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Evaluation of Paraphyletic Assemblages within Lonchophyllinae, with Description of a New Tribe and Genus

Front cover: *Hsunycteris cf. thomasi*, Madre Selva Biological Station, Río Orosa, Loreto, Peru. Photograph courtesy of Heather A. York.

Evaluation of Paraphyletic Assemblages within Lonchophyllinae, with Description of a New Tribe and Genus

Julie A. Parlos, Robert M. Timm, Vicki J. Swier, Horacio Zeballos, and Robert J. Baker

Abstract

In the past decade, seven new species and one new genus have been described in the Lonchophyllinae (Chiroptera: Phyllostomidae), increasing the number of recognized taxa in the subfamily to four genera and 18 species. During this time, three studies, both morphologic and genetic, indicated the genus *Lonchophylla* was paraphyletic with respect to other genera in the subfamily. Using tissues from museum voucher specimens, including the holotypes of specimens of *Xeronycteris vieirai* and *Lonchophylla pattoni*, issues related to the previous paraphyletic assemblages were addressed. A combination of mitochondrial (*Cyt*b), nuclear data (*Fgb*-I7, *TSHB*-I2), chromosome diploid and fundamental numbers, and morphologic characters was used to determine whether all species of *Lonchophylla* share a common ancestor after diverging from other genera in the subfamily. Based on gene sequence data, a basal, monophyletic, statistically supported radiation within the subfamily Lonchophyllinae was observed in all phylogenetic analyses. We conclude that this assemblage merits recognition as a new tribe and genus, and, therefore, present formal descriptions of the genus as *Hsunycteris* and the tribe as Hsunycterini. Several other issues related to paraphyly within both the genus *Hsunycteris* and tribe Lonchophyllini were not resolvable at this time, including that the genus *Lonchophylla* is paraphyletic and *Hsunycteris thomasi* contains four genetic species. A species in the genus *Hsunycteris* remains undescribed because it was not possible to determine which of two lineages the type specimen of *H. thomasi* is actually a member. Until additional genetic and/or morphologic data are available, resolution of all paraphyletic relationships is not possible. Future studies that focus on utilizing morphologic and genetic (both mitochondrial and nuclear) data from the type specimens of species of *Lonchophylla* and species of *Hsunycteris thomasi* are needed to resolve these remaining questions.

Key words: chromosome data, Hsunycterini, *Hsunycteris*, Lonchophyllinae, Lonchophyllini, mitochondrial gene, nuclear genes, paraphyletic assemblages

Introduction

The chiropteran subfamily Lonchophyllinae Griffiths 1982, of the family Phyllostomidae, consists of small, nectarivorous bats distributed from Nicaragua southward into central South America, including Peru, Bolivia, and Brazil. These nectar bats are characterized morphologically by an incomplete zygomatic arch and forwardly projecting upper incisors (Griffiths 1982; Gregorin and Ditchfield 2005). Four genera currently are recognized in the Lonchophyllinae—three are monotypic (*Lionycteris* Thomas 1913; *Platalina* Thomas 1928; and *Xeronycteris* Gregorin and Ditchfield 2005) and the genus *Lonchophylla* Thomas 1903 is comprised of 15 described species (*L. bokermanni* Sazima, Vizotto, and Taddei 1978; *L. cadenai* Woodman and Timm 2006; *L. chocoana* Dávalos 2004; *L. concava* Goldman 1914; *L. dekeyseri* Taddei, Vizotto, and Sazima 1983; *L. fornicata* Woodman 2007; *L. handleyi* Hill 1980; *L. hesperia* G. M. Allen 1908; *L. mordax* Thomas 1903; *L. orcesi* Albuja and Gardner 2005; *L. orienticollina* Dávalos and Corthals 2008; *L. pattoni* Woodman and Timm 2006; *L. peracchii* Dias, Esbérard, and Moratelli 2013; *L. robusta* Miller 1912; and *L. thomasi* J. A. Allen 1904).

The evolutionary position and appropriate taxonomic rank of this group, with respect to other phyllostomids, have been debated since its recognition as a subfamily by Griffiths (1982). However, its genera consistently have been recognized regardless of whether this group has been treated as a tribe of the Glossophaginae (McKenna and Bell 1997; Wetterer et al. 2000; Simmons 2005) or a separate subfamily (Griffiths 1982; Baker et al. 2003a; Datzmann et al. 2010). Much debate and commentary have occurred over whether the Lonchophyllinae and Glossophaginae form collectively a monophyletic lineage or had independent origins and should be recognized as separate subfamilies (Haiduk and Baker 1982, 1984; Hood and Smith 1982; Griffiths 1983; Warner 1983; Smith and Hood 1984; Honeycutt and Sarich 1987; Gimenez et al. 1996; Baker et al. 2000; Wetterer et al. 2000; Baker et al. 2003a). The most recent molecular phylogenetic analyses all support the conclusion that Lonchophyllinae is monophyletic and does not share a common ancestor with the Glossophaginae to the exclusion of other phyllostomid subfamilial-level clades (Solmsen 1998; Baker et al. 2003a; Datzmann et al. 2010; Dumont et al. 2011; Rojas et al. 2011; Baker et al. 2012). We treat the Lonchophyllinae as an independently derived monophyletic lineage of nectar bats to the exclusion of the Glossophaginae.

Although this long debate only recently reached consensus (see citations above), other systematic questions, such as paraphyletic assemblages within *Lonchophylla*, number of genera that should be recognized, and the higher level relationships within the Lonchophyllinae remain to be resolved. Both morphologic and genetic datasets have depicted *Lonchophylla* as a paraphyletic assemblage and the organization of these clades varies with systematic analysis (Dávalos and Jansa 2004; Woodman and Timm 2006; Woodman 2007), with reported paraphyletic arrangements varying among the studies and species of *Lonchophylla* included in the analysis. In these studies, species of *Lonchophylla* are variously paraphyletic with respect to *Lionycteris*, both *Platalina* and *Xeronycteris*, or all three genera (Dávalos and Jansa 2004; Woodman and Timm 2006; Woodman 2007), and few relationships consistently are supported among all genetic and morphologic analyses. Strong support has been demonstrated for the sister relationships between *Platalina* and *Xeronycteris* (Gregorin and Ditchfield 2005) and between *L. robusta* and *L. handleyi* (Dávalos and Jansa 2004). Notably, when the number of recognized species within the evaluated Lonchophyllinae has increased, support for various relationships has decreased (Woodman and Timm 2006; Woodman 2007). In all analyses, specimens treated as members of the "*L. thomasi* complex" (sensu Woodman and Timm 2006) comprise a well-supported, monophyletic clade that is paraphyletic with the remainder of the genus *Lonchophylla* (Dávalos and Jansa 2004; Woodman and Timm 2006; Woodman 2007). Previous studies, however, have not resolved the monophyly, or lack thereof, of *Lonchophylla*. Perhaps this is due in part to a lack of statistical support, lack of discrete morphologic characters, and a need for additional taxon and gene sampling.

In a phylogenetic study of the Lonchophyllini, Dávalos and Jansa (2004) evaluated the mitochondrial cytochrome-*b* (*Cyt*b) gene in combination with morphologic, sex chromosome, and restriction site characters, but statistical support of monophyly was not recovered in their combined analysis. They suggested that saturation at the 3rd codon position was an explanation for the lack of molecular support in the resultant phylogeny (Dávalos and Jansa 2004). Matthee et al. (2001), working with the mitochondrial *Cyt*b gene, generated a phylogeny of Artiodactyla and noted similar results, suggesting that the mitochondrial gene tree does not always generate a species level tree. Their evaluation of nuclear data for the artiodactyls resulted in lower homoplasy indices and well-supported phylogenies, allowing them to draw more robust conclusions from their genetic sequence data set (Matthee et al. 2001). Intron 7 of the nuclear fibrinogen, B beta polypeptide gene (*Fgb*-I7), evolves more slowly than *Cyt*b and therefore can be expected to be more useful for resolving older evolutionary relationships in mammals (Wickliffe et al. 2003; Porter et al. 2007). The second nuclear gene utilized in this study, intron 2 of the thyroid-stimulating hormone gene, beta subunit (*TSHB*-I2), has been useful in resolving phylogenetic relationships from interspecific to interfamilial taxonomic levels (Matthee et al. 2001; Eick et al. 2005; Willows-Munro et al. 2005), even when used alone (Hoofer et al. 2008).

Karyotypic data are available for some species of Lonchophyllinae and may be systematically informative. Karyotypes have been described previously from

Lionycteris, *Lonchophylla robusta*, and *L. thomasi*. It is noteworthy that six karyotypes, of which five are unique, have been described from specimens previously identified morphologically as *L. thomasi*. Karyotypic data generated by recent fieldwork in Latin America permit description of karyotypes for additional species. Comparing the phylogenetic implications of the karyotypic data with those of the sequence and morphologic data—three independent datasets—contributes greatly to understanding the mode and tempo of evolution in this complex of bats.

Given the long-standing controversy over relationships of these nectar bats and the distinct possibility that the currently recognized taxonomy of the Lonchophyllinae does not adequately reflect their diversity, we undertook a generic level reassessment of the subfamily. To assess whether the genus *Lonchophylla* represents a monophyletic lineage, as well as the higher systematic relationships of the genera within the subfamily Lonchophyllinae, we used molecular biology in conjunction with karyotype morphology and morphologically identified specimens. Obtaining tissue for the phylogenetic analysis from all previously described taxa within the Lonchophyllinae was not possible; however, tissues or data were obtained for representatives of all genera and a majority of the described species. Herein, two independent nuclear genes (*Fgb*-I7 and *TSHB*-I2) in combination with the mitochondrial *Cyt*b gene, karyotypic morphology, and cranial characters were used to determine the taxonomic arrangement that would best reflect the evolutionary relationships of these bats. We focused on the genus *Lonchophylla* to determine if it represents a single evolutionary lineage or is a paraphyletic assemblage and how many species, as defined by the Genetic Species Concept (Baker and Bradley 2006), might be present.

MATERIALS AND METHODS

Taxon sampling.—Tissues were sequenced from specimens housed in the following museums: Angelo State Natural History Collections (ASK), Carnegie Museum of Natural History (CM), University of Kansas Natural History Museum (KU), Louisiana State University Museum of Zoology (LSUMZ), Scientific Collection, del Museo de Historia Natural de la Universidad Nacional de San Agustín (MUSA), Museum of Vertebrate Zoology (MVZ), Natural Science Research Laboratory (NSRL) at the Museum of Texas Tech University (TK), Texas Cooperative Wildlife Collection (TCWC), and Museo de Zoología (QCAZ). Data obtained from GenBank included specimens from the Royal Ontario Museum (ROM). Sequence data, available on GenBank, were included to increase geographic and taxon sampling. Sequence data were generated or obtained from GenBank for *Lionycteris*, *Platalina*, *Xeronycteris*, and nine recognized species of *Lonchophylla* (*L. cadenai*, *L. chocoana*, *L. concava*, *L. handleyi*, *L. hesperia*, *L. orienticollina*, *L. pattoni*, *L. robusta*, and *L. thomasi*, plus one taxon that remains to be described; Appendix). No sequence data or tissues were available for *L. bokermanni*, *L. dekeyseri*, *L. fornicata*, *L. mordax*, *L. orcesi*, or *L. peracchii*.

Morphologic evaluations.—Specimens accessioned at the NSRL and KU were morphologically evaluated following recent descriptions (Woodman and Timm 2006; Woodman 2007; Dávalos and Corthals 2008; Appendix). Tissue obtained from specimens morphologically evaluated by Woodman and Timm (2006) and Gregorin and Ditchfield (2005) were included in the genetic analyses. All measurements presented herein are in millimeters, and weights are given in grams. Crania and forearms were measured with digital calipers to the nearest 0.1 mm. Greatest length of skull (GLS), the one cranial measure reported herein, was measured as the length from the anteriormost tip of the upper incisors to the posteriormost projection of the occiput. Length of forearm (FA) was measured from the posterior extension of the radius–ulna to the most anterior extension of the carpals.

Karyotypic methods.—Specimens were karyotyped from bone marrow after 1 h of *in vivo* incubation with the mitotic inhibitor Velban (Sigma-Aldrich, St. Louis, Missouri), following the methods described by Baker et al. (2003b). No yeast stress was employed and animals were karyotyped the morning after capture

from buildings or with mist nets the previous night. Karyotypes were visualized using an Olympus BX51 microscope. Ten spreads per individual were viewed. Images were photographed using an Applied Imaging camera and captured using the Genus System 3.7 from Applied Imaging Systems (San Jose, California).

Molecular methods.—Specimens reported herein were collected on field trips to Ecuador in 2001 and 2004 and Peru in 2010. Whole genomic DNA was extracted from tissue by the phenol method (Longmire et al. 1997). The entire *Cyt*b, *Fgb*-I7, and *TSHB*-I2 genes were amplified via polymerase chain reaction (PCR). *Cyt*b, *Fgb*-I7, and *TSHB*-I2 genes were amplified with the external primers L14724 and H15915 (Irwin et al. 1991) or L14724 and LGL766 (Bickham et al. 2004), B17L-rod2 and B17U-2 (Porter et al. 2007), and THYF and THYR (Eick et al. 2005), respectively. The entire afore-mentioned genes were amplified by PCR using a 50-µL reaction, with approximately 400 ng DNA, 0.30 µM of each primer, 1.25 mM $MgCl_2$, 0.2 mM deoxynucleoside triphosphates, 1X reaction buffer, and 1.25U *Taq* polymerase (Promega Corporation, Madison, Wisconsin). Thermocycling conditions for amplifying *Cyt*b were an initial denaturation at 94°C for 2 min, 35 cycles of denaturation at 94°C for 45 s, annealing of primers at 47°C for 60 s, elongation at 72°C for 75 s, with a final elongation at 72°C for 10 min. Thermocycling conditions for amplifying the nuclear genes *Fgb*-I7 and *TSHB*-I2 were an initial denaturation at 94°C for 2 min, 35 cycles of denaturation at 94°C for 45 s, annealing of primers at 51°C for 60 s, elongation at 72°C for 75 s, with a final elongation at 72°C for 10 min. A nested PCR was performed to eliminate secondary product amplified during the first-round PCR of *Fgb*-I7, following Porter et al. (2007). Products of PCR amplification were purified using ExoSAP-IT® (USB Corporation, Cleveland, Ohio), following manufacturer's specifications. When necessary, gel punches were performed following manufacturer's specifications with the Qiagen Gel Extraction Kit (Qiagen Inc., Valencia, California). Primers used to sequence segments within *Cyt*b varied with species and were MVZ26, MVZ04, and MVZ16 (Smith and Patton 1993); L14648 (Martin et al. 2000); and Glo1L and Glo5L (Hoffmann and Baker 2001). Two internal primers were developed to aid in finalizing the reverse read of *Cyt*b sequences for specimens among the "larger Lonchophyllinae" (see results for taxa; LgLonch650R: 5'-GTRTARTAGGGGTGRAADGGRAT-3') and the "*L. thomasi* complex" (SmLonch600R: 5'-TTGGRT-TRTTTGAWCCTGTTTCATGTA-3'). The first 400bp of the *Cyt*b gene were sequenced for all available specimens. These *Cyt*b sequences were used for calculating genetic distances and the three gene phylogeny because this allowed inclusion of more specimens from more locations in the data sets. The entire *Cyt*b gene preferentially was sequenced for holotypes, specimens with karyotypes, and randomly selected specimens from each species. Sequencing of nuclear genes followed Porter et al. (2007) for *Fgb*-I7 and Hoofer et al. (2008) for *TSHB*-I2. Nuclear genes preferentially were amplified and sequenced for holotypes and specimens with karyotypes. Internal primers developed to aid in areas of *TSHB*-I2 sequence ambiguity were TSHFint (5'-AAATGAGATAAATGACATCC-3') and TSHRint (5'-GAAGAAACAGYTTGCCRTTGATA-3'). Data generated for *Platalina* (MUSA 9383) were done with the help of an author (HZ). Sequences were generated using an ABI Prism 3730 (Applied Biosystems, Grand Island, New York).

Phylogenetic analyses.—Sequence data were submitted to GenBank (Accession numbers KF815280–KF815389) and aligned matrices were submitted to TreeBASE (www.treebase.org; http://purl.org/phylo/treebase/phylows/study/TB2:S14781). Novel sequences were aligned and chromatograms verified by eye using Sequencher 4.9 (Gene Codes Corporation, Ann Arbor, Michigan). Specimens evaluated by Dávalos and Jansa (2004) were included in the *Cyt*b phylogeny. DNA sequences from *Glossophaga* species were included as outgroups for all generated phylogenies. jModelTest (Posada 2008) was used to estimate the best-fit model of nucleotide substitution. Bayesian hypotheses were generated with MrBayes 3.2 (Ronquist et al. 2012). All MrBayes analyses consisted of 10,000,000 generations with a sampling frequency of 5,000. Kimura 2-parameter values were calculated for within and between group mean distances by MEGA 5.05 (Tamura et al. 2011). The first 400bp of the mitochondrial *Cyt*b gene were used to define groups based on clades depicted in the phylogenetic analyses.

This project was undertaken with the approval of the University of Kansas and Texas Tech University's Institutional Animal Care and Use Committees. All animal handling protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

RESULTS

Karyotypic data.—Seven karyotypes from six of the 12 clades were identified among the Lonchophyllinae (Table 1). The karyotype for *L. cadenai* was 2N = 36, FN = 50; the karyotype for *L. concava* was 2N = 28, FN = 50. Images of these karyotypes, previously not available for *L. cadenai* and *L. concava*, are shown in Fig. 1.

Sequence divergence.—All intraspecific sequence divergence values were less than 2.5%, with the exception of those for *Platalina* as well as populations representing what has been known as the "*L. thomasi* complex" (Table 2). Interspecific sequence divergence values were mostly greater than 10% (Table 2). Only one interspecific sequence divergence value was less than 5% (*L. orienticollina–robusta*; Table 2).

Phylogenetic analyses.—The model used in MrBayes 3.2 is based on the model estimated by jModelTest using the Akaike information criteria (AIC). The estimated models of evolution are HKY+I+G for *Cyt*b, TVM+G for both *Fgb*-I7 and *TSHB*-I2, and GTR+G for the concatenated, three gene analysis. The models of evolution evaluated in MrBayes 3.2 were HKY+I+G for the *Cyt*b dataset and GTR+G for the concatenated dataset. Because some estimated models were unavailable in the MrBayes 3.2 package, GTR+G was implemented for both *Fgb*-I7 and *TSHB*-I2 genes.

Two well-supported clades were recovered using specimens of Lonchophyllinae in the *Cyt*b phylogeny (Fig. 2). One clade contains only specimens of the "*L. thomasi* complex" and all other species comprise a second major clade, the "larger Lonchophyllinae" (i.e., *Lionycteris*, *Platalina*, *Xeronycteris*, *Lonchophylla chocoana*, *L. concava*, *L. handleyi*, *L. hesperia*, *L. orienticollina*, and *L. robusta*; see Fig. 2).

In contrast to results obtained in the mitochondrial *Cyt*b data, the nuclear phylogenies recovered multiple well-supported clades (Figs. 3–4). In the nuclear phylogenies, the relationships observed among the "larger Lonchophyllinae" were generally less robust (Figs. 3–4). *Xeronycteris*, as observed in the *Fgb*-I7 phylogeny, was excluded from the monophyletic assemblage containing all other specimens of the "larger Lonchophyllinae" (Fig. 3). The *TSHB*-I2 phylogeny recovers both *Platalina* and *Xeronycteris* as genera independent of the monophyletic assemblage containing all other "larger Lonchophyllinae" (Fig. 4). The concatenated, three gene phylogeny (Fig. 5) was similar to the *Cyt*b phylogeny (Fig. 2) in that the "larger Lonchophyllinae" were supported as a monophyletic group (0.81; Fig. 5). The concatenated, three gene phylogeny, however, was similar to both nuclear phylogenies in that a portion of the genus *Lonchophylla* is paraphyletic with respect to *Lionycteris* (Figs. 2–5).

The genetic distance of species of the "*L. thomasi* complex" to specimens of the other members of *Lonchophylla* is greater than the genetic distances of *Lionycteris–Platalina–Xeronycteris* from each other (>13%; Table 2). This clade was further divided into four well-supported clades of species level rank, one of which coincides with the limits of *L. cadenai* and one of *L. pattoni* (Woodman and Timm 2006), as well as two separate, paraphyletic lineages currently assigned to the species *L. thomasi*. In the interest of taxonomic rank equality for the time of origin of clades and the evolutionary divergence within clades, the "*L. thomasi* complex" merits recognition as a distinct new genus belonging to a distinct new tribe. The new genus and tribe are named and described below.

Family Phyllostomidae Gray 1825
Subfamily Lonchophyllinae Griffiths 1982

Hsunycteris Parlos, Timm, Swier, Zeballos, and Baker 2014, new genus

Lonchophylla: J. A. Allen 1904; part; not *Lonchophylla* Thomas 1903.

Lonchophylla: Dávalos 2004; part; not *Lonchophylla* Thomas 1903.

Lonchophylla: Dávalos and Jansa 2004; part; not *Lonchophylla* Thomas 1903.

Lonchophylla: Lim et al. 2005; part; not *Lonchophylla* Thomas 1903.

Lonchophylla: Woodman and Timm 2006; part; not *Lonchophylla* Thomas 1903.

Table 1. Karyotype data obtained from the literature or described herein. Locality data are provided when available. Abbreviations are: L. = Lonchophylla, H. = Hsunycteris*, 2N = diploid number, FN = fundamental number, Suriname = Republic of Suriname. Gardner (1977) did not include a figure of his karyotype, therefore we were unable to determine whether Peruvian and Republic of Suriname individuals of* H. thomasi *had identical karyotypes.*

Species	Karyotype	Locality of Karyotype Description	Citation
Lionycteris sp.	2N = 28, FN = 50	Colombia	Baker 1979
L. robusta	2N = 28, FN = 50	Nicaragua; Ecuador	Baker 1973, 1979; This study
L. concava	2N = 28, FN = 50	Esmeraldas, Ecuador	This study
H. thomasi	2N = 30, FN = 34	Amazonas, Colombia	Baker 1973, 1979
	2N = 32, FN = 34	Bolívar, Venezuela	Baker et al. 1982, pers. comm.
	2N = 32, FN = 38	Loreto, Peru	Gardner 1977
	2N = 32, FN = 38	Brokopondo, Suriname	Honeycutt et al. 1980
	2N = 32, FN = 40	Suriname	Haiduk and Baker 1982
	2N = 36, FN = 48	East Amazon, Brazil	Ribeiro et al. 2003
H. cadenai	2N = 36, FN = 50	Esmeraldas, Ecuador	This study
Glossophaga, multiple species	2N = 32, FN = 60	Multiple	See Baker 1979 and references therein

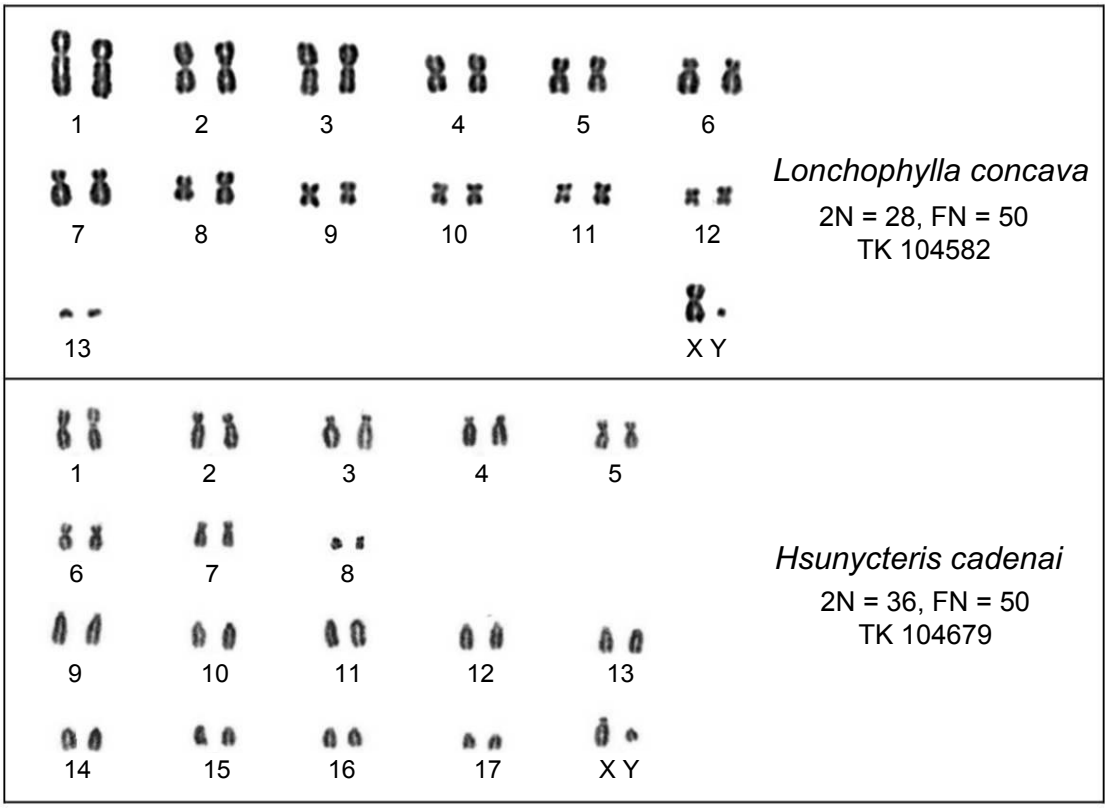

Figure 1. Karyotypes of *Lonchophylla concava* (above) and *Hsunycteris cadenai* (below), reported here for the first time. Specimens were identified morphologically and are included in the cytochrome-*b* gene tree (see Fig. 2). Both specimens are from Esmeraldas Province, Ecuador. Abbreviations are: 2N = diploid number, FN = fundamental number. If you compare the smallest pair (pair 13) of biarms in the *L. concava* karyotype to the smallest pair (pair 8) in the *H. cadenai* karyotype, the karyotype of *H. cadenai* is 2N = 36, FN = 48. However, we consider pair 8 as biarmed autosomes, recovering the karyotype of *H. cadenai* as 2N = 36, FN = 50.

Table 2. Kimura 2-parameter values calculated for within (bolded) and between (below the diagonal) taxa mean distance, calculated using MEGA 5.2.1 and the first 400bp of the mitochondrial Cyt*b gene. Abbreviations are LCh* = Lonchophylla chocoana, *LCo* = L. concava, *LHa* = L. handleyi, *LHe* = L. hesperia, *LO* = L. orienticollina, *LR* = Lonchophylla robusta, *HC* = Hsunycteris cadenai, *HP* = H. pattoni, *HT30* = H. thomasi *in the clade with the 2N = 30; HT32* = H. thomasi *in the clade with the 2N = 32; LS* = Lionycteris spurelli, *PG* = Platalina genovensium, *XV* = Xeronycteris vieirai, *G. spp.* = Glossophaga *species (*G. soricina *and* G. longirostris *used as the outgroup), and NC = not calculated because analyses contained one specimen. Species clades in table were extracted from the* Cyt*b phylogeny (Fig. 2).*

Group		LR	LO	LHa	LCo	LHe	LCh	HC	HP	HT32	HT30	LS	PG	XV	G. spp.
Lonchophylla species (sensu stricto)	LR	**0.011**													
	LO	0.028	**0.008**												
	LHa	0.100	0.101	**0.023**											
	LCo	0.150	0.135	0.151	**0.004**										
	LHe	0.178	0.159	0.179	0.056	**NC**									
	LCh	0.140	0.140	0.172	0.193	0.187	**NC**								
Hsunycteris species	HC	0.200	0.195	0.183	0.208	0.188	0.213	**0.010**							
	HP	0.183	0.224	0.208	0.203	0.215	0.175	0.133	**0.015**						
	HT32	0.211	0.216	0.200	0.191	0.209	0.187	0.137	0.075	**0.011**					
	HT30	0.205	0.203	0.190	0.185	0.204	0.188	0.117	0.074	0.084	**0.018**				
Lionycteris	LS	0.180	0.175	0.170	0.172	0.169	0.189	0.174	0.165	0.170	0.142	**0.023**			
Platalina	PG	0.140	0.139	0.148	0.170	0.173	0.161	0.180	0.156	0.172	0.156	0.137	**0.074**		
Xeronycteris	XV	0.194	0.191	0.198	0.193	0.213	0.195	0.226	0.189	0.203	0.181	0.182	0.162	**NC**	
Glossophaga outgroup	G. spp.	0.195	0.193	0.182	0.184	0.190	0.185	0.177	0.164	0.174	0.163	0.178	0.175	0.226	**0.043**

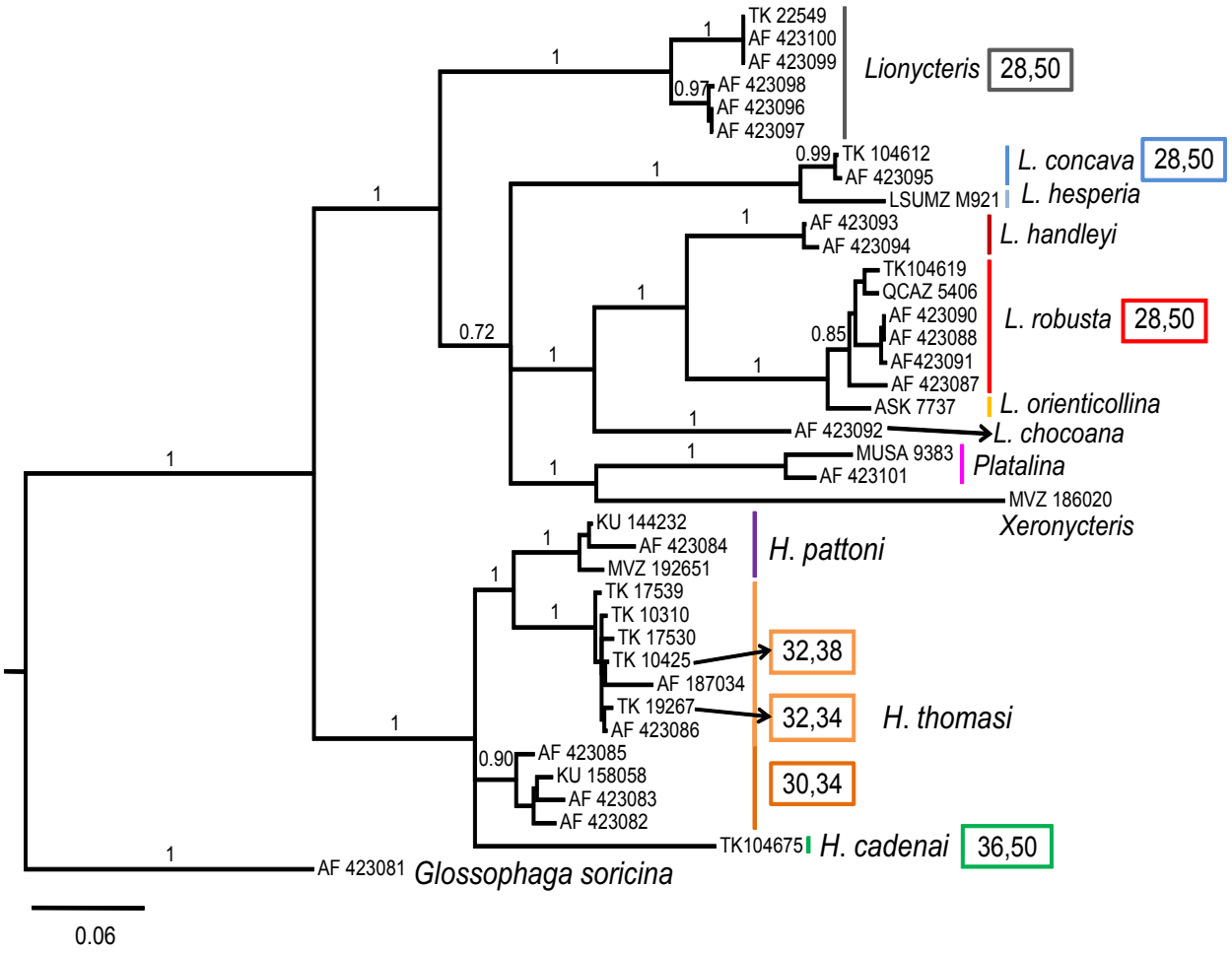

Figure 2. Bayesian phylogeny of the mitochondrial *Cyt*b gene (1140bp). Posterior probabilities are positioned above branches. Model of evolution evaluated was GTR+I+G. Monotypic genera are labeled by genus. Abbreviations are L. = *Lonchophylla* and H. = *Hsunycteris*. Genera of Lonchophyllinae with karyotypic data are depicted (see Table 1 for additional information). Specimen identifications follow assigned GenBank or museum number. TK 10425 is from Brokopondo, Republic of Suriname (Honeycutt et al. 1980), TK 19267 is from Bolívar, Venezuela, and the specimen with the karyotype 2N = 30, FN = 34 is aligned with the clade containing TK 104153 in a 400bp *Cyt*b phylogeny (not shown).

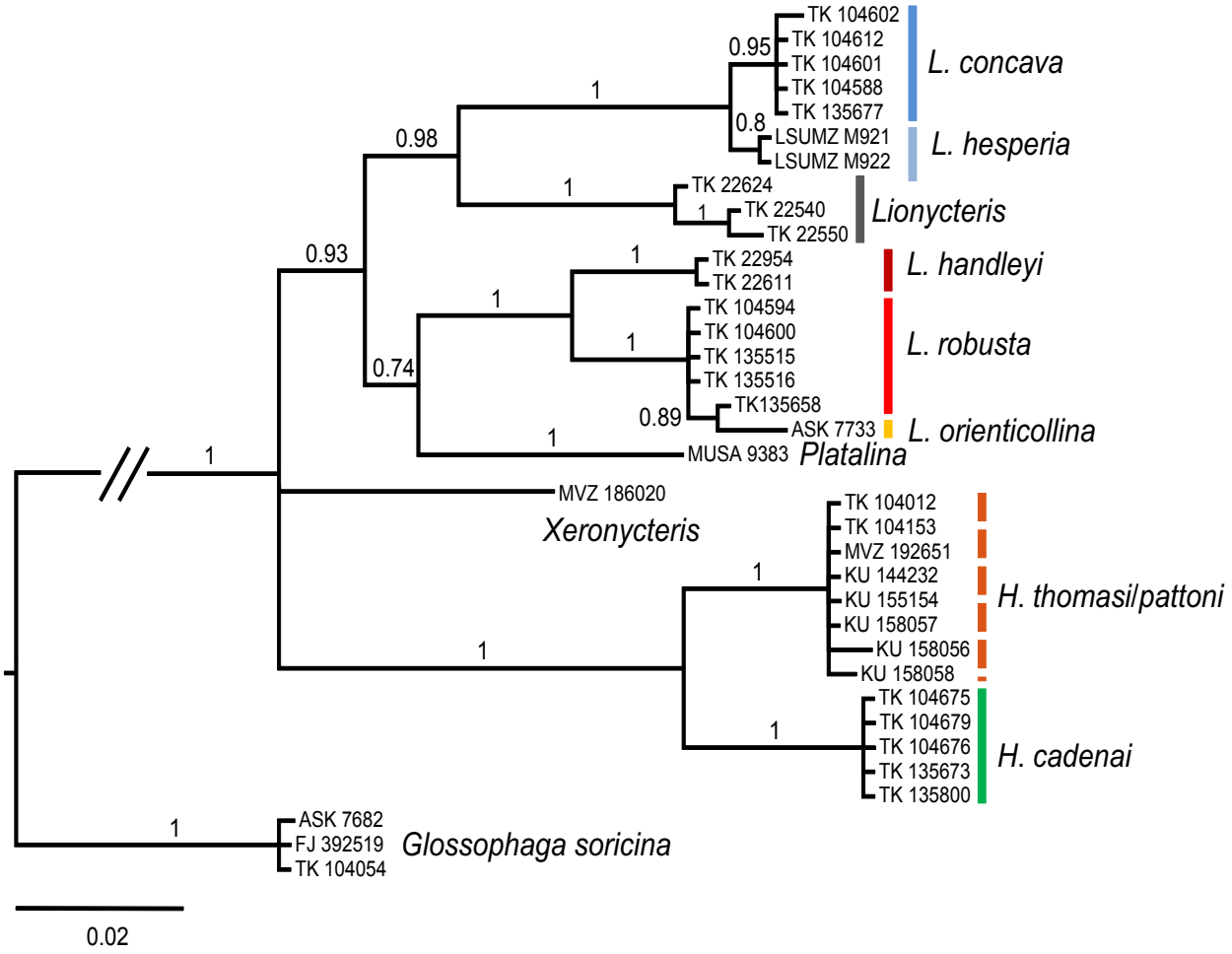

Figure 3. Bayesian phylogeny of the nuclear gene, *Fgb*-I7 (598bp including gaps). Posterior probabilities are positioned above or to the left (i.e., 0.89) of the branches. Model of evolution evaluated was GTR+G. Monotypic genera are labeled by genus. Outgroup is *Glossophaga soricina*. Abbreviations are: *L.* = *Lonchophylla* and *H.* = *Hsunycteris*. Broken bars represent clades including more than one recognized species.

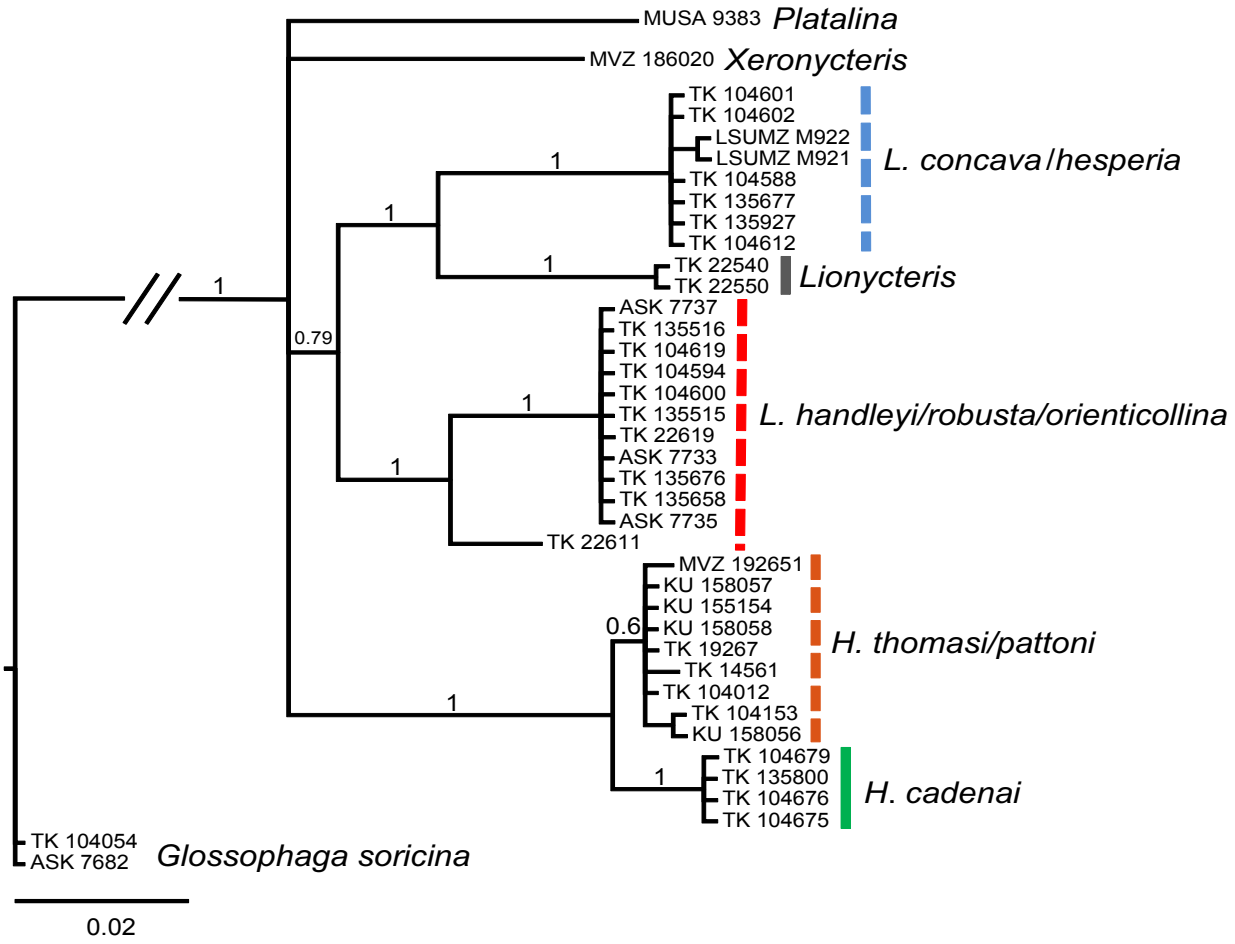

Figure 4. Bayesian phylogeny of the nuclear gene, *TSHB*-I2 (458bp including gaps). Posterior probabilities are positioned above branches. Model of evolution evaluated was GTR+G. Monotypic genera are labeled by genus. Outgroup is *Glossophaga soricina*. Abbreviations are: *L.* = *Lonchophylla* and *H.* = *Hsunycteris*. Broken bars represent clades including more than one recognized species.

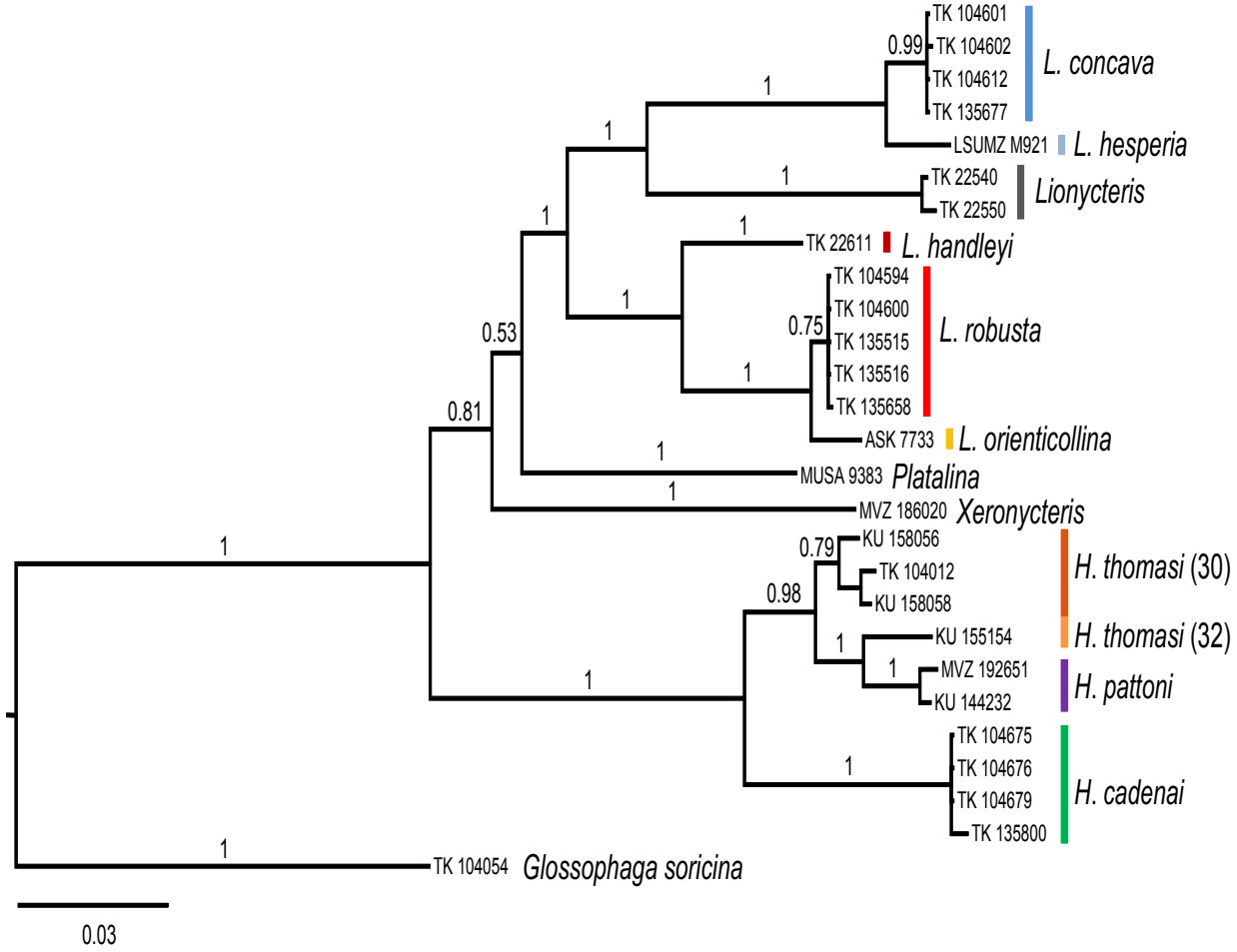

Figure 5. Bayesian phylogeny of the three combined genes, *Cyt*b (400bp), *Fgb*-I7 (598bp including gaps), and *TSHB*-I2 (458bp including gaps). Posterior probabilities are positioned above branches. Model of evolution evaluated was GTR+G. Monotypic genera are labeled by genus. Abbreviations are: *L.* = *Lonchophylla*; *H.* = *Hsunycteris*; (30) = found in clade with karyotype 2N = 30, FN = 34; and (32) = found in clade with karyotype 2N = 32 (see Fig. 1). Outgroup is *Glossophaga soricina*.

Lonchophylla: Griffiths and Gardner 2007; part; not *Lonchophylla* Thomas 1903.

Lonchophylla: Woodman 2007; part; not *Lonchophylla* Thomas 1903.

The above represents a partial synonymy, including relevant usages and based upon specimens that have been confirmed by genetic identifications.

Type species.—*Lonchophylla cadenai* Woodman and Timm 2006.

Type series.—Specimens of *Hsunycteris cadenai*, some of which include karyotypic data— ECUADOR: Esmeraldas; San Jose Farm, E San Lorenzo towards Lita (QCAZ 9095, TK 104671; QCAZ 9096, TK 104675; TTU 85448, TK 104676; TTU 85451, TK 104679; TTU 85459, TK 104687; QCAZ 9564, TK 104689; QCAZ 9565, TK 104690); Comuna San Francisco de Bogotá (QCAZ 9567, TK 135502; TTU 102942, TK 135659; QCAZ 9094, TK 135673); Terrenos Aledanos de la Comuna San Francisco de Bogotá (TTU 103183, TK 135704; TTU 103195, TK 135795; QCAZ 9097, TK 135800; QCAZ 9098, TK 135803).

Included species.—Three described species—*Hsunycteris cadenai*, *H. pattoni*, and *H. thomasi*—and one undescribed species.

Known geographic distribution of the genus.—Southeasternmost Central America to northern and central South America, including Panama, Colombia, Ecuador, Peru, Bolivia, Venezuela, Guyana, Republic of Suriname, French Guiana, and Brazil (see Fig. 6).

Etymology.—Named to honor T. C. Hsu, in recognition of his groundbreaking work on karyotypes of mammals. Dr. Tao-Chiuh Hsu, the Chinese–American cell biologist, was the first to accurately characterize the human karyotype; he pioneered the use of karyotypes in research and is regarded as the father of mammalian cytogenetics. Dr. Hsu discovered and perfected the hypotonic treatment that resulted in *in vivo* bone-marrow preparations producing nonoverlapping chromosomes that more easily distinguished diploid number (2N) and morphology of individual chromosomes. Nearly all published karyotypes, including those presented in this paper, use this hypotonic treatment. The second portion of the name, "nykteris," is derived from the compound Greek word meaning 'bat'. This taxonomic assemblage of bats is appropriate for honoring Dr. Hsu as all species described thus far in *Hsunycteris* have unique karyotypes.

Diagnosis.—Small Lonchophyllinae, GLS 19.5–22.5 mm, length of maxillary toothrows 6.2–7.0; FA 31.0–34.0. Skulls delicate, with incomplete zygomatic arches, rostra shorter than braincases. Tooth morphology primitive: cusps unreduced, contrasting with the reduction seen in most other nectarivorous genera; upper 1st and 2nd premolars elongated, central cuspid of lower premolars not deflected labially, cingula of lower premolars reduced or absent; bases of dorsal pelages paler than tips, uropatagia not conspicuously furred.

Description.—Small Lonchophyllinae with GLS <23.0 mm, FA <34.5 mm, and dorsal pelages ranging from reddish brown to dark brown (Woodman and Timm 2006). Dental formula 2/2, 1/1, 2/3, 3/3 × 2 = 34. *Hsunycteris* is differentiated from the genus *Lonchophylla* by its smaller size, "mesopterygoid fossa short, its anterior margin acutely V-shaped and lacking medial projection of palate; pterygoid process inflated; basisphenoid pits deep; posterior margin of infraorbital foramen anterior to posterior root of P4; large, obvious gap between I1 and I2; coronoid process low" (Woodman and Timm 2006:470).

Comparisons.—Species of *Hsunycteris* are among the smallest members of the Lonchophyllinae, only *Lionycteris* is smaller in some measurements. Greatest length of skull in *Hsunycteris* ranges from 19.5–22.5 mm; in *Lionycteris* 19.0–20.7 mm; in *Lonchophylla* 22.0–30.4 mm; in *Platalina* 27.5–33.7 mm; in *Xeronycteris* 25.5–27.0 mm. Forearms in *Hsunycteris* average the shortest in the subfamily, 29.8–34.4 mm; in *Lionycteris* 33.4–37.5 mm; in *Lonchophylla* 32.3–48.0; in *Platalina* 47.5–52.0; and *Xeronycteris* 35.4–38.1. *Hsunycteris* differs from *Lonchophylla*, *Platalina*, and *Xeronycteris* in that the short, broad rostra are shorter than the braincases, whereas they are as long as or clearly longer than the braincases in *Lonchophylla*, *Platalina*, and *Xeronycteris*. *Hsunycteris* differs from the similarly-sized *Lionycteris* in that in *Hsunycteris* the premolars, especially P3, are flattened laterally and elongated anteroposteriorly, whereas they are not elongated in *Lionycteris*. Exter-

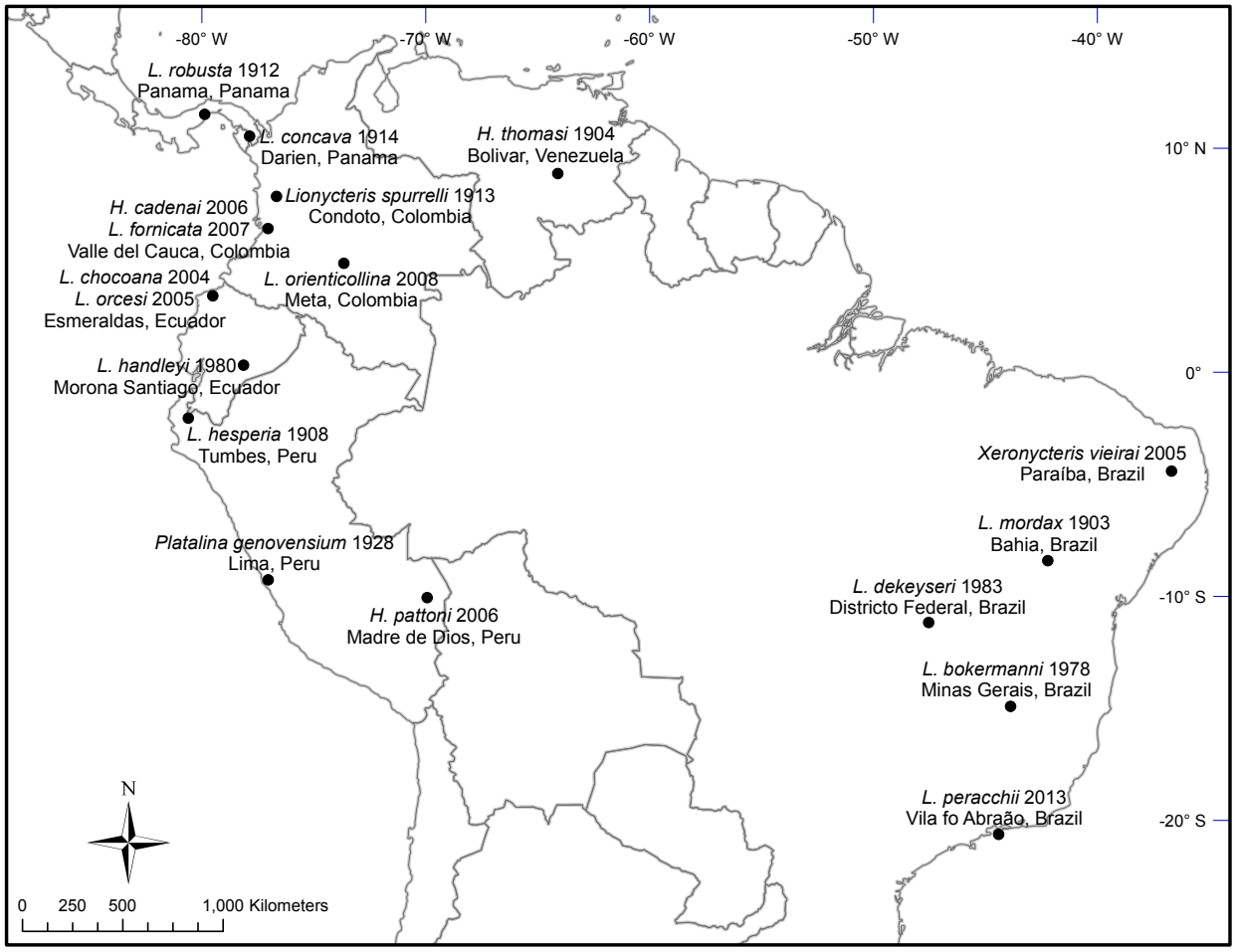

Figure 6. Type localities of Lonchophyllinae. Abbreviations are: *L.* = *Lonchophylla*; *H.* = *Hsunycteris*. Dots represent approximate localities for type specimens.

nally, *Lionycteris* has conspicuous fur on medial 1/2 to 2/3s of uropatagia; whereas *Hsunycteris* has naked uropatagia. *Hsunycteris* is differentiated from the genus *Lonchophylla* by smaller size, short mesopterygoid fossae, palates with rear margin acutely V-shaped and lacking medial projection, inflated pterygoid processes, deep basisphenoid pits, posterior margin of infraorbital foramina anterior to posterior root of P4; an obvious gap between I1s and I2s, and low coronoid processes (Woodman and Timm 2006:470). Additional details of characters, photographs, and/or illustrations of the skins and skulls of these genera are provided by Dávalos and Jansa (2004), Woodman and Timm (2006), Gardner (2007), Griffiths and Gardner (2007), Woodman (2007), and references cited therein.

Species of *Hsunycteris* have a diploid number of 32 to 38, whereas other members of the Lonchophyllinae that have been karyotyped thus far (*Lionycteris* and *Lonchophylla*) have a diploid number of 28. All karyotypes of *Hsunycteris* species have multiple acrocentric autosomes. No other species of Lonchophyllinae have multiple acrocentric autosomes, only a single pair of small dot chromosomes.

Based on the concatenated gene sequence from *Cyt*b and two independent nuclear genes (*Fgb*-I7 and *TSHB*-I2), the genus *Hsunycteris* is recovered as a distinct, statistically well-supported monophyletic clade separate from other members of the Lonchophyllinae (*Lionycteris*, *Platalina*, *Xeronycteris*, *Lonchophylla*

concava, *L. handleyi*, *L. hesperia*, *L. orienticollina*, and *L. robusta*). The matrices and gene sequences deposited on TreeBASE contribute to a genetic diagnosis for *Hsunycteris*. Nonetheless, as outlined in the discussion, *Lonchophylla* still remains a paraphyletic assemblage that cannot be corrected until some additional issues are resolved.

Family Phyllostomidae Gray 1825
Subfamily Lonchophyllinae Griffiths 1982
Tribe Hsunycterini Parlos, Timm, Swier, Zeballos, and Baker 2014, new tribe

Type genus.— *Hsunycteris* Parlos, Timm, Swier, Zeballos, and Baker 2014.

Included genus.—Only a single genus, *Hsunycteris*, is herein included. It contains three described species—*H. cadenai*, *H. pattoni*, and *H. thomasi*—and one undescribed species.

Known geographic distribution of the tribe.— Southeasternmost Central America to northern and central South America, including Panama, Colombia, Ecuador, Peru, Bolivia, Venezuela, Guyana, Republic of Suriname, French Guiana, and Brazil (see Fig. 6).

Diagnosis.— As in the diagnosis of the genus, the Hsunycterini are small Lonchophyllinae, with GLS 19.5–22.5 mm, length of maxillary toothrows 6.2–7.0, FA 31.0–34.0. Skulls delicate, with incomplete zygomatic arches, rostra shorter than braincases; no depression on midline of posterior portion of palates; posterior border of outer margin of anteorbital foramina projecting beyond lateral outline of rostra; basisphenoid pits deep and separated by narrow septum. Tooth morphology primitive, cusps of most teeth unreduced, contrasting with the reduction seen in most other nectarivorous genera; upper 1st and 2nd premolars elongated; lingual cusp on P4s reduced or absent; central cuspid of lower premolars not deflected labially, cingula of lower premolars reduced or absent. Wide, inflated supraorbital regions. Bases of dorsal pelages paler than tips, uropatagia not conspicuously furred.

Species of Hsunycterini have a diploid number of 32 to 38, whereas members of the Lonchophyllini that have been karyotyped thus far (*Lionycteris*, *Lonchophylla*, and *Platalina*) have a diploid number of 28. All karyotypes of Hsunycterini species have multiple acrocentric autosomes, whereas no other species of Lonchophyllinae have multiple acrocentric autosomes, with only a single pair of small dot chromosomes.

Description.—Small Lonchophyllinae with GLS <23.0 mm, FA <34.5 mm, and dorsal pelages ranging from reddish brown to dark brown. Dental formula 2/2, 1/1, 2/3, 3/3 × 2 = 34. Hsunycterini are differentiated from genera of Lonchophyllini by their smaller size, mesopterygoid fossae short, with anterior margin acutely V-shaped and lacking medial projection of palate; pterygoid processes inflated; basisphenoid pits deep, with septum between basisphenoid pits narrow; posterior margin of infraorbital foramina anterior to posterior root of P4s; large, obvious gap between I1s and I2s. Coronoid processes low. Posterior cusp (hypoconid) present on p2s; gap between i2s and canines large, at least as long as length of i2s.

Additional comparisons with members of the Lonchophyllini are provided above in the Comparisons for the generic description of *Hsunycteris*.

DISCUSSION

The Lonchophyllinae differ from the Glossophaginae in that the inner upper incisors in the Lonchophyllinae are prominent, with broad tips, and are conspicuously larger than the outer incisors; the tongues lack bottle-brush tips and there are deep longitudinal grooves along each of its sides. In the Glossophaginae, the inner and outer incisors are similar in size, the tongues have bottle-brush tip of long papillae with filamentous tips, and no deep groove along their sides (Gardner 2007). Griffiths (1982) originally described the Lonchophyllinae as differing from the Glossophaginae in the musculature of the hyoid/lingual region and is to be commended for his detailed anatomical studies of these two subfamilies that first underscored their differences, his understanding their importance, and continuing to stand by his conclusions despite criticism.

Prior to the advent of molecular techniques in systematics, it is quite understandable why the two tribes, Lonchophyllini and Hsunycterini, were considered a single lineage. Both clades are highly specialized morphologically for nectar feeding and with few discrete morphologic characters to define the two tribes. However, the modes and tempos of evolution in *Lonchophylla* and *Hsunycteris* are quite different. These nectar specialists are morphologically best defined by both extreme parallel convergent specializations and reductions of characters, including minute lingual cusps with the size and complexity of the teeth.

Employing the most appropriate systematic arrangement, the goals were to eliminate paraphyly and to document the relationships and phylogenetic distances in regard to this unique clade of nectar-feeding bats. Prior to our studies, the Lonchophyllinae was comprised of four genera—*Lionycteris* (one species), *Platalina* (one species), *Xeronycteris* (one species), and *Lonchophylla* (15 species; Figs. 2–5). Using *Glossophaga* as an outgroup, we found two basal monophyletic clades within the subfamily Lonchophyllinae. A consequence of this phylogeny was that these two major distinct clades should be recognized, and no generic name was available for the "small-sized" members of Lonchophyllinae. The concatenated DNA sequence data from the mitochondrial *Cyt*b gene and two nuclear genes recover the "*H. thomasi* complex" (*H. cadenai*, *H. pattoni*, and *H. thomasi*; sensu Woodman and Timm 2006) as a monophyletic lineage separate from a monophyletic clade consisting of the remainder the genus *Lonchophylla* (*L. bokermanni*, *L. chocoana*, *L. concava*, *L. dekeyseri*, *L. fornicata*, *L. handleyi*, *L. hesperia*, *L. mordax*, *L. orienticollina*, *L. orcesi*, *L. peracchii*, and *L. robusta*) and three monotypic genera (*Lionycteris*, *Platalina*, and *Xeronycteris*; Fig. 5). Based on these phylogenies, the subfamily Lonchophyllinae is now regarded as comprising two monophyletic clades. The first includes the now redefined Lonchophyllini (as noted above), and the second clade, constituted by members of the new genus *Hsunycteris*, the sole genus in the tribe Hsunycterini. Two tribes are recognized because the modes and tempos of evolution are distinctively different in the two monophyletic clades and there are both morphologic and genetic characters defining the two lineages. At least three niche shifts sufficient to merit description of different genera with different ecological adaptations have occurred and are observable among the variable morphologic adaptations of genera in the tribe Lonchophyllini. However, few such morphologic differences have been noted among clades within the Hsunycterini, but these clades have multiple chromosomal differences, a phenomenon that is absent in the Lonchophyllini thus far karyotyped. Therefore, these differences are interpreted as support for recognizing these two evolutionary clades as tribes, following the logic of McKenna and Bell (1997).

McKenna and Bell (1997) were the first to formally recognize the tribe Lonchophyllini, acknowledging Koopman, treating it as one of four tribes along with Brachyphyllini, Phyllonycterini, and Glossophagini in the subfamily Glossophaginae. Wetterer et al. (2000) defined the tribe Lonchophyllini as including the genera *Lonchophylla*, *Lionycteris*, and *Platalina*, which was followed by Simmons (2005). In their description of *Xeronycteris* (Gregorin and Ditchfield 2005), this new genus of nectar bat from Brazil was placed in the tribe Lonchophyllini within the subfamily Glossophaginae. We now define the tribe Lonchophyllini Griffiths 1982, as including *Lonchophylla* (as delimited above), *Lionycteris*, *Platalina*, and *Xeronycteris*. The Lonchophyllini does not include members of the other basal monophyletic clade herein described as the tribe Hsunycterini.

The Lonchophyllini contains substantial morphologic evolution, sufficient to justify recognition of four genera, with the possibility of a fifth genus. Based on gross chromosome morphology, diploid (2N = 28) and fundamental numbers (FN = 50), all species and genera of the Lonchophyllini karyotyped to date appear to have similar karyotypes (Table 1), although some minor centromeric position variation is present in three or four of the medium-sized biarmed chromosomes. In all described karyotypes, members share 14 chromosomal linkage groups, which are comprised of 12 biarmed elements and a small pair of acrocentrics or near acrocentrics. The *Cyt*b genetic distances of the genera and species within the Lonchophyllinae range from 2.8–22.6%.

The evolutionary diversification within the two clades (Hsunycterini and the Lonchophyllini), however, is strikingly different even though the time of origin of the two monophyletic groups is essentially equal. In comparison to the tribe Lonchophyllini, the "*H. thomasi*

complex" does not contain sufficient morphologic characters to merit recognition of multiple genera. In fact, until recently, this clade was considered to be comprised of a single species (Woodman and Timm 2006). Two unique characteristics indicate that more genetic variation exists within the "*H. thomasi* complex" than would be expected from the level of morphologic distinctions present. First, the number of karyotypes documented for specimens previously identified as *H. thomasi* is greater than the number of the currently recognized species of the "*H. thomasi* complex" (Table 1). Second, the intraclade pairwise comparisons between the *Cyt*b gene of specimens within the "*H. thomasi* complex" ranges from 7.4–13.7%, greater than the interspecific pairwise comparison of the morphologically described species of *L. robusta–L. orienticollina* (2.8%; Table 2). These two unique, genetic characters (chromosome and sequence divergence data), justify the conclusions that the "*H. thomasi* complex" is a unique, basal radiation separate from its previous congeners (species in *Lonchophylla*).

Our data document that one undescribed genus exists among specimens within the tribe Lonchophyllini; however, the taxonomic boundaries of an unrecognized genus cannot be determined without a genetic resolution of the type species of *Lonchophylla*, *L. mordax*. These assemblages include two separate clades comprising specimens of *Lionycteris–L. concava–L. hesperia* and *L. robusta–L. orienticollina–L. handleyi* (Figs. 2–5). The available genetic data categorized as *L. mordax concava* (GenBank accession number AF423095; Dávalos and Jansa 2004) are those for *L. concava*, based on geography and recent elevation to full species status of *L. mordax* (Albuja and Gardner 2005). We were unable to obtain tissue of *L. mordax*, but we are convinced that it should not be included as a member of the clade containing *Hsunycteris*, based on morphologic analyses (Woodman and Timm 2006; Woodman 2007).

Woodman and Timm (2006) described *H. cadenai* and *H. pattoni* based on morphologic features. These two species, statistically supported in our mitochondrial and concatenated phylogenies (Figs. 2, 5), validate the conclusions of Woodman and Timm (2006) in recognizing *H. cadenai* and *H. pattoni* as genetically and morphologically defined species (da Silva and Patton 1998). However, the phylogenetic tree resulting from the concatenated data and the mitochondrial data alone distributes specimens of *H. thomasi* on more than one clade. Additional study, utilizing genetic data on the holotype of *H. thomasi*, is necessary to resolve the paraphyly of *H. thomasi* as both clades contain specimens from near the type locality of *H. thomasi* (Bolívar, Venezuela; Fig. 2). As specimens from both clades are found in Bolívar, Venezuela, these two clades of *H. thomasi* are likely sympatric.

The Peruvian endemic long-snouted bat, *Platalina genovensium*, occurs across an extensive geographic and altitudinal range in arid western Peru. This monotypic genus is known from throughout the length of the country and an altitudinal range of 700–2,600 m. Both specimens included herein are from southwestern Peru's Departamento de Arequipa (Caravelí, AMNH 257108; Atiquipa, MUSA 9383), suggesting that simple geographic distance is not expected to explain the genetic variation we observed between the two specimens. The genetic divergence between these two specimens (7.4%, Table 2) is greater than any value observed within a species currently recognized in the Lonchophyllinae. When the entire *Cyt*b gene is evaluated, the intraspecific genetic divergence decreases to 3.8% (data not shown). The genetic distance between these two specimens of *Platalina* is greater than the one mutation in 500 bases calculated following Williams et al. (1999). Several explanations are possible for the observed genetic variation between these two specimens of *Platalina*, but these remain to be tested. First, one of these specimens represents a distinct, undescribed taxon genetically distinct from *P. genovensium*. The second possible explanation is that artificial mutations may have been sequenced from the formalin-preserved specimen at the American Museum of Natural History (Dávalos and Jansa 2004). The third possible explanation is that there is a large polymorphism, not typical of phyllostomid bats, present in *Platalina*. The fourth possible explanation regards observed changes in population size, and, subsequently, the potential of genetic drift having an effect on the genetic diversity of *Platalina*. Sahley and Baraybar (1996) documented considerable population size fluctuation in *Platalina*, which they attributed to an El Niño Southern Oscillation event. This caused a severe drought that affected flowering in the cactus that is the primary food source of these bats. The two specimens of *Platalina* reported herein were collected during or prior to 1987 (Caravelí)

and in 2010 (Atiquipa), dates surrounding the drought discussed in Sahley and Baraybar (1996). Finally, the specimen from Atiquipa is from approximately 325 m in elevation, whereas the specimen from Caravelí is from approximately 1,780 m in elevation, so perhaps altitudinal divergence explains this genetic variation. Considering the morphologic uniqueness of *Platalina*, and the lack of phyllostomids similar in appearance in the region, there seems to be a low probability that one of these specimens is misidentified and not a *Platalina*. Future studies using genetic data and morphologic characters from specimens throughout the range will no doubt shed considerable insights into the geographic variation and relationships between populations in this enigmatic and poorly known bat.

Our analyses focused on specimens of the "*H. thomasi* complex," *Platalina*, and the existence of another genus based on the paraphyletic assemblage containing *Lionycteris*, *Lonchophylla concava*, and *L. hesperia*. Future investigations into Lonchophyllinae should aim to incorporate more species to define the geographically distributed karyotypes of species in *Hsunycteris* (Table 1). Much remains to be learned about the relationships of these nectar-feeding bats that can best be addressed with a variety of genetic techniques.

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APPENDIX

Specimens examined.

Glossophaga soricina (8).—ECUADOR: Napo; Jatún Sacha Biological Station (QCAZ 8515, ASK 7682); Pastaza District; Puyo, Finca el Pigual (TTU 84826, TK 104054). FRENCH GUYANA: Paracou (AMNH 267950, GenBank AF423081). TRINIDAD AND TOBAGO: Trinidad; Nariva, Ecclesville (TK 25212, GenBank FJ392519). VENEZUELA: Bolívar; 0.5 km E El Manteco (CM 78384, TK 19072; CM 78387, TK 19094; CM 78378, TK 19240). PERU: Huánuco; 6 km N Tingo María (TCWC 55948, TK 22596).

Hsunycteris cadenai (14).—ECUADOR: Esmeraldas; San Jose Farm, E San Lorenzo towards Lita (QCAZ 9095, TK 104671; QCAZ 9096, TK 104675; TTU 85448, TK 104676; TTU 85451, TK 104679; TTU 85459, TK 104687; QCAZ 9564, TK 104689; QCAZ 9565, TK 104690); Comuna San Francisco de Bogotá (QCAZ 9567, TK 135502; TTU 102942, TK 135659; QCAZ 9094, TK 135673); Terrenos Aledanos de la Comuna San Francisco de Bogotá (TTU 103183, TK 135704; TTU 103195, TK 135795; QCAZ 9097, TK 135800; QCAZ 9098, TK 135803).

Hsunycteris pattoni (4).—BOLIVIA: La Paz; 1 mi W Puerto Linares (TTU 34812, TK 14561); Beni (AMNH 209358, GenBank AF423084). PERU: Madre de Dios; 14 km E of Puerto Maldonado, Reserva Cuzco Amazónico, 200 m (KU 144232—holotype); Río Alto Madre de Dios, Hacienda Erika, opposite Salvación, 350 m (MVZ 192651).

Hsunycteris thomasi (38).—ECUADOR: Napo (ROM 104064 and ROM 105527, GenBank AF423082–83); Pastaza; 5 km E Puyo, Safari Hosteria Park (TTU 84784, TK 104012); Amazonas Military Fort (TTU 84925, TK 104153). FRENCH GUIANA: Paracou (AMNH 267943, GenBank AF423086). GUYANA: Potaro–Siparuni; Iwokrama Reserve, Kurupukari Base Camp, 70 m (KU 155157); Iwokrama Reserve, 5 km SW of Kurupukari, Giaconda Camp, 75 m (KU 155152–55); Iwokrama Reserve, Burro Burro River, 25 km WNW of Kurupukari, el 90 m (KU 155156). PERU: Loreto; San Jacinto, el 175 m (KU 158056–61); Teniente López, el 175 m (KU 158062–63); Madre de Dios; 14 km E of Puerto Maldonado, Reserva Cuzco Amazónico, 200 m (KU 144233). SURINAME: Brokopondo; Brownsberg Nature Park, 8 km S, 2 km W of Brownsweg (CM 63713, TK 10425); Marowijne; 3 km SW of Albina (CM 76778, TK 17530; CM 76779, TK 17539; CM 77202, TK 17580); Saramaca; Bitagron, 5°06′N, 56°04′W (TK 10299); Sipaliwini; 24 km S, 60 km E of Apoera (CM 63717, TK 10320; CM 63718, TK 10322; CM 63719, TK 10321; CM 63720, TK 10323); Bitagron (Kayserberg Airstrip) (CM 68722, TK 17067; CM 63723, TK 10310); Oelemarie (CM 77207, TK 17991); Raleigh Falls, 4°44′N, 56°12′W (CM 68776, TK 17098); Sipaliwini Airstrip (CM 77210, TK 17837); Voltzberg (CM 68778, TK 17148; CM 68779, TK 17177, GenBank AF187034). VENEZUELA: Bolívar (ROM 107906, GenBank AF423085) Río Grande, 28 km E El Palmar (CM 78396, TK 19267).

Lionycteris spurrelli (16).—GUYANA: Potaro–Siparuni; Iwokrama Reserve, Burro Burro River, 25 km WNW of Kurupukari, el 90 m (KU 155140–44). PANAMA: Darién; Cana (TTU 39121, TK 22524; TTU 39123, GenBank AF423099, TK22531; TTU 39123, TK 22540; TTU 39137, GenBank AF423100, TK22548; TTU 39128, TK 22549; TTU 39129, TK 22550). PERU: Huánuco; Leoncio Prado, 1 km S Tingo María (CM 98650, TK 22624); Madre de Dios (MVZ 166628 or MVZ 166630 or MVZ 166632, GenBank AF423096–98); Río Alto Madre de Dios, Hacienda Erika, opposite Salvación, 350 m (MVZ 192645).

Lonchophylla chocoana (1).—ECUADOR: Esmeraldas; 2 km S Alto Tambo (ROM 105786, GenBank AF423092—holotype).

APPENDIX (CONT.)

Lonchophylla concava (13).—ECUADOR: Esmeraldas (ROM 105798, GenBank AF423095); E San Lorenzo, banana plantation (TTU 85354, TK 104582; TTU 85360, TK 104588; QCAZ 9087, TK 104601; QCAZ 9568, TK 104602); E San Lorenzo, La Guarapera banana farm and pasture (QCAZ 9088, TK 104612); Comuna San Francisco de Bogotá (QCAZ 9086, TK 135517; TTU 102960, TK 135677; QCAZ 9089, TK 135926; QCAZ 9563, TK 135973); Mataje, Navy Base (TTU 103120, TK 135927). PANAMA: Darién; Cana (LSUMZ 25498, M 549; LSUMZ 25540, M 572).

Lonchophylla handleyi (10).—ECUADOR: Morona Santiago; Sucua, 850 m (TK 105276); Puente Limitrofe entre Morona Santiago y Pastaza (lado sur del Río Pastaza), 662 m (TK 105314). PERU: Huánuco; Junín (AMNH 230214, GenBank AF23093); Leoncio Prado, 9 km S, 2 km E Tingo María (CM 98648, TK 22954; TCWC 59019, TK 22956); 6 km N Tingo María (TTU 46164, GenBank AF423094, TK 22598; TTU 46169, TK 22611; TTU 46172, TK 22616; TTU 46173, TK 22617; TCWC 55947, TK 22620).

Lonchophylla hesperia (2).—PERU: Lambayeque; Las Juntas, in Quebrada La Pachinga, ca. 14 km N, 25 km E Olmos, el 1,000 ft (LSUMZ 27253, M 921; LSUMZ 27254, M 922).

Lonchophylla orienticollina (5).—ECUADOR: Pastaza: Cueva de los Tayos, 692 m (QCAZ 8566, ASK 7733; QCAZ 8568, ASK 7735; QCAZ 8570, ASK 7737). PERU: Huánuco; Leoncio Prado, 6 km N Tingo María (TTU 46168, TK 22609; TCWC 55946, TK 22619).

Lonchophylla robusta (16).—COLOMBIA: Tabito (MHN512, GenBank AF423088; MHN514, GenBank AF423090; MHN515, GenBank AF423091). ECUADOR: Esmeraldas; E San Lorenzo, banana plantation (TTU 85353, TK 104581; TTU 85355, TK 104583; TTU 85366, TK 104594; QCAZ 9085, TK 104600); E San Lorenzo, La Guarapera banana farm and pasture (TTU 85391, TK 104619); Comuna San Francisco de Bogotá (TTU 102832, TK 135513; QCAZ 9091, TK 135515; QCAZ 9092, TK 135516; QCAZ 9093, TK 135518; TTU 102941, TK 135658; TTU 102959, TK 135676); Pichincha; Mejía, La Unión del Toachi, Ontongachi, 937 m (QCAZ 5406). PANAMA: Altos de Campana (ROM 104268, GenBank AF423087).

Platalina genovensium (2).—PERU: Arequipa; Caravelí (AMNH 257108, GenBank AF 423101); 2 km NE of Atiquipa, "El Castillo," 15.7811°S, 74.34767°W (WGS84), 418 m (MUSA 9383).

Xeronycteris vieirai (1).—BRAZIL: Paraiba; Fazenda Espírito Santo, near Campina Grande, Municipio de Solidade (MVZ 186020).

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