lorenzo (TTU 85302 [TK 104530]); PERU: *Loreto*, Quebrada Aguas Negras (MUSM uncataloged [TK 46010]).

Carollia perspicillata. ECUADOR: *Esmeraldas*, San Lorenzo (TTU 85385 [TK 104613]); GUATEMALA: *El Peten*, Poptun (ROM 99259 [FN 31809]).

Carollia sowelli. HONDURAS: *Comayagua*, Cueva de Taulabe (TTU 82495 [TK 101341]), *Francisco Morazán*, Parque Nacional La Tigra (TTU 82497 [TK 101013]).

Carollia subrufa. EL SALVADOR: *Ahuachapan*, El Refugio (ROM 35506 [TK 15818]); MEXICO: *Jalisco*, Chamela (TTU 37719 [TK 19550]).

Glyphoncteris sylvestris. GUYANA: Siparuni, Iwokrama Reserve (ROM 107445 [TK 16374]).

Trinycteris nicefori. VENEZUELA: *Guarico*, 45 km S Calabozo (Universidad Central de Venezuela, UCV [TK 15189]).



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