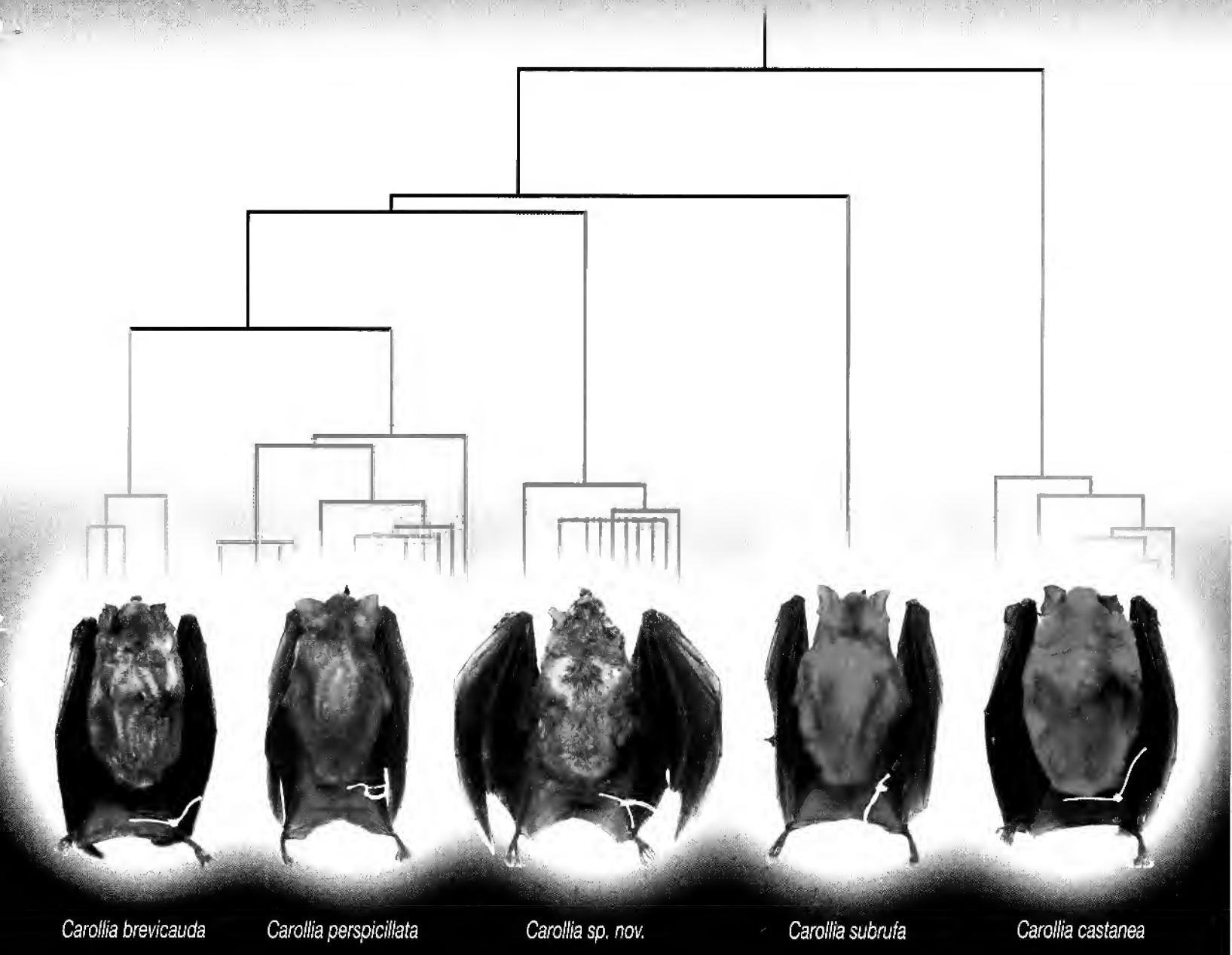
Occasional Papers

Museum of Texas Tech University

Number 217 31 October 2002



A New Central American Species from the *Carollia brevicauda* Complex

Editor's Comment: This paper describes a previously unrecognized species in the genus *Carollia*. Although it is probable that morphological differences distinguish this new species from the remainder of the genus, it is clear that this species would not have been recognized based on morphology alone. Methods developed since 1986 allow easy access to DNA sequence data from native species permit scientists to employ data other than morphological to document biological uniqueness and species boundaries. The use of the mitochondrial cytochrome-*b* gene to indicate biological species in mammals was recently reviewed by Robert Bradley and Robert Baker (Journal of Mammalogy, vol. 82:960-973). If their conclusions are correct, there will be numerous currently unrecognized species that will be detected through studies of DNA sequence and application of the genetic species concept. The total may be 25% more than the current list in Wilson and Reeder, 1992 (Mammals Species of the World, Smithsonian Institution Press, Washington, DC). Clearly, there is a substantial need for detailed studies of the implications of genetic variation to species boundaries in natural populations of mammals. One important implication to the hypothesis that many biological species remain unrecognized is that museum collections, especially those that archive material for DNA analysis, are not sufficient to resolve many of these systematic and biodiversity issues. Additional museum collections that save a maximum amount of material for genetic studies will be needed. Collections of mammal specimens for this purpose should be archived (voucher specimens and tissues) in accredited collections that are funded for perpetuity. Storage of samples in individual laboratories greatly increases the likelihood that these specimens will be unavailable for research by others to better understand the diversity of life on Earth.
RJB

Front cover: Color representation of the cytochrome-*b* branding pattern of the *Carollia brevicauda* complex. Specimens are: *Carollia brevicauda*, TTU 85130; *Carollia perspicillata*, TTU 63655; *Carollia sp. nov.*, TTU 82495; *Carollia subrufa*, TTU 63681; and *Carollia castanea*, TTU 84903.

A New Central American Species from the *Carollia brevicauda* Complex

Robert J. Baker, Sergio Solari and Federico G. Hoffmann

In a study of the sequence divergence in the mitochondrial cytochrome-*b* gene, Wright et al. (1999) suggested that the species *Carollia brevicauda* as recognized currently may consist of two biological species primarily because *C. brevicauda* was paraphyletic relative to *C. perspicillata*. Because of the sample size of the proposed new species (N=1) as compared to *C. brevicauda (sensu stricto)* (N=3) and the geographic areas represented in the Wright et al. (1999) study, it was impossible to estimate the limits of geographic distribution as well as the range of genetic variation within and among populations and clades. From a taxonomic standpoint, it was necessary to establish the geographic limits of each clade and relate them to available species-level names. Here we further examine the biogeography of the two clades that Wright et al. (1999) suggested might represent biological species.

To do this we sequenced 1140 base pairs of the mitochondrial cytochrome-*b* gene from 21 additional individuals of the *C. brevicauda* complex representing as many geographic localities as were available to us for DNA samples. Additionally, we sequenced the cytochrome-*b* gene from 30 specimens of the other recognized species of *Carollia*. The new sequences were combined with the 10 reported by Wright et al. (1999) to generate a phylogenetic tree, which provides additional information concerning the extent of geographic variation within members of the genus *Carollia*. The new data are consistent with the proposal that a major subdivision exists in what currently is recognized as *Carollia brevicauda* (Fig. 1). Three methods (neighbor-joining, parsimony and likelihood, as implemented by PAUP*, Swofford, 1999) all produce a tree with the same topology as shown in figure 2. The results and implications of these additional data beyond the resolution of the possibility of two biological species within the *Carollia brevicauda* complex will be published elsewhere. Based on the cytochrome-*b* data, the South American clade of *C. brevicauda* shares a common ancestor with *Carollia perspicillata* after diverging from the Central American representatives of *Carollia brevicauda*. One clade of *C. brevicauda* (*sensu lato*) is restricted to Central America, north of Panama, and includes Western Panama. The other clade of *C. brevicauda* is distributed from Eastern Panama to Bolivia (Fig. 1).

The potential application of the sequence data from the cytochrome-*b* gene to predicting situations where unrecognized biological species might exist was reviewed by Bradley and Baker (2001) and the conclusion that *C. brevicauda* comprises two biological species is supported by both distance values, and the observation that samples from *C. brevicauda* (*sensu lato*) do not form a monophyletic clade (genetic species concept, Dobzhansky, 1950; phylogenetic species concept, Cracraft, 1983). In fact, *C. brevicauda* (*sensu stricto*) is sister to *C. perspicillata*, whereas the Central American portion of *C. brevicauda* (*sensu lato*) is sister to the common ancestor of *C. perspicillata* and *C. brevicauda* (*sensu stricto*).

This resolution of the geographic distribution of the two clades permits assignment of the species level names that have been recognized as available for *Carollia brevicauda* (*sensu lato*). The type locality of *brevicauda* is Rio do Espirito Santo, Brazil. The four synonyms that are available (Koopman, 1993) are *bicolor* (Wagner, 1840), type locality Brazil; *grayi* (Waterhouse, 1838), type locality Pernambuco, Brazil; *lanceolatum* (Gray, 1843), type locality South America; and *minor* (Gray, 1866), type locality Bahia, Brazil. However, according to Pine (1972) the name *lanceolatum* is a *nomen nudum*. There is no name available for representatives of the clade of *C. brevicauda* (*sensu lato*) from Central America. Below we describe a new taxon to fill this need.

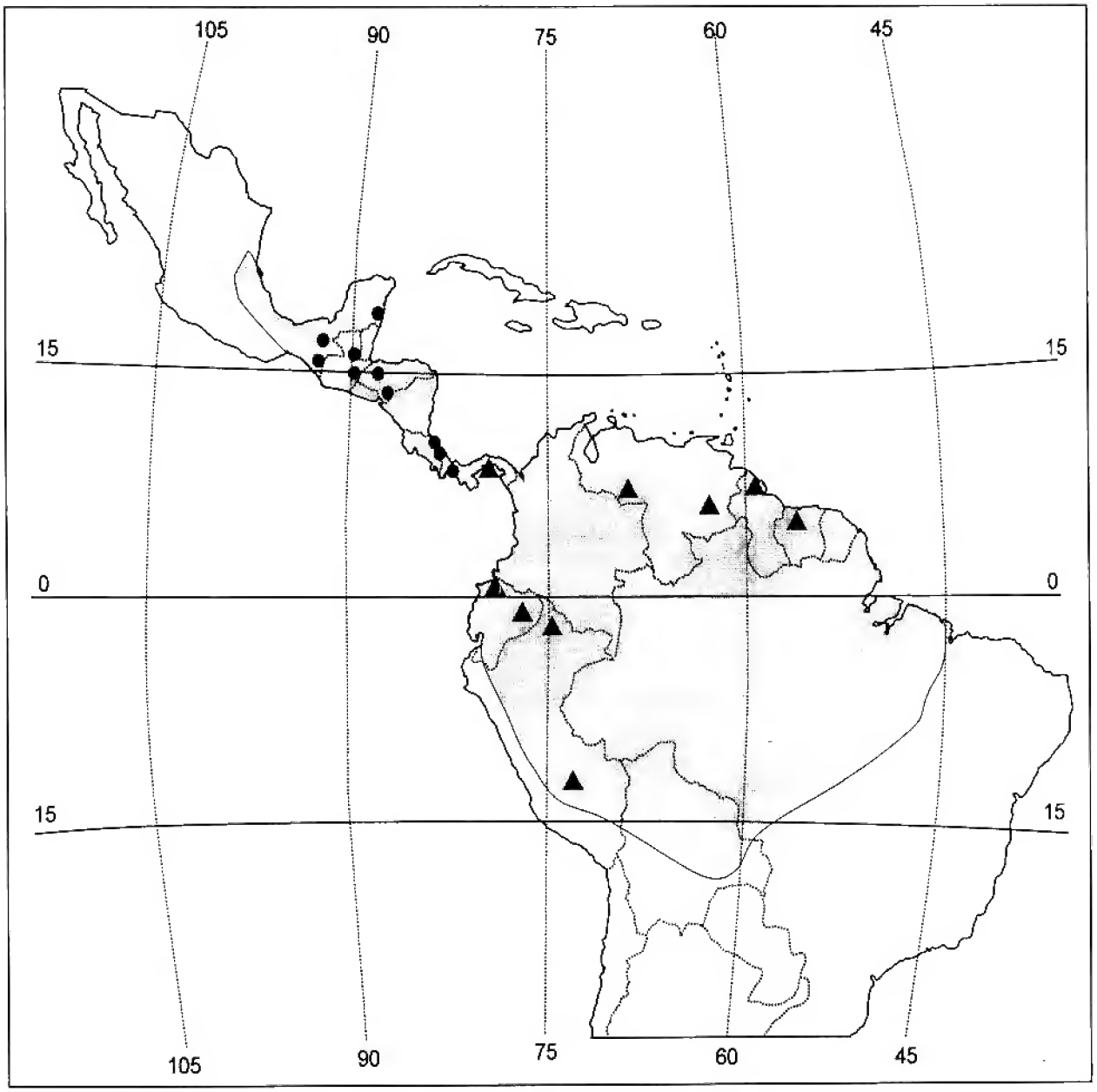


Figure 1. Geographic distribution of *Carollia brevicauda sensu* Koopman (1993). Triangles and dots correspond to collecting localities of individuals for which we have cytochrome-*b* sequence that relate to the two clades defined by Wright et al. (1999).

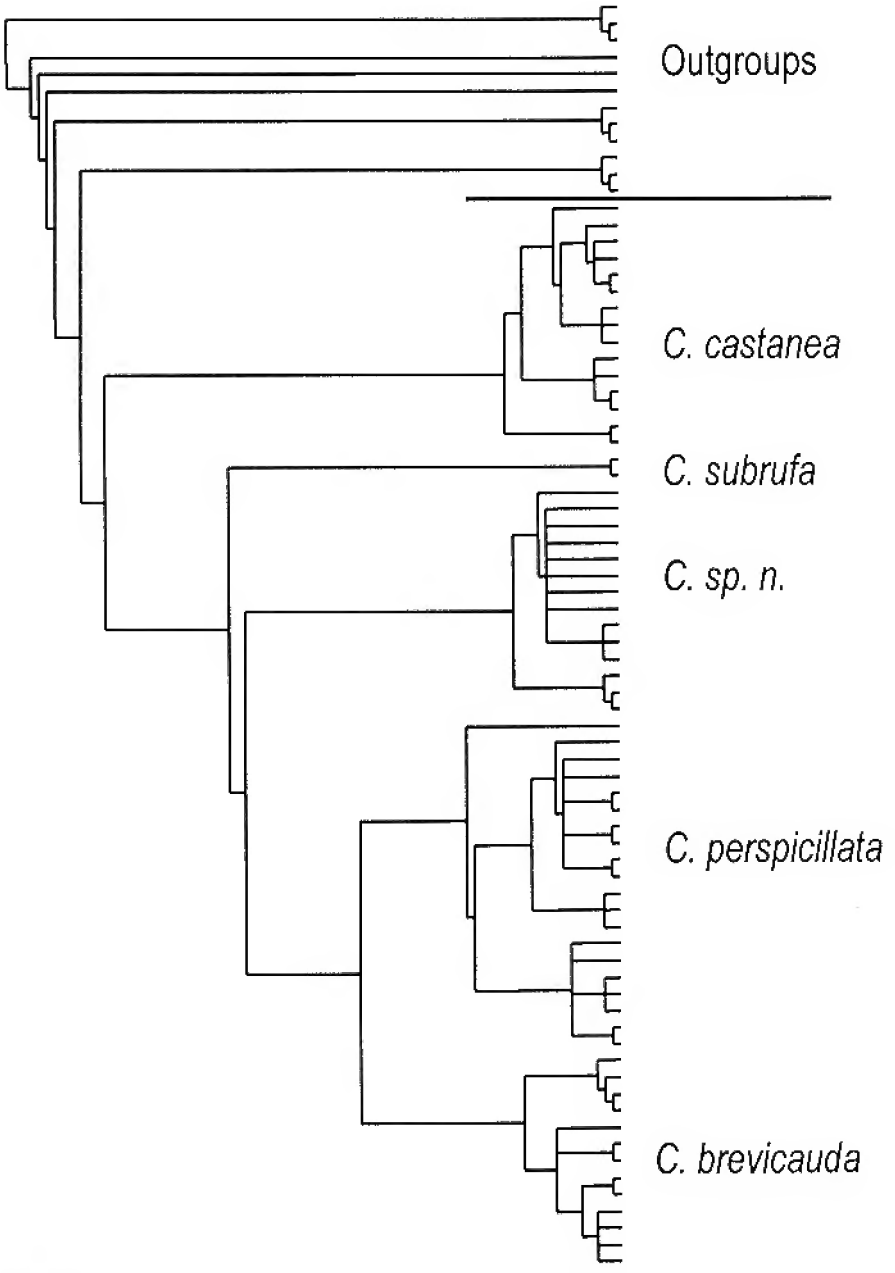


Figure 2. Parsimony tree depicting phylogenetic relationships among the species of *Carollia*.

Carollia sowelli, New Species

Holotype.– Adult male, skin, skull and skeleton, Museum of Texas Tech, TTU 82495 from Honduras, Comayagua, Cueva de Taulabe,(14°41'42"N, 87°57'07"W), (UTM zone 16:397511 E 1624803 N), collected on 11 July, 2001, by a Texas Tech field party on the Sowell Expedition 2001 led by Robert D. Bradley. Original number, Ronald A. Van Den Bussche 1869, TK number 101341 identifies tissue samples and karyotype preparations that are deposited in the Natural Science Research Laboratory, Texas Tech University.

Distribution.– From Western Panama, north through Middle America to the states of Veracruz and San Luis Potosi in Mexico on the Atlantic versant and to the state of Oaxaca on the Pacific versant (Fig. 3).

Diagnosis.– The initial diagnosis is based on nucleotide order in the mitochondrial cytochrome-*b* gene. These sequences are deposited in GenBank (pending) along with the sequences of *C. brevicauda* (*sensu stricto*). The differences between these two involve nucleotide characters at positions in the cytochrome-*b* gene (Table 1). A summary of pairwise comparisons within and between *C. sowelli*, *C. brevicauda* and *C. perspicillata* can be found in Table 2.

Morphologically, *C. sowelli* can be distinguished from *C. perspicillata, C. subrufa* and *C. castanea* by the same morphological suite of characters used to distinguish *C. brevicauda.* These include a pelage that is long and thick with the size of the shafts of the individual hairs being fine; forearm hairy, hair on nape of neck with broad, dark band contrasting strongly with and demarcated from a broad whitish band distal to it (Hall, 1981).

This is a large species of *Carollia*, slightly larger than *brevicauda* but smaller than *perspicillata*, with long and lax dorsal fur. Fur on back tricolor, almost like *brevicauda*, but *sowelli* lacks the dark brown tips that would make conspicuous its medial light band. Consequently, the appearance is lighter than *brevicauda*. Forearm haired but not furred. Forearm, tibia, and feet almost the same length as those of *brevicauda*, but smaller than those of *perspicillata*.

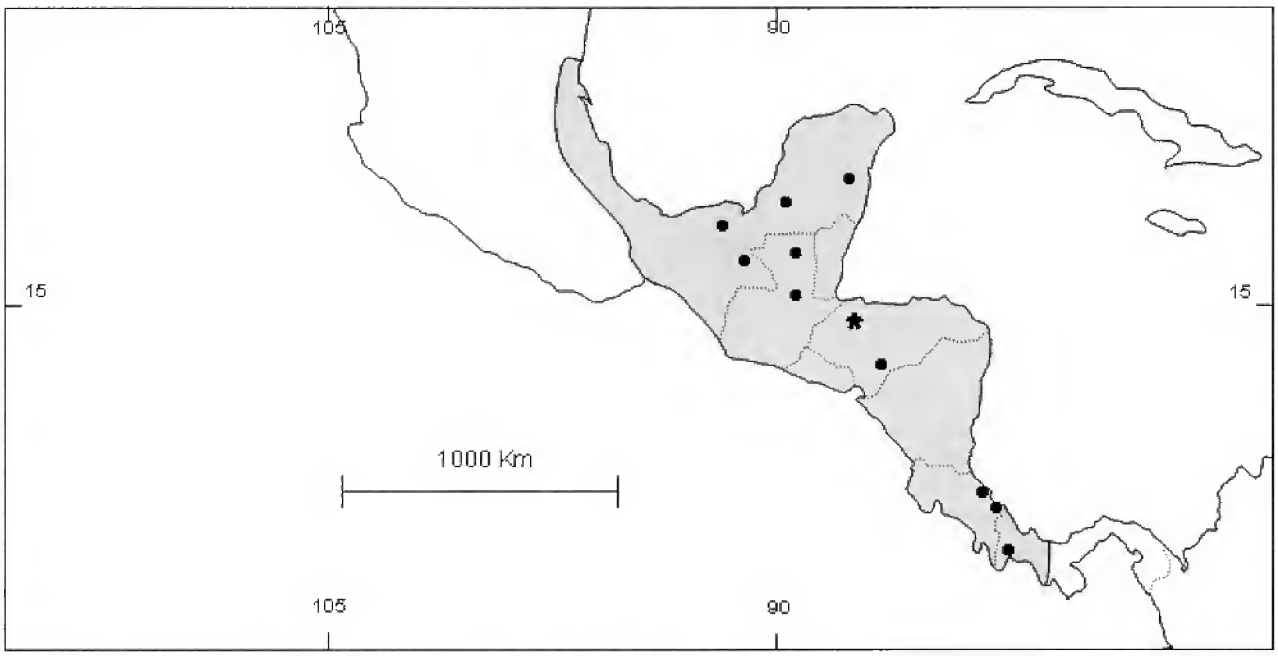


Figure 3. Geographic distribution of *Carollia sowelli*. Dots indicate sample localities for which cytochrome-*b* sequence data are available. Type locality is identified by an asterisk.

Table 1. List of fixed changes in the mitochondrial cytochrome-b gene among Carollia sowelli, C. brevicauda *and* C. perspicillata. *A = adenine, C = cytosine, G = Guanine, and T = Thymine.*

Position	*C. brevicauda*	*C. perspicillata*	*C. sowelli*
39	T	T	C
72	C	T	C
102	C/T	T	C
183	T	C	C
207	C	T/C	T
276	C	T	C
309	T	C	C
348	C	C/T	T
363	C	T	T
390	A	A	C
483	C	A	T
573	T	C	C/T
585	G	A/G	C
588	C/T	T	C
603	C	C	T
630	C	C	T
675	C/T	T	C
708	C	C	T
711	T	T/G	C
759	T	T/C	C
777	G/T	C	T
816	G	G	A
885	T	T	C
888	G	G	A
912	A	A	G
925	G/A	G	A
999	C	C	T

Skull larger than *brevicauda* especially in its total length; but also with a longer palate, longer maxillary and mandibular toothrow, mandibular length, and coronoid height (Table 3). There is a gap between the upper premolars, but the space is highly variable. It is because the posterior edge of the anterior premolar (PM3), which is almost straight, and the anterior projection of the cingulum of the posterior premolar (PM4), which is not well developed but, always present (Fig. 4). Basisphenoidal pits are elongated. Supraorbital processes are well-developed, and the interorbital (postorbital) breadth is conspicuously narrower. The posterior palate is long and wide and not as slender as in *perspicillata*. Lateral projection of the mastoid process is evident on the external side of the skull, forming a low crest that connects with the lambdoidal crest. The anterior projection of this process is low, and fused to the side of the skull just behind the middle ear.

Selected measurements.– External measurements (in millimeters) recorded in the field by Ronald A. Van Den Bussche are: total length – 66; tail length – 6; hind foot – 10; ear – 20; tragus – 10. Weight was 16.5 grams. Length of forearm on the dried specimen is 41.8. Cranial measurements (in millimeters) of the holotype (Fig. 4) are as follows: Greatest length of skull – 23.1; condylobasal length – 21.2; breadth of brain case – 9.1; depth of brain case – 9.0; mastoid breadth – 11.5; length of mandibular toothrow – 8.5; length of maxillary toothrow – 7.4; post-orbital breadth– 5.6; width across upper canines – 5.6; length of mandible – 14.6 (see also Table 3).

Karyological Data.– The karyotype of the holotype is indistinguishable from that reported by Patton and Gardner (1971) for *C. brevicauda*. The diploid number is 21 and the fundamental number is 36. The X is a subtelocentric and the 2 Ys are acrocentric.

Lower jaw and the lower toothrows are bowed, but not to the same extent as seen in *brevicauda*. Base and cingulum of lower canines conceal in part the external lower incisors. The middle lower incisors are enlarged, and bigger than the external ones, but not as much as those of *perspicillata*. Little or no space between the premolars although some variation is present. As seen in other species of *Carollia*, there is some evidence of sexual dimorphism, with development of processes and crests more conspicuous in the males.

A full comparison of *Carollia sowelli*, with its congeners is beyond the scope of this description. There is a previously recognized wide range of morphological (Pine, 1972; Owen et al., 1984; Lim and Engstrom, 1998) and morphometric (McLellan, 1984; Owen et al., 1984) variation between and within species of *Carollia*. McLellan (1984) provides a reference for the scale of the morphometric variation in terms of the geographic range of the species, even recognizing the existence of a large difference between populations of the northern range (our new species, see above) and the southern range (*C. brevicauda* as here restricted) of her concept of *C. brevicauda*.

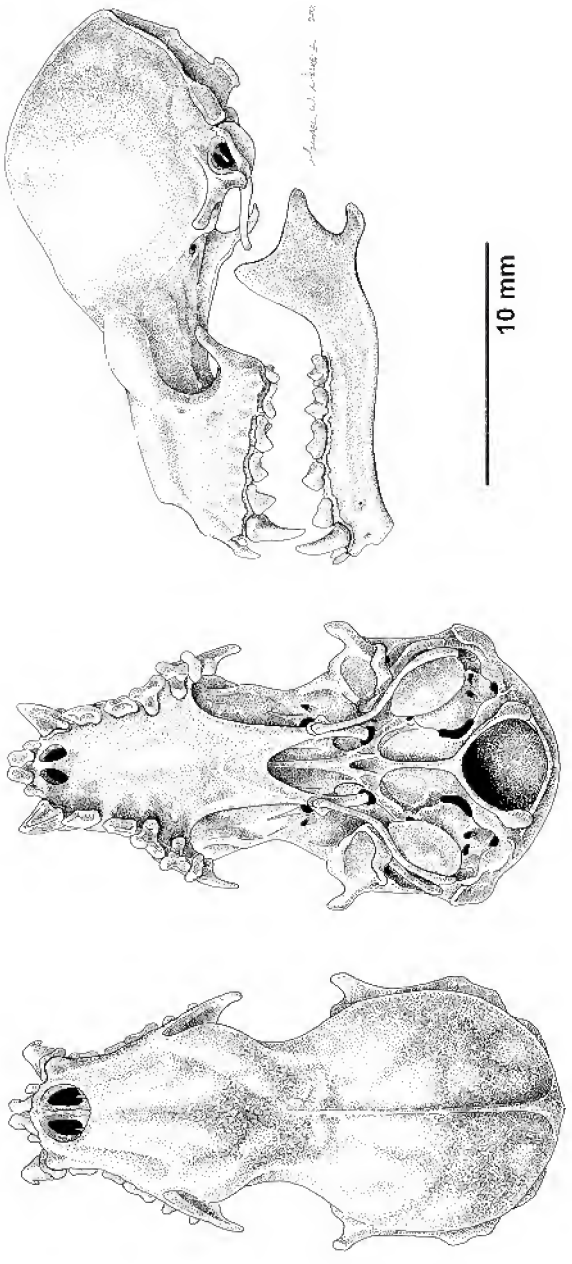


Figure 4. Dorsal, ventral and lateral views of the skull and lower jaw of the holotype (TTU 82495) of *Carollia sowelli*. Drawing by Michael W. Nickell.

Table 2. Average genetic distance (uncorrected) between and within samples of Carollia sowelli, C. brevicauda *and* C. perspicillata.

	C. brevicauda	*C. perspicillata*	*C. sowelli*
C. brevicauda	1.98 ± 0.11 %		
C. perspicillata	3.67 ± 0.02 %	1.46 ± 0.05 %	
C. sowelli	4.95 ± 0.03 %	4.79 ± 0.02 %	1.58 ± 0.17 %

Table 3. Measurements of Carollia sowelli *new species (n=15) and* C. brevicauda *(n=10). For each measurement, the average plus/minus one standard deviation is shown. Differences are significant (P < 0.05) in the variables marked with *.*

	brevicauda	*sowelli*
Braincase breadth (BRB)	9.570 ± 0.190	9.595 ± 0.177
Coronoid height (CH)*	4.821 ± 0.175	5.005 ± 0.240
Greater skull length (GSL)*	21.711 ± 0.465	22.095 ± 0.360
Least interorbital breadth (LIB)	5.492 ± 0.131	5.465 ± 0.150
Breadth of upper M2 (M2M2)	7.548 ± 0.248	7.482 ± 0.238
Mandibular length (MDL)*	13.973 ± 0.503	14.498 ± 0.470
Mastoid breadth (MST)	10.797 ± 0.295	10.980 ± 0.300
Maxillar toothrow (MTR)*	6.934 ± 0.195	7.131 ± 0.113
Mandibular toothrow (MDTR)*	7.508 ± 0.265	7.788 ± 0.165
Palate length (PL)*	9.036 ± 0.326	9.495 ± 0.220
Rostral breadth (RB)	4.817 ± 0.211	4.787 ± 0.169
Supraorbital breadth (SOB)	6.340 ± 0.225	6.362 ± 0.231

Intraspecific Genetic Variation in the Cytochrome-*b* gene within *Carollia sowelli*

We have sequenced 14 individuals from Middle America that are referable to *C. sowelli*, and the cytochrome-*b* variation is partitioned into 2 lineages that are quite distinct. The average distance values that separate those clades are 3.6%. Perhaps the most striking aspect of these data is the nature of the changes relative to the codon positions when compared to the differences that distinguish *C. sowelli* from *C. brevicauda*. Of the 19 fixed changes between *C. sowelli* and *C. brevicauda* (Table 1) all are in 3rd codon positions, involving 17 transitions and 2 transversions and no fixed amino acid replacements. Within *C. sowelli*, (Table 4) the 2 clades are distinguished by 23 fixed differences, which involve 8 fixed changes in 1st codon positions, 1 in the 2nd codon position, and 14 in 3rd codon positions. These fixed differences include 22 transitions and 1 transversion, and involve 4 amino acid replacements. In each of these amino acid changes one clade of *C. sowelli* is unique from *C. brevicauda*, whereas the other shares the amino acid condition in *C. brevicauda*. In all 4 examples the unique condition is present in the specimens from western Panama and Costa Rica.

The application of genetic data to taxonomic recognition is a relatively unexplored field, but the general ideas have been presented philosophically (Avise and Walker, 1999; Bradley and Baker, 2001; Cracraft 1983, Templeton, 1989, 2001). Clearly the magnitude of differences that separate the *C. sowelli* clades typically is present in other species of mammals that have been recognized on a morphological basis (Bradley and Baker, 2001). Indeed, *C. sowelli* may be a composite species

*Table 4. Fixed changes in the cytochrome-*b *between the 2 lineages of* C. sowelli. *A = adenine, C = cytosine, G = Guanine, and T = Thymine.*

Position	Northwest	Southeast
27	C	A/G
84	T	C
117	C	A
180	T	C
264	C	T
291	C	T
304	T	C
444	C	T
459	T	C
489	A	G
573	C	T
609	T	C
672	C	T
685	A	G
688	T	C
721	A	G
795	C	T
846	C	T
886	C	T
1066	A	G
1069	C	T
1078	T	C
1106	T	C

or alternatively, may be comprised of two subspecies. While all these are intriguing possibilities, the best solution to these questions must await resolution from other forms of data (morphology, nuclear genes, etc.).

Etymology – It is our pleasure to name this species in honor of Mr. James E. Sowell, who has been a major benefactor to Texas Tech University. Mr. Sowell has funded the Sowell Expeditions, which have tremendously benefited the Natural Science Research Laboratory's research collections and provided an opportunity for many Tech students to experience the natural history and ecology of the tropics.

ACKNOWLEDGMENTS

We thank Robert Bradley for leading the expedition that collected the holotype as well as other specimens valuable to this study. We thank Ron A. Van Den Bussche for preparing the holotype and Meredith Hamilton for karyotypic preparation. We thank Miguel Quintana for logistical and organizational support for the trip. Other members of the field party were Brian Amman, Darin Carroll, Nevin Durish, Carl Dick, Steve Hoofer, Francisca Mendez-Harclerode, Lisa Mitchell, Serena Reeder, John Suchecki, with the collaboration of Reyna Teresa Velasquez and Catalina Sherman of the Honduras Secretaria de Salud. For discussions on the description of species using genetic data we thank Robert Bradley, David Hafner, Enrique Lessa and Bruce Patterson.

List of Specimens Examined

Specimens examined and their geographic localities are given below: TK numbers correspond to samples from the frozen tissue collection at the Natural Science Research Laboratory from Texas Tech University, Lubbock, Texas; MVZ numbers correspond to samples from the Museum of Vertebrate Zoology, Berkeley, California; NK to the Museum of Southwestern Biology (Albuquerque), FMNH and MDE numbers correspond to samples from the Field Museum of Natural History, Chicago, Illinois. Voucher number are given in parentheses.

Carollia brevicauda.– BOLIVIA: Santa Cruz, Buen Retiro NK 12171 (MSB 55142); Santa Cruz NK 15417 (MSB 59775); ECUADOR: Esmeraldas, San Lorenzo TK 104530 (TTU 85302); Napo, Parque Nacional Yasuni FMNH 37060; GUYANA: North West District, Baramita TK 86502; PANAMA: Panama, Parque Nacional Altos de Campana FMNH 38117; PERU: Loreto, Aguas Negras TK 46009, TK 46010; Cuzco, La Convencion TK 70412; SURINAME: Saramacca, Raleigh Falls TK 10218 (CMNH 63727); VENEZUELA: Barinas, Barinitas TK 19316 (CMNH 78409); Bolivar, El Palmar TK 19273 (CMNH 78400).

Carollia castanea.– BOLIVIA: Beni, Yucumo NK 25385 (MSB 68356); Cochabama, Villa Tunaria NK 30033 (MSB 70298); Sajta NK 30150 (MSB 70297); COSTA RICA: Limon, Estacion Biologica Cano Palma FMNH 44029; Tortuga Lodge FMNH 44016; ECUADOR: Esmeraldas, San Lorenzo TK 104506 (TTU 85278); TK 104508 (TTU 85280), TK 104681 (TTU 85453); Napo, Parque Nacional Yasuni FMNH 37061, FMNH 37065; HONDURAS: Comayagua, Cueva de Taulabe TK 101378 (TTU 84037); Atlantida, Lancetilla TK 101462 (TTU 84121); PANAMA: Chiriqui, Ojo de Agua FMNH 38156; Darien, Parque Nacional Darien FMNH 38195.

Carollia perspicillata.– BRAZIL: Minas Gerais, Municipio de Caratinga MVZ 185533; Pernambuco, Municipio Tamandare MVZ 185518; Rio Grande do Norte, Municipio Baia Formosa MVZ 185806; Sergipe, Municipio Santo Amaro Das Brotas MVZ 185813; ECUADOR: Esmeraldas, San Lorenzo TK 104613 (TTU 85385), TK 104631 (TTU 85403); Napo, Parque Nacional Yasuni FMNH 37084, FMNH 37107; GUATEMALA: El Peten, Poptun FMNH 31809; GUYANA: Berbice District, Dubulay Ranch TK 86671, TK 86691; North West District, Baramita TK 86503; MEXICO: Campeche, Escarcega FMNH 33206; Chiapas, Agua Azul NK 8644 (MSB 55645), NK 8645 (MSB 55643); Quintana Roo, Laguna Noh-Bec FMNH 30973; Tulum MDE 6004; PERU: Cuzco, La Convencion TK 70435; SURINAME: Nickerie, Kabalebo TK 17466 (CMNH 68804); VENEZUELA: Barinas, Barinitas TK 19315 (CMNH 78397).

Carollia sowelli.– COSTA RICA: Limon, Estacion Biologica Cano Palma FMNH 44027; Tortuga Lodge FMNH 44017; GUATEMALA: El Peten, Poptun FMNH 31769; Poptun FMNH 31805, FMNH 31824; HONDURAS: Francisco Morazan, Parque Nacional La Tigra TK 101005 (TTU 83668), TK 101010 (TTU 82496), TK 101013 (TTU 82497); Comayagua, Cueva de Taulabe TK 101341 (TTU 82495), TK 101377 (TTU 82498); MEXICO: Chiapas, Agua Azul NK 8641 (MSB 55644); Quintana Roo, Laguna Noh-Bec FMNH 30976; Tabasco, Jonuta FMNH 30002; PANAMA: Chiriqui, Ojo de Agua FMNH 38140.

Carollia subrufa.– EL SALVADOR: Auachapan, El Refugio TK 15818; MEXICO: Jalisco, Chamela TK 19550 (TTU 37719), TK 19551 (TTU 37720).

Loan of Tissues

Tissue loans were generously provided by C. Cicero and J. Patton from the Museum of Vertebrate Zoology (Berkeley), C. Parmenter, J. Salazar and T. Yates from the Museum of Southwestern Biology (Albuquerque), M. Engstrom and B. Lim from the Royal Ontario Museum (Ontario), and R. Monk from the Natural Science Research Laboratory at Texas Tech University.

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PUBLICATIONS OF THE MUSEUM OF TEXAS TECH UNIVERSITY

It was through the efforts of Horn Professor J Knox Jones, as director of Academic Publications, that Texas Tech University initiated several publications series including the Occasional Papers of the Museum. This and future editions in the series are a memorial to his dedication to excellence in academic publications. Professor Jones enjoyed editing scientific publications and served the scientific community as an editor for the Journal of Mammalogy, Evolution, The Texas Journal of Science, Occasional Papers of the Museum, and Special Publications of the Museum. It is with special fondness that we remember Dr. J Knox Jones.

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Layout and Design: Jacqueline B. Chavez
Cover Design: R. Richard Monk

This book was set in Times New Roman and printed on acid-free paper that meets the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources.

Printed: 31 October, 2002

Library of Congress Cataloging-in-Publication Data

Occasional Papers, Number 217
Series Editor: Robert J. Baker

A NEW CENTRAL AMERICAN SPECIES FROM THE *CAROLLIA BREVICAUDA* COMPLEX

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ISSN 0149-175X

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