

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 construidos para los representantes de la tribu de glosófagos 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

Nectarivorous bats within the tribe Lonchophyllini are characteristic members of mammalian assemblages in the Biogeographic Chocó. Lonchophylline 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*,

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 lonchophylline 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) recognizes a monophyletic arrangement of 15 glossophagine genera divided into three main tribes: Phyllonycterini, including *Phyllonycteris* and *Erophylla*; Glossophagini, including *Anoura*, *Choeroniscus*, *Choeronycteris*, *Glossophaga*, *Hylonycteris*, *Leptonycteris*, *Lichonicterys*, *Monophyllus*, *Musonycteris*, and *Scleronycteris*, and Lonchophyllini, 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 Phylloonycterini (*Erophylla* and *Phylloonycteris*). 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 Lonchophyllines. 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 species 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 correlation between Lonchophyllini richness and elevation ($R = 0.477$, R square = 0.228; significance one tail analysis 0.000)

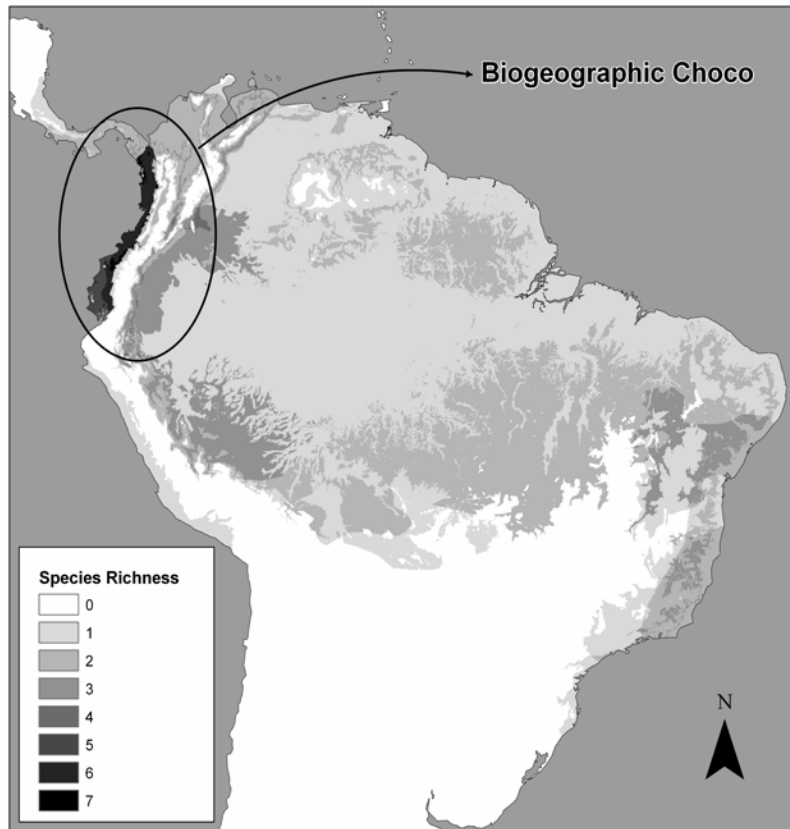


Figure 1. Reichness concentration of bats within the tribe *Lonchophyllini* in the biogeographic Chocó.

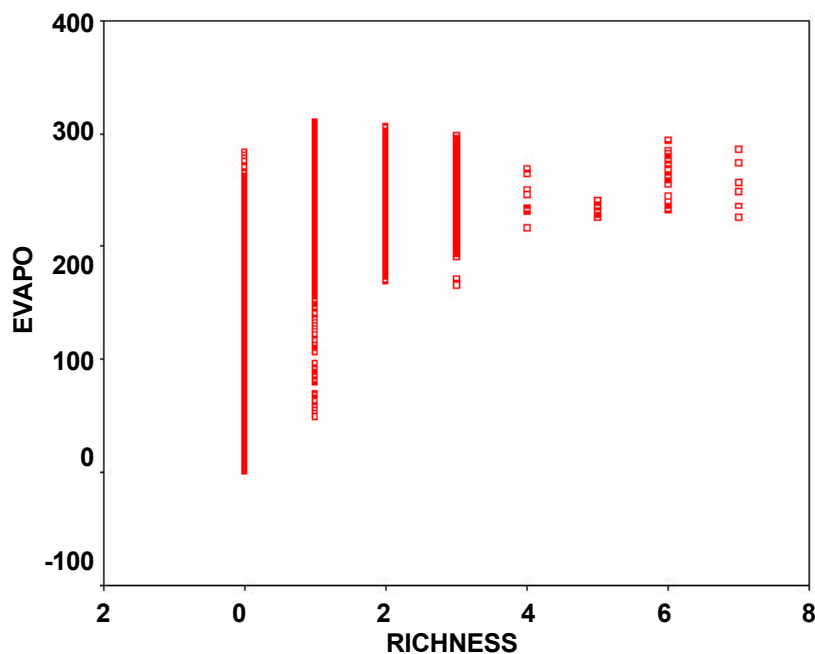


Figure 2. Positive correlation between species richness and evapotranspiration.

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

(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 glossophagine 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 Lonchophyllini. 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 conditions of the Chocó region.

Dávalos and Jansa (2004) suggest a polyphyletic origin for the tribe Lonchophyllini with representatives 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 geographic 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 *Lionycteris* in addition to *Platalina* restricted to western Peru. A third clade is composed by *L. chocoana*, *L. handleyi*, *L. robusta*. In their morphological analysis Woodman 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 Chocó and isolated by the uplifting of the northern Andes making bat assemblages in the Chocoan region unique.



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

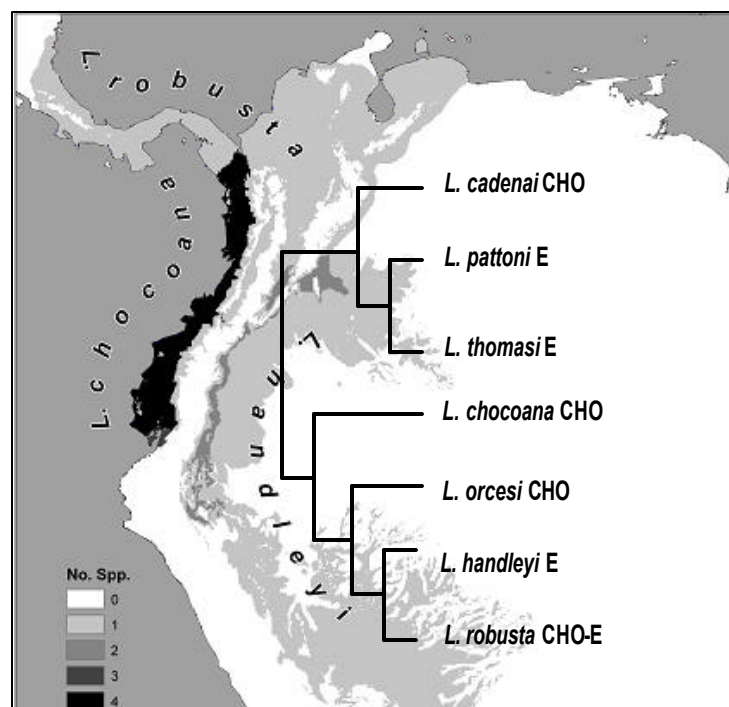


Figure 4. Effect of the Andes in the isolation of Chocoan populations of Lonchophyllini. Parsimony analysis 65 morphological characters adapted from (Woodman and Timm 2006). (CHO) Chocó, (E) East, (CHO-E) Chocó-East.

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Apenndix I

Sp./Country	Brazil	Bolivia	Colombia	Costa Rica	Ecuador	Guyana	Nicaragua	Panama	Peru	Suriname	Venezuela
<i>L. spurrelli</i>	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
<i>P. genovensium</i>									10,15,28,29		
<i>L. bokermanni</i>	30										
<i>L. concava</i>			3,29	29	2,3			1,29			
<i>L. dekeyseri</i>	29	29									
<i>L. handleyi</i>		1,8,20,21		2,10				10,24,25,27,29			
<i>L. hesperi</i>								15,28,29			
<i>L. mordax</i>	5,12,23, 29	23	1,11,20,21	23	22,2				6,13,28		
<i>L. robusta</i>			1,6,8,10,11,20 23,30	23	2		23	6,10	15,27,28,29		14,18,23
<i>L. thomasi</i>	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
<i>L. chocoana</i>			29		16,25						
<i>L. orcesi</i>			3		3						
<i>L. cadenai</i>			9		9,10						
<i>X. vieirai</i>	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), Koopman 1978. (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).