

Evolutionary Relationships Among Tropical Nectar-feeding Bats (Glossophaginae: Lonchophyllini), Based on Morphological Characters



Figure 1. Close up of Dekeyser's Nectar Bat (*Lonchophylla dekeyseri*). The fleshy appendage ("nose leaf") on the end of the muzzle is characteristic of the Neotropical bat family Phyllostomidae.

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Abstract

Nectar-feeding bats serve an essential role in lowland tropical rain forests, acting as pollinators for plants, seed dispersers, and predators on insects. Knowledge of the diversity of this group and its evolution is the necessary to understanding the development of the ecological relationships of these bats and the species with which they typically interact. The discovery of two new species of lonchophylline nectar-feeders in Colombia and Peru prompted me to undertake a study of the phylogenetic relationships in this branch of the group. I completed a series of analyses of a matrix of 177 characters with the computer program PAUP. These analyses used a variety of outgroup taxa that reflect the diversity of opinions regarding the closest relatives of the Lonchophyllini. Results support the contention that lonchophyllines represent a distinct group of nectar-feeders. However, relationships within this group remain poorly resolved. Characteristics that define individual species in this group show complex patterns of evolution that suggest convergence in a number of characters as a result of common feeding strategies in a variety of environments.



Figure 2. An Orange Nectar Bat (*Lonchophylla robusta*) approaching a night-flowering plant. In addition to feeding on pollen, nectar, and flower parts, nectar-feeding bats seasonally consume large quantities of insects.

Introduction

Recent molecular and morphological analyses (e.g., Wetterer et al., 2000; Baker et al., 2003) of the family Phyllostomidae (leaf-nosed bats—Fig. 1) strongly suggest a radiation within the guild of nectar-feeding bats (subfamily Glossophaginae) that has resulted in two successful groups occupying the modern New World Tropics: the "long-tongued bats" of the tribe Glossophagini and the "nectar bats" of the tribe Lonchophyllini. These two taxonomically distinct groups of bats appear to have diverged genetically from a common ancestor, then converged morphologically as a result of their common, specialized feeding strategies.

As their names suggest, nectar-feeding bats visit flowers to forage on nectar, pollen, and flower parts (Fig. 2). In doing so, they act as the primary and secondary pollinators for a large number of night-blooming tropical plants, including some economically important crops, such as bananas and plantains. Nectar feeders consume a variety of fruits and thereby serve as important dispersers of seeds for those plants. In addition, these bats are important seasonally as predators of insects (Howell and Burch, 1974; Gardner, 1977; Coelho and Marinho-Filho, 2002). Hence, the health of specific segments of tropical rain forests may be closely tied to the presence, diversity, and abundance of this feeding guild. Understanding species diversity within this group is crucial for accurately determining the ecological roles these bats play in the environment and gauging their impact on the reproductive lives of the plants with which they interact.

The identification of two new species of *Lonchophylla* in Colombia and Peru raised questions regarding the distribution and evolutionary history of members of the tribe Lonchophyllini, and it provided the impetus to study phylogenetic relationships in this group. Understanding the genetic relationships among these species will provide the framework necessary for understanding both the biogeography of these bats and the evolution of specific bat-plant interactions.

Materials and Methods

I investigated the phylogeny of the Lonchophyllini (genera *Lionycteris*, *Lonchophylla*, *Platalina*, *Xeronycteris*) using the computer program PAUP 4.0b10 for Macintosh computers to analyze a data matrix of 177 characters from 16 species of lonchophyllines and 7 outgroup taxa. The dataset included the entire suite of 137 morphological and 13 mtDNA restriction site characters from Wetterer et al.'s (2000) analysis of Phyllostomidae, as well as 27 additional cranio-mandibular and dental characters determined by me or adapted from other sources (Carstens et al., 2002; Dávalos and Jansa, 2004; Gregorin and Ditchfield, 2005). I used Wetterer et al.'s (2000) original codings, except for their characters #12 and #21, for which I followed Dávalos and Jansa (2004). For lonchophylline taxa not included in Wetterer et al.'s (2000) study, I scored characters using specimens available to me whenever possible. I secondarily relied upon some character codings reported by Carstens et al. (2002), Dávalos and Jansa (2004), and Gregorin and Ditchfield (2005).

Previous analyses of the Phyllostomidae (Baker et al., 2003; Wetterer et al., 2000; Carstens et al., 2002) have suggested a variety of complex relationships between the Lonchophyllini and other groupings of phyllostomids. To encompass as many potential outgroup relationships as possible, I included in all analyses seven taxa inferred to have a relatively close relationship with Lonchophyllini: *Anoura geoffroyi* (Choronycterini), *Glossophaga soricina*, *Monophyllus redmani* (Glossophagini), *Carollia perspicillata* (Carollinae), *Erophylla sezekorni*, *Phyllonycteris poeyi* (Phyllonycterini), *Brachyphylla cavernum* (Brachyphyllini). For each of seven analyses, one of these species was designated the outgroup, and the effects on the composition and relationships exhibited by the resulting tree for the Lonchophyllini were compared. Carstens et al. (2002), Dávalos and Jansa (2004), and other authors used the name *L. mordax* for *L. concava*. I concur with the view of Albuja and Gardner (2005) that the two names represent distinct species, and I adjusted the data matrix accordingly. Specimens of *L. bokermanni*, *L. orcesi*, and *Xeronycteris vieirai* were unavailable to us, and I inferred all characters from their original descriptions and accompanying illustrations (Sazima et al., 1978; Albuja and Gardner, 2005; Gregorin and Ditchfield, 2005). I used parsimony analyses using the heuristic search option with a random addition sequence of 1000 replicates. Robustness of parsimony trees were evaluated with bootstrap heuristic analyses of 500 replicates. Starting trees were via stepwise addition, and the branch-swapping algorithm was tree-bisection-reconnection (TBR). All characters were equally weighted and unordered.

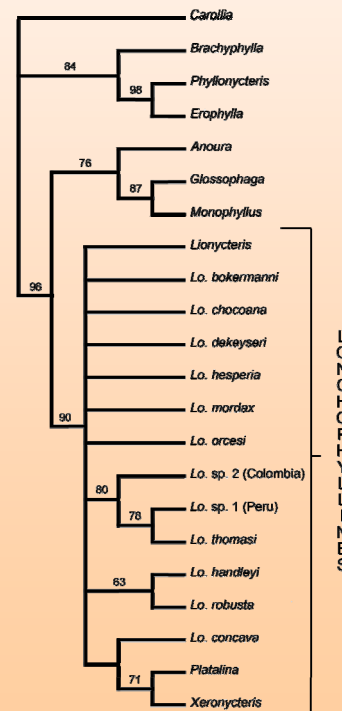


Figure 3. Strict consensus of 261 shortest-length trees from phylogenetic analysis using *Carollia* as the outgroup (218 steps; consistency index = 0.606; retention index = 0.698; G-fit = -64.551). Bootstrap supports > 50% are shown above branches. This tree represents the results of one of 7 analyses using 7 different outgroups. All 7 analyses provided the same unresolved topology for the Lonchophyllini, although the topology of the other taxa varied. Abbreviation: *Lo.* = *Lonchophylla*.

Results and Discussion

Regardless of the outgroup taxon employed, each parsimony analysis resulted in 261 shortest-length trees with 218 steps. Tree statistics were equivalent for each tree (Fig. 3). Topology among the 7 non-lonchophylline taxa varied considerably among the 7 analyses, as would be expected given each was rotated to act as the outgroup. In contrast, the membership and topology of the lonchophylline group remained stable among all analyses, and there was good bootstrap support (88–90%) for this branch. In general, all analyses support the recognition of this group as a clade.

Within the lonchophylline clade, the resulting trees are marked by a lack of resolution. The only exceptions include moderate to good (80–91%) bootstrap support for a clade consisting of the two new species and *Lonchophylla thomasi*, and within that grouping, moderate support (75–78%) for the new species from Colombia having a sister relationship to the group comprising the new species from Peru and *L. thomasi*. There is also weak (61–65%) support for a clade consisting of *L. handleyi* and *L. robusta*, and for another comprised of the two most derived taxa, *Platalina genovesium* and *Xeronycteris vieirai* (68–71%).

The lack of resolution among the Lonchophyllini probably reflects complex patterns of evolution marked by convergence and homoplasy. Additional analyses using mtDNA and nuclear DNA characters, in collaboration with USGS Ornithologist Terry Chesser, are currently being undertaken. A more completely resolved phylogeny with assist with evaluating convergent characteristics within the Lonchophyllini.

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