**LONCHOPHYLLINI:
LOS MURCIÉLAGOS DEL CHOCÓ**

ABSTRACT

Models of potential distribution for representatives of the glossophagine tribe Lonchophyllini were constructed to investigate the ecological and evolutionary history within this group of bats. Models created pointed on a concentration of species richness on the northwestern portion of South America with high richness values in the Chocó Biogeographic region. Evapotranspiration and precipitation were positively correlated with Lonchophyllini richness, at the same time species richness was inversely correlated with altitude. Ecological data support a process of geographic isolation by niche partitioning within nectar feeding bat tribes. Based upon phylogenetic, geologic, and ecological data, a model of evolutionary radiation for members of the tribe Lonchophyllini is proposed.

Keywords: Bats; Chocó; Ecology; Evolution; Lonchophyllini; Models; Reconstruction; Species richness.

RESUMEN

Modelos de distribución potencial fueron construi-dos para los representantes de la tribu de glosofaginos Lonchophyllini con la finalidad de investigar la historia ecológica y evolutiva de este grupo de murciélagos. Los modelos creados señalan una concentración de la riqueza de especies en la parte nor-occidental de Sur América con altos valores de riqueza sobre la región del Chocó Biogeográfico. La riqueza de especies de Loncofilinos tuvo una correlación positiva con la evapotranspiración y la precipitación, al tiempo que presentó una correlación negativa con la altitud. Estos datos ecológicos apoyan un proceso de aislamiento geográfico por partición de nicho entre las tribus de murciélagos nectarívoros. Con base en datos filogenéticos, geológicos y ecológicos, un modelo de radiación evolutiva es propuesto para los miembros de la tribu Lonchophyllini.

Palabras clave: Chocó; Ecología; Evolución; Murciélagos; Modelos; Reconstrucción; Riqueza de especies.

LONCHOPHYLLINI, THE CHOCOAN BATS

Hugo Mantilla-Meluk*

INTRODUCTION

Nectarivourous bats within the tribe Lonchophyllini are characteristic members of mammalian assemblages in the Biogeographic Chocó. Lonchophilline bats include the genera *Lochophylla, Lionycteris, Platalina,* and *Xeronycteris*. In the Chocó region seven lonchophylline bat species have been reported *L. cadenai, L. chocoana, L. handleyi, L. mordax, L. orcesi L. thomasi,* and *L. spurrelli* (Mantilla-Meluk and Jiménez-Ortega 2006; Woodman and Timm 2006).

The great morphological variation found among nectarivorous bats suggests a rapid radiation of original glossophagine forms followed by an also rapid and effective niche partitioning. Rapid evolution has been associated with global environmental changes that result in landscape fragmentation and population isolation (Bush *et al*. 1977). Population isolation is thought to be an important component of the process of speciation in the Neotropics. An indirect method to recover those historical patterns promoting isolation is the study of current patterns of species distribution and species richness. It has been proposed that centers of diversification used to enclose higher numbers of species than areas recently colonized (Jetz *et al*. 2004). In the present analysis the species distribution of members of the tribe Lonchophyllini and their associated ecological limiting factors are investigated to reconstruct the mode of geographic radiation for this group of bats in the northwestern portion of South America.

METHODS

Models of potential distribution

Models of potential distribution were created for fourteen of the fifteen currently recognized lonchophylline species: *L. spurrelli, L. bokermani,*

* Department of Biological Sciences Texas Tech University, Lubbock TX, 79409-1313 USA. e-mail: hugo.mantilla@ttu.edu.

L. dekeyseri, L. handleyi, L.hesperia, L. mordax, L. robusta, L. thomasi and P. genovensium (Simmons 2005), as well as the recently described species *L. chocoana* (Davalos 2004), *L. orcesi* (Albuja and Gardner 2005), *Xeronycteris vieirai* (Gregorin and Ditchfield 2005), and *L. cadeanai* (Woodman and Timm 2006). In addition *L. concava* (Goodman 1914) was also included in the present analysis based upon Carter and Jones (1976), Albuja and Gardner (2005), and Woodman and Timm (2006). Digital polygon maps were created based upon confirmed species distribution data reported in the literature. *Lonchophylla pattoni* (Woodman and Timm 2006) was not included in the analysis due to the lack of information on distributional limits of the species. Basic polygons were corrected based on ecological criteria including species altitudinal limits as well as ecoregion limits. Elevation data was obtained from a Digital Elevation model created for the Neotropics based upon the Digital Chart of the World data available at: http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html. The «Ecoregions» layer was obtained from: http://www.natureserve.org/explorer/eodist.htm#ecoregions. Sources of information on species distribution included in the analysis are summarized in Appendix I. Final polygon maps on species distributions were transformed into raster format layers and added using the *Spatial Analyst* extension of ArcGIS 9.1 to create a raster layer representing lonchophylline species richness accumulation.

Environmental variables

In order to investigate the potential effect of environmental heterogeneity on species isolation among bats of the tribe Lonchophyllini data on altitude, precipitation, evapotranspiration, and maximum temperature representing important niche dimensions for mammals (Wang *et al*. 2003) were derived from raster layers (GTOPO30 and MAXENT, http://www.cs.princeton.edu/~schapire/maxent/).

ArcGIS 9.1 was used to create a grid of points (N=5,047) evenly distributed across the study area (32.70,-58.49 Lat.; -118.48,-26.27 Lon.), the function

extract values from points was then used to extract values contained in raster layers of: lonchophylline richness, altitude, precipitation, evapotranspiration, and maximum temperature. Values in associated attribute tables were exported as excel files and a multiple correlation analysis (Pearson correlations) was performed between species richness and environmental variables with the help of SPSS (http://www.spss.com/registration/login/login009.cfm).

RESULTS

Species Richness

The obtained model of richness distribution of lonchophilline bat species is presented in Figure 1.

Environmental variables

Results of the Pearson Correlations are summarized in Table 1 and Figure 2.

DISCUSSION

The phylogenetic relationships among glossophagine bats have been largely debated (Griffith 1982; Haiduk and Baker 1982; Carstens *et al*. 2002). Different sets of data and different phylogenetic approaches used to define appropriate outgroups have resulted in different topologies opening multiple interpretations of the actual placement of representatives of major divisions inside the subfamily Glossophaginae. Simmons (2005) following Koopman (1993) and Wetterer et al. (2000) recognizes a monophyletic arrangement of 15 glossophagine genera divided into three main subfamilies: Brachyphyllinae, including *Brachyphylla*, Phyllonycterinae, including *Phyllonycteris* and *Erophylla*; and Glossophaginae, including the tribes Glossophagini: *Anoura*, *Choeroniscus*, *Choeronycteris*, *Glossophaga*, *Hylonycteris, Leptonycteris, Lichonicterys, Monophyllus. Musonycteris*, and *Scleronycteris*, and the tribe Lonchophillini, including *Lonchophylla*, *Platalina*, and *Lionycteris*. Based upon new molecular evidence Baker *et al*. (2000) suggested that this

arrangement results in a classification that is paraphyletic at several levels. In a more complete molecular analysis using both mitochondrial and nuclear genes including a taxon sampling with almost all phyllostomid genera Baker *et al*. (2003) arranged phyllostomid nectarivorous species into two monophyletic groups the subfamilies: Glossophaginae and Lonchophyllinae. The subfamily Glossophaginae includes the Cheoronycterini (*Anoura, Choeronycteris, Musonycteris, Scleronycteris*, and *Hylonycteris*), and the Glossophagini (*Glossophaga, Leptonycteris, Monophyllus*) the Brachyphyllini (*Brachyphylla*), and the Phyllonycterini (*Erophylla* and *Phyllonycteris*). On the other hand, the subfamily Lonchophyllinae includes the Lonchophyllini (*Lochophylla, Lionycteris* and *Platalina*). Morphological characters of 35 phyllostomid nectar feeding bat species were used by Carstens *et al*. (2002) to test Griffiths (1982) and Baker (1967) hypotheses of morphological convergence among nectar feeding bats. In their analysis Carsten *et al*. (2002) also recovered the division between Glossophaginae and Lonchophyllinae. The monotypic genus *Xeronycteris* (Gregorin and Ditchfield 2005) has been recently added to the list of Lochophyllines. Based upon morphological data *X. vieirai* has been associated with the genus *Platalina*. Both species *P. genovensium* and *X. vieirai* are adapted to xerophytic conditions (Gregorin and Ditchfield 2005).

In the present work richness distribution of species within the tribe Lonchophyllini was concentrated on the northern portion of South America with highest values of richness in the Biogeographic Chocó region (Figure 1). The model obtained from the Pearson Correlation analysis show a positive correlation between Lonchophyllini richness *vs*., evapotranspiration, and precipitation and a negative
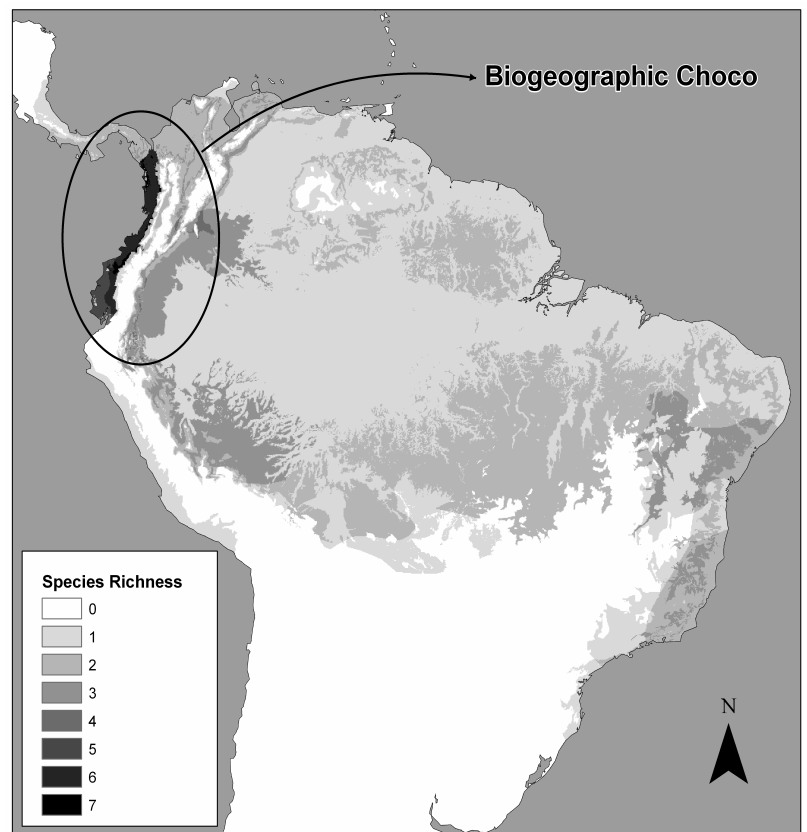

Figure 1. Reichness concentration of bats within the tribe *Lonchophyllini* in the biogeographic Chocó.
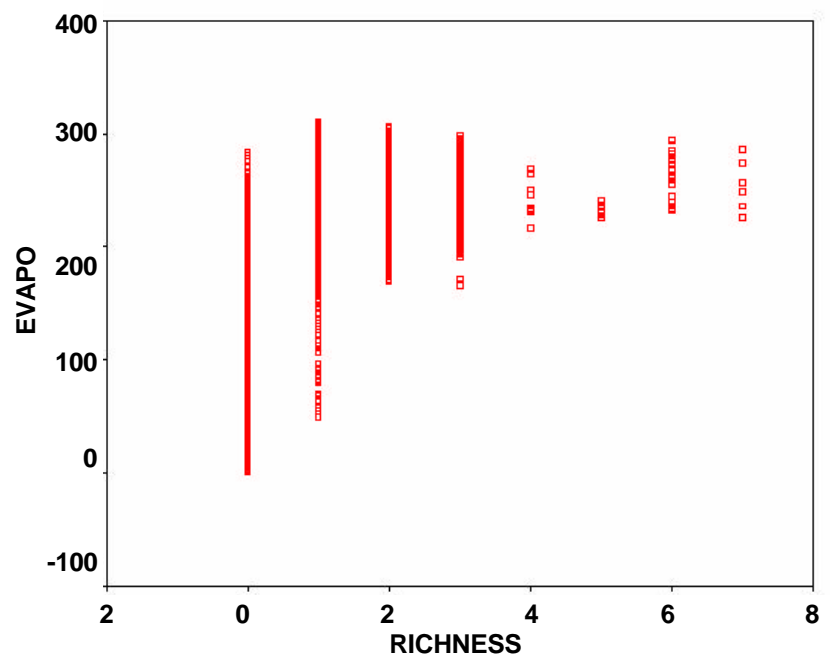

Figure 2. Positive correlation between species richness and evapotranspiration.

Table 1
Pearson correlation values between richness and environmental variables

	Richness	Precipitation	Max temperature	Elevation	Evapotranspiration	Vegetation
Richness	1.000					
Precipitation	0.408	1.000				
Max temperature	0.320	0.381	1.000			
Elevation	-0.336	-0.467	-0.901	1.000		
Evapotranspiration	0.459	0.702	0.806	-0.830	1.000	
Vegetation	-0.261	-0.423	-0.418	0.460	-0.546	1.000

correlation between Lonchophyllini richness and elevation (R=0.477, R square=0.228; significance one tail analysis 0.000) (Figure 2) (Table 1). These data support the hypothesis of niche partitioning among the recognized continental tribes of nectar feeding bats in the Neotropics since Choeronycterini bats mainly include highland specialist bat species (Mantilla-Meluk and Baker 2006) and Glossophagini bats mainly include species adapted to xerophytic conditions (Fleming 2002). It is difficult to determine the phylogeographic affinities of the tribe Lonchophyllini. Fossil evidence available of glosso-phagine bats are very scarce making difficult to reconstruct the evolutionary history of nectar feeding bats. The only nectar feeding bat fossil record known from the northern part of South America corresponds to *Palynephyllum antimaster* recovered from the Miocene deposits of La Venta, Colombia dated between 13 and 12 mya. *Palynephyllum antimaster* corresponds to a choeronycterine intermediate form between *Lonchophylla handleyi* and *Anoura caudifer* (Czaplewski *et al*. 2003). This evidence confirmed the presence of already well differentiated glossophagine bats from middle Miocene and suggests a mid Tertiary origin for lonchophylline forms. *Anoura caudifer* represents bats adapted to the highlands (Mantilla-Meluk and Baker 2006) while *Lonchophylla handleyi* is common at mid elevations and lowlands (Eisenberg 1989). The isolation of Lonchophyllini includes an environmental component associated with the unique ecological combination of variables found in the Biogeographic Chocó. Although representatives of the tribe Lonchophyllini include some species adapted to xerophytic conditions such as *P. genovensium* and the *X. vieirai* (Gregorin and Ditchfield

2005) the majority of the species in the northern portion of South America are adapted to lowland humid forests, which is particularly true for Chocoan representatives of the group. It is possible that lonchophylline species were widespread distributed on the lowlands of South America prior the uplifting of the Andes. The uplifting of the Andes was also followed by other significant geologic events that took place during the Miocene such as the completion of the Isthmus of Panama, and the creation of the Circumpolar Antarctic Current(Orsi *et al*. 2005). These events could also have potential effects on the distribution of original bat forms within the tribe Lochophyllini. With the completion of the Circumpolar Current due to the separation of the Antarctic land from the southern part of the South America (23 Mya.) cold currents coming from the south resulted in an arid belt which connected the Pacific and the Atlantic coasts of South America around the current Chaco region (Orsi *et al*. 2005).

The cold Antarctic currents freely circulated from west to east in central and southern South America due to the absence of the high elevations of the Andean system. The prevailing xerophytic connection between eastern and western coasts across central South America before the Andean uplifting could explain the affinities that have been suggested between members of the genus *Platalina* and *Xeronycteris* today separated by the Amazon basin in semi isolated arid enclaves on coastal Peru and coastal Brazil respectively (Gregorin and Ditchfield 2005). A paleo-reconstruction of the South American landscape for the Miocene (17–9 mya) in its northern portion also suggests a connection between the eastern and western

versants of the Andes system know as the Cuenca Basin. Trans-Andean gene flow among lowland species across the Cuenca Bridge was terminated 3 mya with the major uplifting events of the northern Andes during the Late Miocene (Figure 3) (Wesselingh 2006).

Widespread lonchophylline forms adapted to more humid conditions in the northern range of South America seem to be separated into two vicariant groups between the two versants of the Andes by the uplifting of the system. In a parallel way, with the completion of the Panamanian Isthmus and the associated deviation of the Humboldt Current from the Pacific coast of South America in its north-western portion resulted in the super humid condtions of the Chocó region.

Dávalos and Jansa (2004) suggest a polyphyletic origin for the tribe Lonchophyllini with repre-sentatives of the genera *Platalina* and *Lionycteris* nested in between two separated clades of *Lonchophylla*. The basal group corresponds to *L. thomasi* separated into two phylogroups one enclosing *L. thomasi* populations from Guayanas and Bolivia, and another clade with *L. thomasi* populations from Ecuador and Venezuela. This geo-graphic signal found in Dávalos and Jansa (2004) is also supported by the model of distribution proposed for the lonchophyllines in the present work. A second clade included the widest spread distributed *L. mordax* and *Lionyceris* in addition to *Platalina* restricted to western Peru. A third clade is composed by *L. chocoana*, *L. handleyi, L. robusta.* In their morphological analysis Wood-man and Timm (2006) also suggest a polyphyletic origin of *Lonchophylla*. One remarkable aspect in Woodman and Timm's analysis (2006) is the sister group relationship that exists between eastern and western representatives among their Chocoan clade (Figure 4). This evidence suggests a process of speciation in isolation among lonchophyllines. Species on the western versant of the Andes were selected to the conditions of the Biogeographic
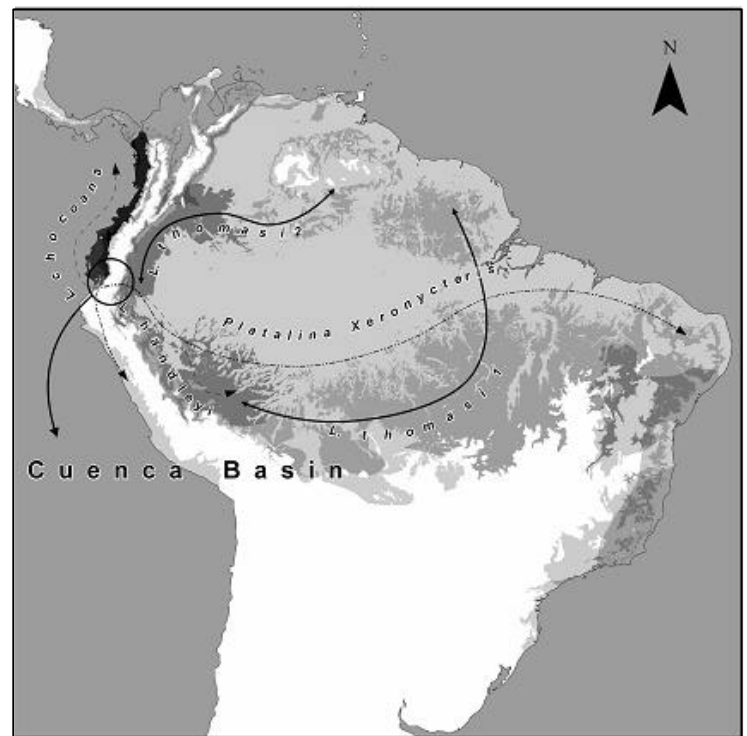

Figure 3. Suggested connection routes among Lonchophillini. Dashed line represent the potential routes interconnecting representatives of Chocoan clades.
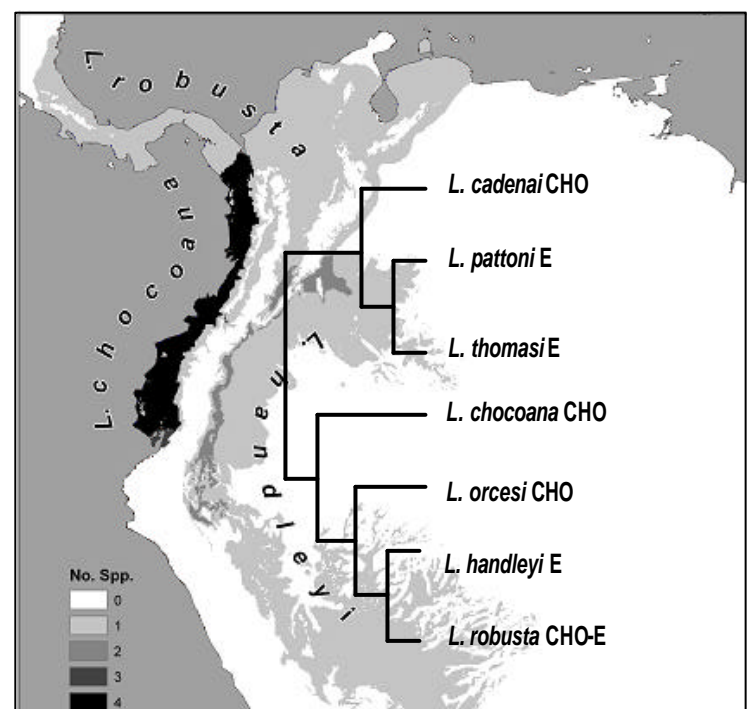

Figure 4. Effect of the Andes in the isolation of Chocoan populations of Lonchophyllini. Parsimony analysis 65 morphological characters adapted from (Woodman and Timm 2006). (CHO) Chocó, (E) East, (CHO-E) Chocó-East.

ACKNOWLEDGEMENTS

CITED LITERATURE

ALBERICO, M., A. CADENA, J. HERNÁNDEZ-CAMACHO, and Y. MUÑOZ-SABA. 2000. Mamíferos (Synapsida: Theria) de Colombia. Biota Colombiana 1 (1) 43-75.

ALBUJA. L. 1999. Murciélagos del Ecuador. Cicetrónic Cia. Ltds. Quito, Ecuador. 288 pp.

ALBUJA, L. and A. L. GARDNER. 2005. A new species of *Lonchophylla* Thomas (Chiroptera: Phyllostomidae) from Ecuador. *Proceedings of the Biological Society of Washington:* Vol. 118, No. 2, pp. 442–449.

ANDERSON, S. 1997. Mammals of Bolivia, taxonomy and distribution. Bulletin of the American Museum of Natural History No 231, 652 pp.

BAKER R. J. 1967. Karyotypes of bats of the family Phyllostomidae and their taxonomic implications. Southwestern Naturalist 12:407-428.

BAKER R. J., C. A. PORTER, J. C. PATTON, and R. A. VAN DEN BUSCHE B. 2000. Systematics of the family Phyllostomidae based on RAG-2 DNA sequences. *Occ. Pap. Mus. Tex. Tech Univ*. 202: 1–16.

BAKER R. J., S. R. HOOFER, C. A. PORTER, and R. A. VAN DEN BUSCHE B. 2003. Diversification among New World leaf-nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230:i þ 1–32.

BERNARD, E. A. L. K. M, ALBERNAZ, and W. E. MAGNUSSON. 2001. Bat species composition in three localities in the Amazon Basin. Studies on Neotropical Fauna and Environment Vol. 36. No. 3, pp. 177-184.

BUSH G. L., S. M. CASE, A. C. WILSON, and J.L. PATTON. 1977. Rapid speciation and chromosomal evolution in mammals (evolutionary rates / effective population size / vertebrates / cytogenetic isolating mechanisms /social structuring). *Proc. Natl. Acad. Sci.* Vol. 74, No. 9, pp. 3942-3946.

CABRERA, A. 1957. Catálogo de los Mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales, Bernardino Rivadavia. Tomo IV No. 1.

CARSTEN, B. C., B. L. LUNDRIGAN, and P. MEYERS. 2002. A phylogeny of the neotropical nectar-feeding bats (Chiroptera: Phyllostomidae) based on morphological and molecular data. Journal of Mammalian Evolution 9:23–53.

CHARLES-DOMINIQUE, P., A. BROSSET, and S JOUARD. 2001. Les chauves-souris de Guyane. Publications Scientifiques du Museum National D'Historie Naturelle. Paris. 172 pp.

CUARTAS-CALLE, C. A. and J. MUÑOZ-ARANGO. 2003. Lista de los mamíferos (Mammalia: Theria) del departamento de Antioquia, Colombia. Biota Colombiana 4(1) 65-78. (19) G

CZAPLEWSKI N. J., M. TAKAI, T. M. NAEHER, N. SHIGEHARA, and T. SETOGUSHI. 2003. Additional bats from the middle Miocene La Venta fauna of Colombia. Revista Academia Colombiana de Ciencias. Volumen XXVII, No. 103.

DÁVALOS L. M. 2004. A new Chocoan species of *Lonchophylla* (Chiroptera: Phyllostomidae). American Museum Novitates 3426, 1-14.

DÁVALOS L. M., and S. A. JANSA. 2004. Phylogeny of the Lonchophyllini (Chiroptera: Phyllostomidae). Journal of Mammalogy: Vol. 85, No. 3 pp. 404–413.

EISENBERG, F. J. 1989. Mammals of the northern Neotropics Volume 1. Panama, Colombia, Venezuela, Guyana, Suriname, French Guyana. The University of Chicago Press. 449 pp.

FARIA, D. B. SOARES-SANTOS, and SAMPAIO E. 2006. Bats from the Atlantic rainforest of southern Bahia, Brazil. Biota Neotrópica Vol. 6. No. 2. pp 1-13.

FLEMING, T. H. 2002. Pollination biology of four species of Sonoran Desert columnar cacti. In: FLEMING, T. and VALIENTE, A. eds. Columnar cacti and their mutualists: evolution, ecology and conservation. Tuscon: University of Arizona Press, 207–225.

GREGORIN, R. andDITCHFIELD, A. D. 2005. New genus and species of the nectar feeding bat in the tribe Lonchophyllini (Phyllostomidae: Glossophaginae) from northeastern Brazil. Journal of Mammalogy. 83(2): 403-414 pp.

HANDLEY, Ch. O. Jr. 1966a. Checklist of the mammals of Panamá. Pp. 753-795. In: Ectoparasites of Panama (R. L. WENZEL AND V. J. TIPTON, eds.) Field Museum of Natural History Chicago, 861 pp.

HANDLEY, Ch. O. Jr. 1967. Bats of the canopy of an Amazonian forest. Zoologia Vol. 5. 211-215.

HANDLEY. Ch. O. Jr, 1976. Mammals of the Smithsonian Venezuelan project. Briham Young University. Science Publications of Biological Series, 20: 1-89 pp.

HAIDUK, M. W. and BAKER. R. J. 1982. Cladistical analysis of G-banded chromosomes of nectar feeding bats (Glossophaginae: Phyllostomidae). Systematic Zoolology, 31:252-265.

JETZ, W. RAHBEK, C. and Zoological Museum, University of Copenhagen, Copenhagen, Denmark Colwelll, r. K. 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. Ecology Letters 7 (12), 1180–1191.

JONES, J. K. Jr. and CARTER, D. C. 1976. Annotated checklist, with keys to subfamilies and genera. Part I. Pp. 7–38, *in* Biology of bats of the New World family Phyllostomatidae (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Special Publication, The Museum, Texas Tech University Press, Lubbock, 10:1–218.

KOOPMAN, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. American Museum Novitates No. 2651. Ameican Museum of Natural History.

LIM, B. and ENGSTROM, M. 2005. Mammals of the Iwokrama Forest. Proceedings of the Academy of Natural Science of Philadelphia 154: 71-108 pp.

LIM, B. and ENGSTROM, M. 2001. Bat community structure at Iwokrama Forest, Guyana. Journal of Tropical Ecology 17:647-665.

LINARES. J. O. 1998. Mamíferos de Venezuela. Sociedad Conservacionista Audubon de Venezuela 691 pp.

MANTILLA-MELUK, H. and BAKER, R. J. 2006. Systematics of small *Anoura* (Chiroptera: Phyllostomidae) from Colombia, with description of a new species. Occasional Papers of the Museum of Texas Tech University. No. 261.

MANTILLA-MELUK, H. and JIMÉNEZ-ORTEGA, A.M. 2006. Estado de Conservación y algunas consideraciones biogeográficas sobre la quirópterofauna del Chocó Biogeográfico Colombiano. Revista Institucional. Universidad Tecnológica del Chocó Diego Luís Córdoba. No. 25. 10-17 pp.

MARÍN-VASQUEZ, A. and AGUILAR-GONZÁLEZ, A. V. 2005. Murciélagos (Chiroptera) del departamento de Caqueta-Colombia. Biota Colombiana 6(2) 211-218.

MUÑOZ-ARANGO, J. 2001. Los murciélagos de Colombia, Sistemática, distribución, descripción, historia natural y ecología. Univerisidad de Antioquia. 391.

MUÑOZ-SABA, Y. and ALBERICO, M. 2004. Mamíferos en el Chocó Biogeográfico. In: Colombia diversidad biotica IV. RANGEL Ch. J. O. El Chocó biogeogáfico / Costa Pacífica. Instituto de Ciencias Naturales. Bogotá. 997 pp.

ORSI, A.H., T. WHITWORTH, and W.D. NOWLING. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current, Deep Sea Research, Series I, 42, 641-673 pp.

PACHECO, V. PATTERSON, B. PATTON, J. EMMONS, L. SOLARI, S. and ASCORRA, C. 1993.

List of mammal species known to occur in Manu Biosphere Reserve, Peru. Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos No. 44: 1-12 pp.

REID, F. 1997. A field guide to the mammals of Central America and southeast Mexico. Oxford University Press. 344 p.

SAZIMA, I. VIZOTTO, L. D. and TASDDEI, V. A. 1978. Uma nova espécie de Lonchophylla da Serra do Cipó, Minas Gerais, Brasil (Mammalia, Chiroptera, Phyllostomidae). Revista Brasiliera de Biologia, vol. 38, no. 1. 81-89.

SIMMONS, N. B. 2005. Order Chiroptera. In: WILSON D. E. and D. M. REEDER. Mammals Species of the World, a taxonomic and geographic reference. Third Edition. Volume 1. The John Hopkins University Press, Baltimore. 2142 pp.

SOLARI, S. VIVAR, E. VELAZCO, P.M. RODRÍGUEZ, J.J .WILSON, D. E. BAKER, R. J. and MENA, J.L. 2001. The small mammal community of the lower Urubamba Region, Peru. Pp. 171–181. In: Urubamba: the biodiversity of a Peruvian Rainforest. SI/MAB Series 7 (A. ALONSO, F. DALLMEIER, and P. CAMPBELL, eds.). SI/MAB Biodiversity Program, Smithsonian Institution, Washington, D.C., 204 pp.

SOLARI, S. PACHECO, V. LUNA, L. VELAZCO, P. and PATTERSON, B. 2006. Mammals of teh Manu Biosphere Reserve. Fieldiana Zoology, N. S., No. 110. pp. 13-22.

SOLARI, S. A. and PINTO, M. 2007. A rapid assessment of mammals of the Nassau and Lely plateaus. Eastern Suriname. In: A rapid biological assessment of Lely and Nassau Plateaus, Suriname (with additional information on the Brownberg Plateau). ALONSO, L. E. and. Mol, J. H. Eds. Conservation International.

SOLARI, S. PACHECO, V. and VIVAR, E. 1999. Nuevos registros distribucionales de murciélagos peruanos. Revista Peruana de Biología Vol. 6. No. 2.

TUTTLE, M. D. 1970. Distribution and zoogeography of Peruvian btas, with comments on natural history. The University of Kansas Science Bulletin. Vol. XLIX No. 2 45-86 pp.

WESSELINGH F. P. 2006. Miocene long-lived lake Pebas as a stage of mollusc radiations, with implications for landscape evolution in western Amazonia. Evolution of Miocene Amazonian landscapes and biota. Scripta Geologica, 133. 1-17 pp.

VAN DEN BUSCHE, R. 1992. Restriction-Site Variation and Molecular Systematics of New World Leaf-Nosed Bats. *Journal of Mammalogy*, Vol. 73, No. 1. 29-42. pp.

WANG, G. OWEN, R, SÁNCHEZ-CORDERO, C. ALMARAZ, M. L. 2003. Ecological charcaterization of bat species distribution in Michoacán, México, using geographic information system. Global Ecology and Biogeography. 12, 65-85 pp.

WESSELINGH, F. P. and SALO, J. A. 2006. A Miocene perspective of the evolution of the Amazonian biota. Evolution of Miocene Amazonian landscapes and biota. Scripta Geologica., 133. 439-453 pp.

WETTERER, A.L., ROCKMAN, M., and SIMMONS, N. 2000. Phylogeny of phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites, Bulletin of the American Museum of Natural History, No. 248, issue 1, 200 pp.

WOODMAN, N. and TIMM, R. 2006. Characters and phylogenetic relationships of nectar-feeding bats, with descriptions of new *Lonchophylla* from western South America (Mammalia: Chiroptera: Phyllostomidae: Lonchophyllini). Proceedings of the Biological Society of Washington 19(4): 437-476.

Apenndix I

Sp./Country	Brazil	Bolivia	Colombia	Costa Rica	Ecuador	Guyana	Nicaragua	Panama	Peru	Suriname	Venezuela
L. spurrelli	5,12, 30		1,3,6,8,11, 19,20,21			6,7,11, 16,17,29		10	10,13,15,22 24,25,27,28	26	11,14,18,29
P. genovensium									10,15,28,29		
L. bokermani	30										
L. concava			3,29	29	2,3			1,29			
L. dekeyseri	29	29									
L. handleyi		1,8,20,21		2,10					10,24,25,27,29		
L. hesperi								15,28,29			
L. mordax	5,12,23, 29	23	1,11,20,21	23	22,2				6,13,28		
L. robusta			1,6,8,10,11,20 23,30	23	2		23	6,10	15,27,28,29		14,18,23
L. thomasi	5,23,29	4,10,22, 29	1,8,11,19,20, 21,23,29		2,10,22	10,16,17, 7,29		23,29	29		29
L. chocoana			29		16,25						
L. orcesi			3		3						
L. cadenai			9		9,10						
X. vieirai	31										

Sources of information in the literature used to construct the distribution models: Alberico *et al.* 2000. (1), Albuja 1999. (2), Albuja and Gardner 2005. (3), Anderson 1997. (4), Bernard *et al.* 2001. (5), Cabrera 1957. (6), Charles-Dominique *et al.* 2001. (7), Cuartas-Calle and Muñoz-Arango 2003. (8), Davalos 2004. (9), Davalos and Jansa 2004. (10), Eisenberg 1989. (11), Faria *et al.* 2006. (12), Handley 1967. (13), Handley 1976. (14), Koopman1978. (15), Lim and Engstrom 2005. (16), Lim and Engstrom 2001. (17), Linares 1998. (18), Marín-Vásquez and Aguilar-González 2005. (19), Muñoz-Arango 2001. (20), Muñoz-Saba and Alberico 2004. (21), Pacheco *et al.* 1993. (22), Reid 1997. (23), Solari *et al.* 2001. (24), Solari *et al.* 2006. (25), Solari and Pinto 2007. (26), Solari *et al.* 1999. (27), Tuttle 1970. (28), Woodman and Timm 2006. (29), Sazima *et al.* 1978. (30), Gregorin and Ditchfield 2005. (31).