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Phylogenetics and Historical Biogeography

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Introduction

The single largest change in the number of phyllostomid subfamilies took place in a 293-day span between 1 March and 19 December in 2000. The first date marks the publication of Wetterer et al. (2000) comprehensive character-based phylogeny based primarily on morphological variation among genera and recognizing only seven subfamilies. The second corresponds to the first analyses based on DNA sequences from as many genera as could be sampled (Baker et al. 2000) that would eventually lead to subfamily classification for 11 clades (Baker et al. 2003). Together, both phylogenies stand as bookends signaling the end of one set of assumptions about the evolution, biogeography and adaptation of bats in the phyllostomid radiation and the beginning of another, whose full implications, reviewed here, have not yet been fully explored.

The shock inflicted by molecular phylogenies to the established phyllostomid phylogeny cannot be overstated. To understand the repercussions of those first well-resolved family-level analyses requires reviewing the culmination of multiple prior analyses and character sets in Wetterer et al. (2000). A preview of Andrea Cirranello's dissertation, Wetterer et al. (2000) assembled the largest data set to date to resolve phyllostomid phylogeny. With new morphological characters scored from the vast specimen holdings at the American Museum of Natural History and other North American collections, Wetterer et al. (2000) were able to include genera neglected by most previous efforts, from the monotypic nectar-feeding *Platalina* and *Scleronycteris*, to the diverse fruit-feeding *Artibeus* and *Platyrrhinus*. The character compilation was equally ambitious, compiling various sources to code, and in some cases describe for the first time, 150 characters from the skull, skeleton, soft tissues, fur, skin, and published accounts of restriction sites and karyotypes. By amassing such a large character matrix and including all the known genera, Wetterer et al. (2000) sought to generate a robust estimate of the phyllostomid phylogeny, comprehensive in the scope of both the characters and lineages included. The main result showed taxa that shared feeding

specializations formed clades resulting in the support for and recognition of the seven traditionally recognized subfamilies.

The first indication that long-standing relationships within phyllostomids would be upended by analyses of DNA sequences arrived with the phylogeny based on the autosomal locus encoding for the recombination-activating protein 2 or RAG2 by Baker et al. (2000). While some of the phylogenetic relationships uncovered were unsurprising and in line with previously debated clades (e.g., the lack of monophyly among nectarivorous genera; Griffiths 1982, 1983), others were breathtakingly novel. Instead of being a "phyllostomine," *Macrotus*—and not the desmodontines—emerged as the sister to all other phyllostomids. *Lonchorhina*, a morphologically distinctive genus of primarily insectivorous bats, was sister to the nectarivorous *Lonchophylla* and *Lionycteris*. Instead of being sister taxa, the phenotypically and ecologically similar *Carollia* and *Rhinophylla* were paraphyletic, and *Carollia* was more closely related to the gleaning insectivores *Glyphonycteris* and *Trinycteris*. And the latter two genera, formerly part of a monophyletic "*Micronycteris*," were now only distant relatives rendering the genus polyphyletic.

Rejecting three paraphyletic subfamilies long thought to be monophyletic—"Phyllostominae," "Glossophaginae," and "Carolliinae"—the Baker et al. (2000) phylogeny was groundbreaking. But with poor support for relationships among newly redefined subfamilies, and its reliance on a single locus, the comparative implications of this phylogeny were not immediately grasped. A single gene tree can fail to reflect the species tree through incomplete lineage sorting of ancestral polymorphisms (Rosenberg and Nordborg 2002), lateral gene transfer (Sjöstrand et al. 2014), introgression (Litsios and Salamin 2014), paralogy (Roy 2009), or ecologically adaptive convergence (Liu et al. 2010). Instead of reflecting the evolutionary history of phyllostomids, the single-locus gene tree might reflect some idiosyncratic features of the RAG2 protein or its history.

With relationships among higher clades in flux, the historical biogeography of the family was not a priority for research. Nevertheless, the implications of the change from the morphology-based phylogeny to one based on sequences were noted early on. A possible North American origin for the family based on the position of *Macrotus* was first highlighted by Dávalos (2006), and the DNA-based phylogeny was adopted from the start in analyses of ecological biogeography by Stevens (2006). Despite several phylogenies for individual genera (e.g., Hoffmann and Baker 2001; Hoffmann et al. 2003; Porter et al. 2007), implementation of model-based biogeographic analyses has been relatively recent (Cuadrado-Ríos and Mantilla-Meluk 2016; Velazco and Patterson 2008, 2013). In short, the task of fleshing out the historical biogeography of phyllostomids has not yet been completed.

The purpose of this chapter is to review the literature since 2000, thereby summarizing the key changes between the two landmark studies of Wetterer et al. (2000) and Baker et al. (2000), as well as new discoveries published since then. In particular, we compare and contrast phylogenies introducing sources of phylogenetic characters or those including previously excluded lineages. In the process, we also identify outstanding questions on the phylogenetics and historical biogeography of the family and highlight areas of overlap between historical and ecological approaches.

Methods

The literature review by Wetterer et al. (2000) synthesized phylogenies, whether character or distance based, published until that point. Additionally, the character analyses they introduced directly related the systematics of the family to phylogenies through character changes defining nodes. This strictly phylogenetic approach had been applied to phyllostomids before (e.g., Baker et al. 1989; Griffiths 1982), but phylogenetic resolution resulting from those early analyses was poor. The taxonomic comprehensiveness and character-based approach of Wetterer et al. (2000) set a template for subsequent studies of relationships among subfamilies. The taxonomic scope of Wetterer et al. (2000) has guided our phylogenetic review of character-based analyses including multiple phyllostomid subfamilies. Additionally, we focus special attention on those studies introducing new sets of characters since 2000.

In contrast to phylogenetic analyses, most historical biogeographic analyses since 2000 have focused on particular genera with only recent interest in applying biogeographic models to the entire family. Some comprehensive biogeographic analyses tended to include historical signal incidentally, as part of studies of eco-

logical biogeography analyzing diversity gradients and community structures. For these reasons, our biogeographic review has a broader taxonomic and thematic scope, including both genus-level historical biogeography studies and ecological biogeography analyses whose conclusions touch on historical aspects.

To visualize the differences between key phylogenies, we used the *cophylo* routine in the phytools v.0.5–38 R package (Revell 2012). The algorithm uses a matching table to present phylogenies with tips connected despite different input names or topologies. Nodes are then rotated as many times as needed to maximize the correspondence between different phylogenies. These analyses do not substitute for topology tests, which would reveal the statistical significance and source of conflict between resolutions (Dávalos et al. 2012). As these require reanalyses of all data sets, they are beyond the scope of this review.

For biogeographic analyses, we summarized the main findings of individual analyses, emerging common themes, and outstanding questions. Although there is an important body of work on classical phylogeography (Avise 2000) of certain lineages (e.g., Hoffmann and Baker 2001; Hoffmann et al. 2003; Larsen et al. 2007), our focus is on comparative, multi-species approaches. Hence we discuss phylogeographic studies only if they pertain to multiple species (e.g., Hoffmann and Baker 2003).

Results

Phylogenies of family-wide relationships published since the Wetterer et al. (2000) review are summarized in table 6.1. A comparison between the Wetterer et al. (2000) phylogeny and the first multilocus whole-family phylogeny based on DNA sequences by Baker

Table 6.1. Annotated phyllostomid phylogenies published since the comprehensive review by Wetterer et al. (2000)

Data type(s)	Loci	Analytical method	Notes	Source
DNA sequences	*rag2*	Parsimony	Phylogeny only	Baker et al. 2000
DNA sequences	*rag2*, mtr 12S, $tRNA^{val}$, 16S	Bayesian	Phylogeny and systematics	Baker et al. 2003
DNA sequences	*rag2*, mt *cytb*, 12S, $tRNA^{val}$, 16S	Likelihood, Bayesian	Dated phylogeny	Hoffmann et al. 2008
DNA sequences	*brca1*, *pepck*, *rag2*, *vwf*, mt *nd1*, *cox1*, *cytb*, 12S, $tRNA^{val}$, 16S	Parsimony, likelihood, Bayesian	Dated phylogeny	Datzmann et al. 2010
DNA sequences	*rag2*, mt 12S, $tRNA^{val}$, 16S, *cytb*	Likelihood, Bayesian	Dated phylogeny and ancestral traits	Rojas et al. 2011
DNA sequences	mt *cytb*	Bayesian	Dated phylogeny	Agnarsson et al. 2011
DNA sequences on fixed tree	*adra2b, rag1*, *rag2*, *vwf*, mt 12S, $tRNA^{val}$, 16S	Relative-rate fitting	Relative dates	Baker et al. 2012
DNA sequences	*rag2*, mt 12S, $tRNA^{val}$, 16S, *cox1*, *cytb*	Bayesian	Dated phylogeny and diversification	Dumont et al. 2012
DNA sequences, morphological characters	*rag2*, mt 12S, $tRNA^{val}$, 16S, *cox1*, *cytb*	Parsimony, likelihood, Bayesian	Phylogeny and method comparison	Dávalos et al. 2012
DNA sequences	*vwf*, *rag2*, mt genome	Likelihood, Bayesian	Phylogeny only	Botero-Castro et al. 2013
DNA sequences	*rag2*, mt 12S, $tRNA^{val}$, 16S, *cox1*, *cytb*, *nd2*	Bayesian	Dated phylogeny	Yu et al. 2014
DNA sequences, dental characters	*atp7a*, *bdnf*, *plcb4*, *rag2*, *stat5a*, *thy*, mt 12S, $tRNA^{val}$, 16S, *cox1*, *cytb*	Likelihood, Bayesian	Phylogeny only	Dávalos et al. 2014
DNA sequences	*atp7a*, *bdnf*, *plcb4*, *rag2*, *stat5a*, *thy*, mt 12S, $tRNA^{val}$, 16S, *cox1*, *cytb*	Bayesian	Dated phylogeny and selection analyses	Dumont et al. 2014
DNA sequences	*atp7a*, *bdnf*, *plcb4*, *rag2*, *stat5a*, *thy*, mt 12S, $tRNA^{val}$, 16S, *cox1*, *cytb*	Bayesian	Dated phylogeny and diversification	Rojas et al. 2016

Note: Abbreviations in column 1 above are as follows: adra2b, alpha-2B adrenergic receptor; *atp7*, X chromosome ATPase-7A gene; *bdnf*, brain-derived neurotrophic factor gene; *brca1*, breast cancer susceptibility gene 1; cox1, cytochrome oxidase 1 gene; *cytb*, cytochrome b gene; mtr, mitochondrial ribosomal RNAs 12S, $tRNA^{val}$ and 16S; *nd1*, mitochondrial NADH dehydrogenase subunit 1 gene; *nd2*, mitochondrial NADH dehydrogenase subunit 2 gene; *pepck*, phosphoenolpyruvate carboxykinase gene; *plcb4*, phospholipase C beta 4 gene; *rag1*, recombination-activating gene 1; *rag2*, recombination-activating gene 2; *stat5a*, signal transducer and activator of 5A gene; *thy*, thyrotropin beta chain gene; *vwf*, von Willebrand factor gene.

et al. (2003) is shown in figure 6.1. Figure 6.2 compares two multilocus strictly molecular phylogenies (Botero-Castro et al. 2013; Datzmann et al. 2010), while figure 6.3 shows comparisons among recent phylogenies analyzing a combination of DNA sequences and morphological characters or DNA sequences alone (Dávalos et al. 2014; Rojas et al. 2016).

Rojas et al. (2016) provided model-based inferences of phyllostomid biogeography. Those analyses are based on the geographic distribution of extant taxa, fitting with rates for five biogeographic processes: vicariance, anagenetic dispersal, cladogenetic dispersal, founder-event speciation, and speciation in the same area. The rates are estimated based on branch lengths from the dated phylogeny, together with the observed and inferred geographic distribution of tips and nodes. The result is a phylogeny with a probabilistic inference of the geographic range of each node of the tree, summarized in figure 6.4.

Discussion

Shaking Up the Bat Tree

Despite Wetterer et al.'s (2000) search for a fully resolved phylogeny, several phylogenetic challenges persisted. First, support for deep relationships was weak, with <50% bootstrap support for the earliest divergence separating desmodontine vampire bats from other phyllostomids, "Phyllostominae" from its sister taxon, and "Carolliinae" from Stenodermatinae (fig. 6.1). Second, the position of the enigmatic Antillean endemic genus *Brachyphylla* (Silva Taboada and Pine 1969) was unresolved relative to all other phyllosto-

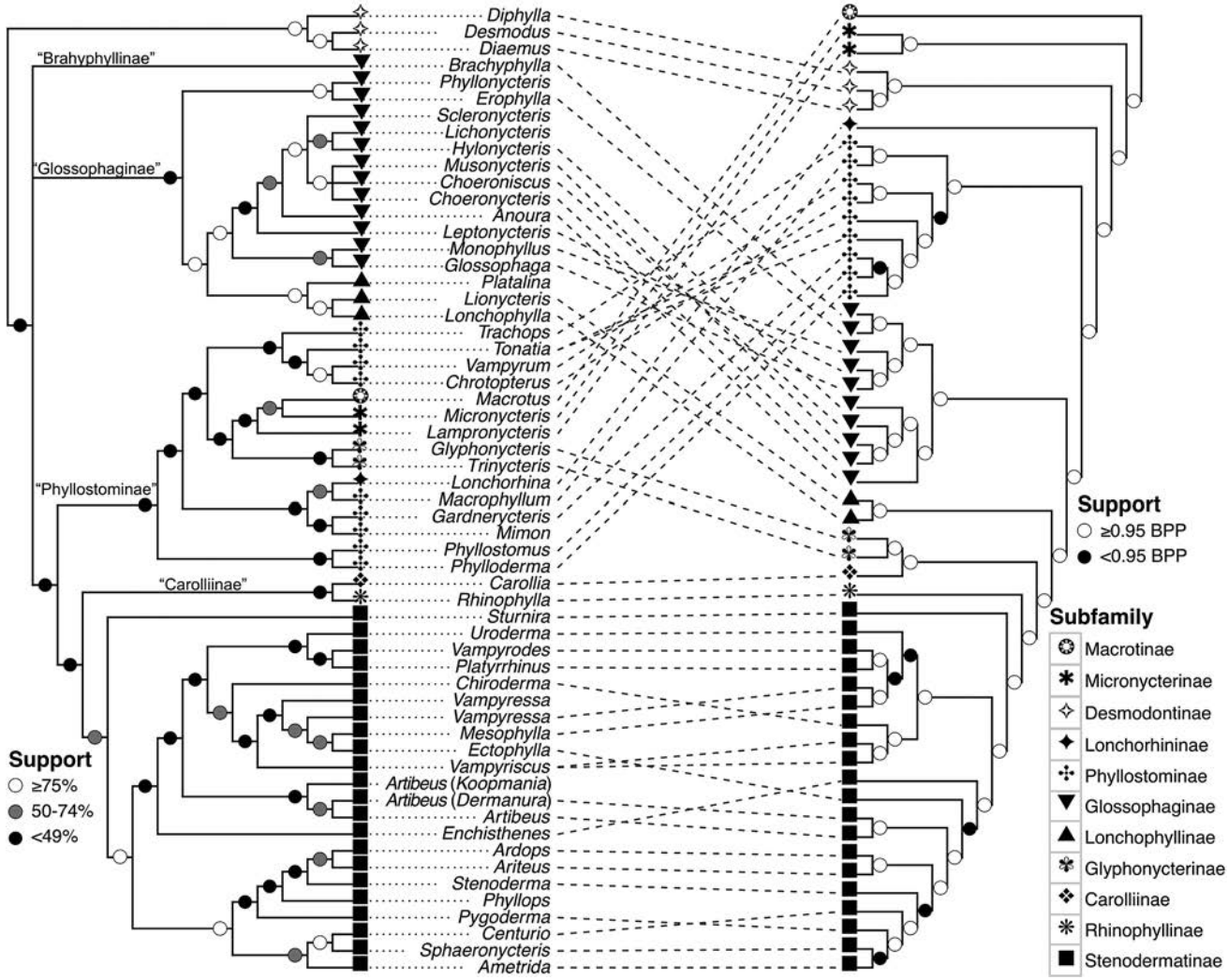

Figure 6.1. Co-phylogeny of the results of Wetterer et al. (2000, fig. 49) (*left*) and Baker et al. (2003, fig. 5) (*right*). Current subfamily classification and genus taxonomy follows Cirranello et al. (2016), former (traditional) subfamily classification is shown in quotations.

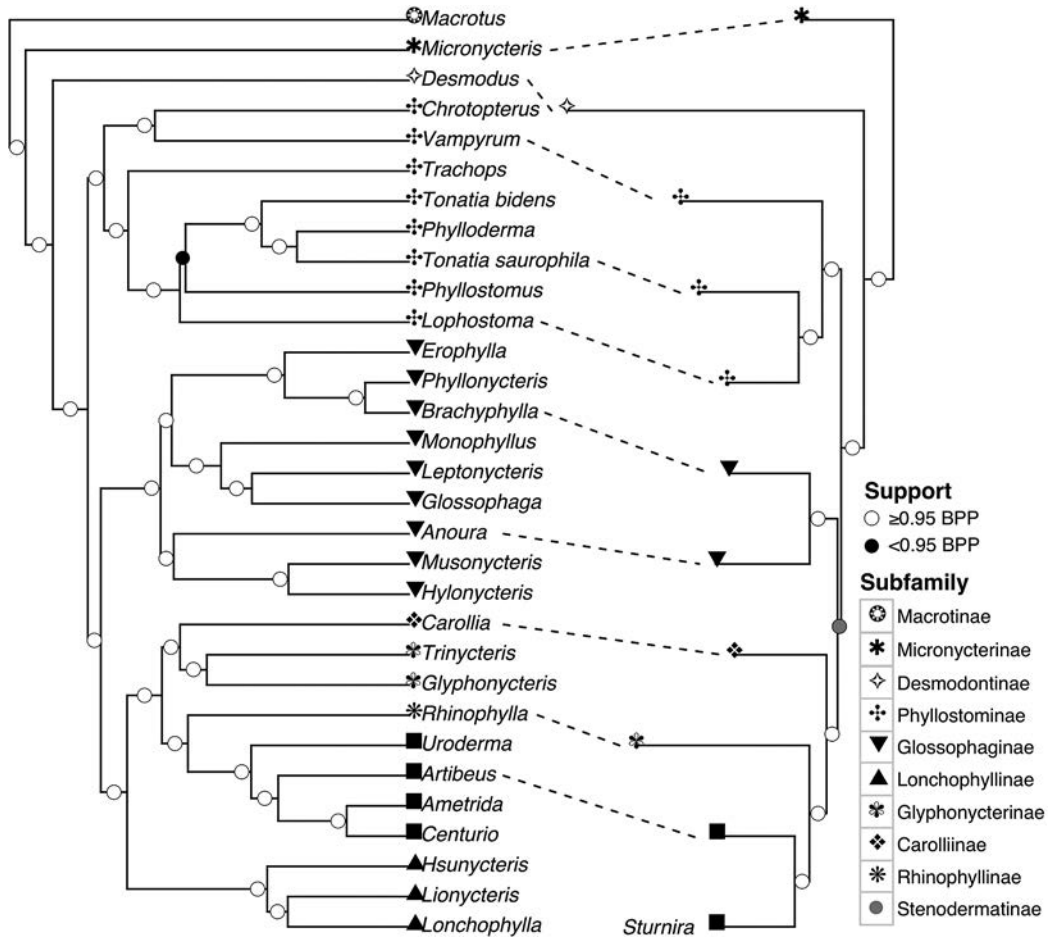

Figure 6.2. Co-phylogeny of the results of Datzmann et al. (2010, fig. 4) (*left*) and Botero-Castro et al. (2013, fig. 2) (*right*). Current subfamily classification and genus taxonomy follows Cirranello et al. (2016).

mids except for desmodontines. Finally, most relationships among genera in the "Phyllostominae" clade were weakly supported, reflecting both the lack of shared derived character states and the conflict in signal from different suites of characters (Dávalos et al. 2012).

Strongly supported clades identified by Wetterer et al. (2000) also posed a challenge for comparative analyses, a subject discussed in the next chapter. With monophyletic clades corresponding to nectarivory ("Glossophaginae"), animalivory ("Phyllostominae"), and soft ("Carolliinae") and hard (Stenodermatinae) fruits specialists, ecological adaptation and phylogeny were perfectly correlated. As a result, comparisons between species accounting for the correlations in residuals arising from shared history lacked statistical power, yielding nonsignificant results (e.g., Cruz-Neto et al. 2001). The exceptions were cases in which many predictions were tested simultaneously, resulting in a series of matches validating an adaptive hypothesis for renal and digestive features (Schondube et al. 2001).

Ultimately, the character analyses of Wetterer et al. (2000) were based on dozens of previous studies compiling mostly phenotypic characters, reflecting the underlying biases of those data sets. The most influential of these are the saturation of character states relative to steps in the phylogeny (Dávalos et al. 2012), a sign of exhaustion in phenotypes that can arise for structural or selective reasons (Wagner 2000; Wake 1991). Another indication of the correspondence between the Wetterer et al. (2000) phylogeny and the many phyllostomid phylogenies from which its characters were drawn is the congruence between the character-based results and the supertree of Jones et al. (2002). Although the analyses of Jones et al. (2002) differ from that of Wetterer et al. (2000), the two phylogenies match in the monophyly of all previously named subfamilies, differing only in the position of *Brachyphylla*, sister to a clade comprising *Phyllonycteris* and *Erophylla* in the supertree (fig. 6.1).

While the single-locus phylogeny of Baker et al. (2000) could be questioned as the result of lineage sorting of ancestral polymorphisms or the result of a

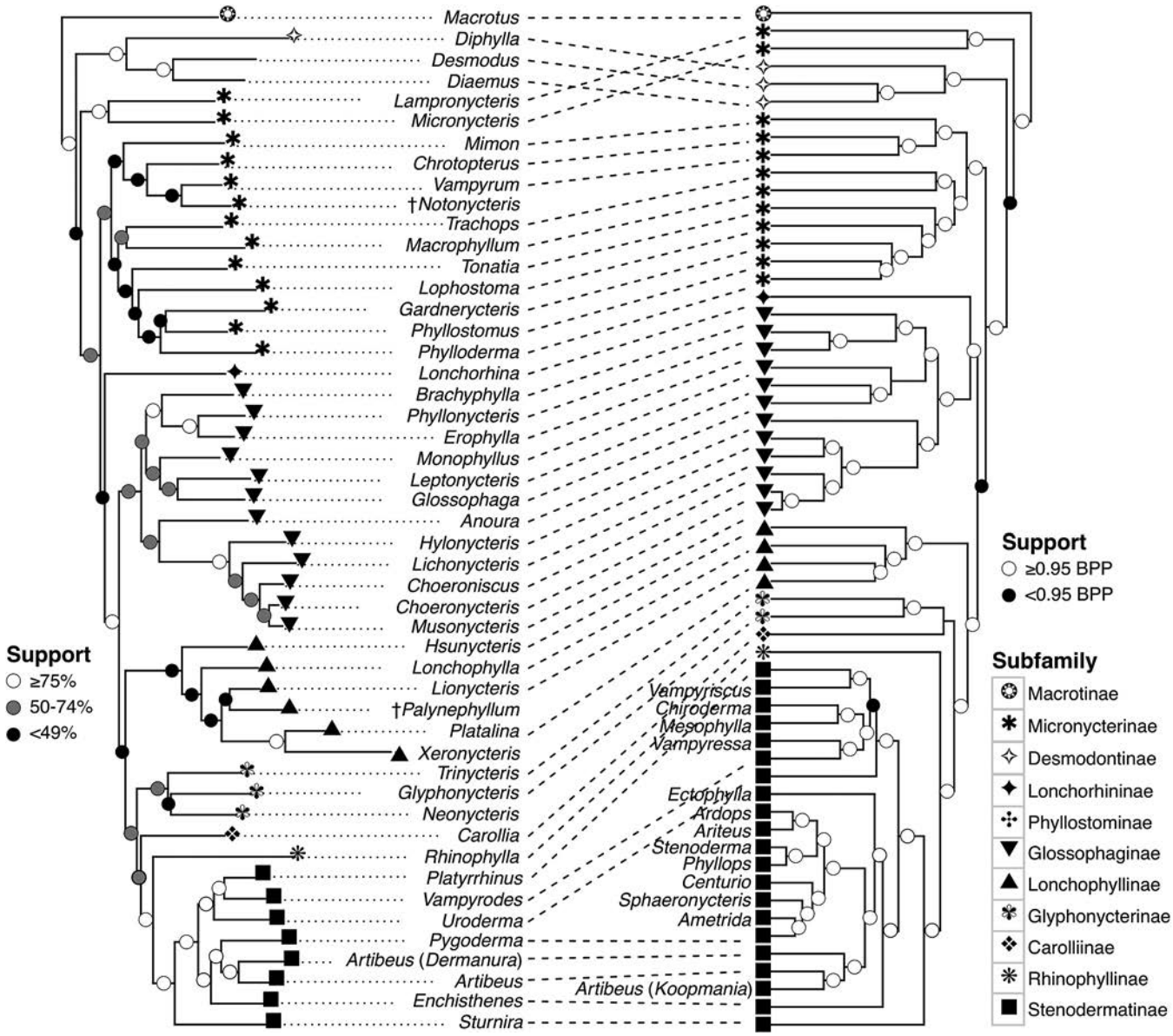

Figure 6.3. Co-phylogeny of the results of Dávalos et al. (2014, fig. S*B*) (*left*) and Rojas et al. (2016, fig. 2) (*right*). Current subfamily classification and genus taxonomy follows Cirranello et al. (2016).

misleading gene tree, these explanations for phylogenetic conflict could no longer hold after the publication of Baker et al. (2003). Using a new Bayesian implementation of models of nucleotide evolution for two loci, RAG2 and the mitochondrial ribosomal RNAs 12S, $tRNA^{val}$, and 16S (mtr), their results confirmed the break-up of "Phyllostominae," "Glossophaginae," and "Carolliinae" and resolved the early phyllostomid divergences with posterior probabilities close to 1 (≥0.95, fig. 6.1). Many of the most important changes to the phyllostomid phylogeny first introduced by Baker et al. (2000) were confirmed including *Macrotus* as the earliest-diverging extant branch of phyllostomids, polyphyly of "Phyllostominae," polyphyly of "*Micronycteris*," paraphyly of "Glossophaginae," paraphyly of "Carollinae," and the sister relationship between *Carollia* and Glyphonycterinae (*Glyphonycteris* and *Trinycteris*). One of the puzzling results from the earlier gene tree was dispelled, separating *Lonchorhina* as its own separate subfamily (fig. 6.1). Except for the stable Desmodontinae and Stenodermatinae, formerly monophyletic subfamilies with similar feeding ecologies were revealed to be collections of distant relatives united by ecologically convergent phenotypes.

The Baker et al. (2003) phylogeny represents a turning point in the phylogenetics and systematics of

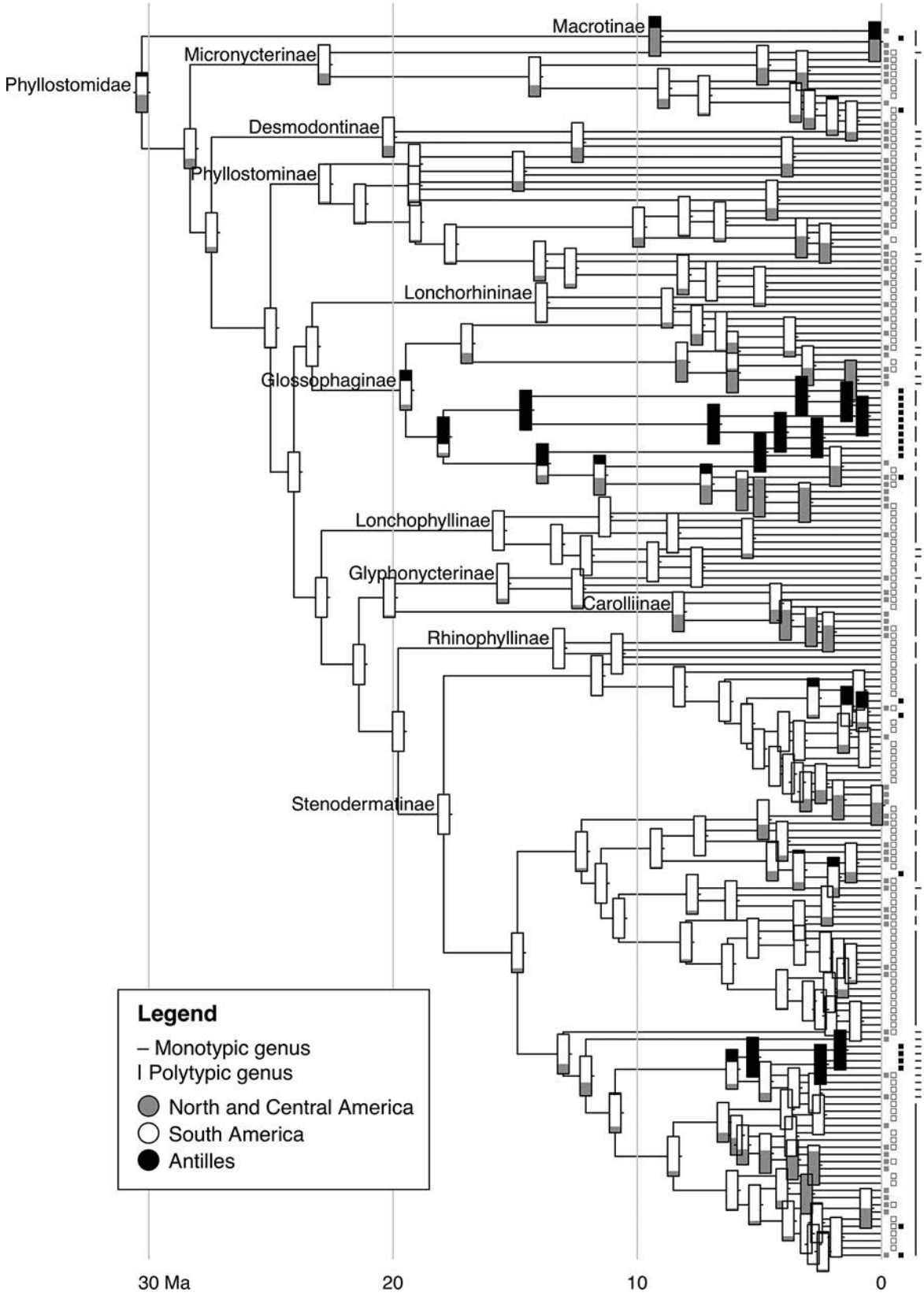

Figure 6.4. Historical biogeography of phyllostomids inferred by applying the best-fit model of dispersal-extinction-cladogenesis and jump speciation (Matzke 2013) on the dated phylogeny of Rojas et al. (2016). Subfamilies are shown along the branch defining the most recent common ancestor.

the family. Before that phylogeny, the traditional subfamily designations could be applied and the phylogeny might still uphold traditionally recognized subfamilies. After it, successive efforts to include new characters (e.g., Datzmann et al. 2010), or other lineages (e.g., Dávalos et al. 2014), left the contours of the phyllostomid phylogeny largely unchanged (figs. 6.2 and 6.3). These unchanging contours include the confirmation of Desmodontinae and Stenodermatinae as the only two monophyletic subfamilies inferred from both morphological data and DNA sequences (fig. 6.1); the separation of primarily nectar-feeding bats into the subfamilies Glossophaginae and Lonchophyllinae; the break-up of primarily insectivorous and carnivorous genera into the subfamilies Macrotinae, Micronycterinae, Lonchorhininae, Phyllostominae, and Glyphonycterinae; and the division of *Piper* and similar fruit specialists into the subfamilies Carolliinae and Rhinophyllinae (Cirranello et al. 2016).

Datzmann et al. (2010), in particular, helped strengthen support for the new phyllostomid phylogeny. In addition to the two loci used by Baker et al. (2003) and the published sequences encoding the mitochondrial cytochrome b *cytb* and cytochrome oxidase I *coi* genes, Datzmann et al. (2010) collected data for four other autosomal loci from fragments of the von Willebrand factor gene *vwf*, the breast cancer susceptibility gene 1 *brca1*, the 3′ untranslated region of the phospholipase C beta 4 gene *plcb4*, and an intron of the phosphoenolpyruvate carboxykinase gene *pepck*, as well as the mitochondrial NADH dehydrogenase subunit 1 gene *nd1* and its adjacent $tRNA^{leu}$. With its focus on establishing relationships among nectarivorous lineages, the Datzmann et al. (2010) phylogeny also corroborated the sister relationship between a clade formed by *Brachyphylla* and *Erophylla*, and *Glossophaga*, *Leptonycteris* and *Monophyllus* (figs. 6.1 and 6.2), and the paraphyly of *Lonchophylla*, which had previously been reported based on the mitochondrial *cytochrome b* (*cytb*) gene tree (Dávalos and Jansa 2004). A paraphyletic *Tonatia* (fig. 6.2) is an uncorroborated result from Datzmann et al. (2010), as no subsequent study has inferred similar relationships despite including multiple *Tonatia* species (Dávalos et al. 2014). Outside of this single node, the relationships among subfamilies obtained in the multilocus analyses have been supported in subsequent analyses.

The first genomic analysis by Botero-Castro et al. (2013) is similarly important in consolidating the new molecular phylogeny of phyllostomids (fig. 6.2). Based on the entire mitochondrial genome and applying second-generation sequencing techniques, the new data confirmed the subfamily relationships of Baker et al. (2003), while highlighting the relatively short internode uniting glossophagines, *Carollia*, *Rhinophylla* and stenodermatines, and separating that clade from phyllostomines (fig. 6.2). Despite >16 kb of mitochondrial DNA and 2.6 kb of the *rag2* and *vwf* genes, this branch was only moderately supported with a posterior probability of 0.91 and maximum likelihood bootstrap of 76%. This result highlighted the difficulties in resolving a few ancient phyllostomid nodes, analyzed in depth by Dávalos et al. (2012) and discussed in the next chapter.

Besides collecting new data, the Datzmann et al. (2010) analyses also applied relaxed molecular clock models to estimate divergence times among lineages. The relaxed clocks were calibrated at three nodes based on fossil phyllostomids from the Middle Miocene of La Venta in Colombia (Czaplewski et al. 2003) and a mormoopid fossil from the Early Oligocene of Florida and by constraining the divergence between Vespertilionidae and Molossidae. Applying relaxed molecular clocks with branch-specific rates of evolution drawn from an uncorrelated lognormal prior distribution and fitted to the entire alignment (Drummond et al. 2006), those analyses inferred substantially older divergence dates than alternative methods. For example, the divergence date between the vampire bats (Desmodontinae) and their sister group was estimated at 32 Ma (95% high probability density = 28, 36), while previous estimates using the Thorne and Kishino (2002) model of uncorrelated rates across loci estimated this divergence at 26 Ma (95% high probability density = 21, 30) (Teeling et al. 2005). Applying a rate-smoothing method to obtain branch- and partition-specific rates from "absolute" dates at constrained nodes (Bininda-Emonds 2007), the same node corresponds to 26 Ma (95% confidence interval = 21–31) (Baker et al. 2012). The disparate results suggest modeling different genes or partitions by drawing their rates from different distributions accommodates the between-gene variance in rates and reduces estimates of divergence times. Considering the much faster rates of change at mitochondrial loci, ensuring a sufficiently large variance in rates among loci is indispensable for dating future phylogenies.

While the analyses of Datzmann et al. (2010) and Botero-Castro et al. (2013) focused on expanding the sequence data available to infer phyllostomid phylogeny, only two analyses introduced new morphological characters (Dávalos et al. 2012, 2014). The challenges of combining DNA sequences and morphological characters in phyllostomid phylogeny had been analyzed in depth before by using likelihood-based statistical analyses to compare the phylogenies and data of Wetterer et al. (2000) and Baker et al. (2003) (fig. 6.1). Briefly, excluding morphological characters for which there is evidence of convergent evolution reduced conflict between the results of Wetterer et al. (2000) and those of Baker et al. (2003) and produced better-supported phylogenies combining both character types (Dávalos et al. 2012). Based on that insight, and aiming to adequately model the statistical behavior of morphological characters, Dávalos et al. (2014) investigated both rates of change and patterns of correlated change in character state in the dental data. The morphological rate of change was higher than the median substitution rate of DNA sequences by an order of magnitude. Coupled with evidence of character-state exhaustion or saturation and evidence for excess correlated changes in the dental data, the results implied the need to model the high rate of change and exclude characters for which convergence could be demonstrated. Dávalos et al. (2014) then developed two new methods to combine characters: one constraining morphological analyses based on the posterior sample of molecular trees and the other by identifying and excluding morphological characters significantly supporting ecologically convergent nodes. Results from the latter approach are in line with previous DNA-based phylogenies and, therefore, are in conflict with phylogenies based exclusively on morphological characters (fig. 6.3).

The Dávalos et al. (2014) phylogenies were the first to include the La Venta Miocene fossils using characters from multiple subfamilies. The results confirmed the close relationship between *Notonycteris* and *Vampyrum* (Czaplewski et al. 2003) and placed *Palynephyllum* within the Lonchophyllinae (fig. 6.3). These analyses of the Miocene fossils provide the first data sets for applying tip dating methods to the phyllostomid phylogeny (e.g., Herrera and Dávalos 2016). Until now, all dating analyses have relied on node dating methods (table 6.1), constraining particular nodes based on taxonomy or presumed phylogenetic placement, but without including fossil taxa as tips or fitting models of evolution to morphological characters (Heath et al. 2014; Ronquist et al. 2012). Thus, tip dating remains an unexplored frontier in estimates of the phyllostomid tree.

In addition to dental characters, Dávalos et al. (2014) introduced new markers for resolving the phyllostomid phylogeny, including introns in the thyrotropin beta chain gene or *thy* and the signal transducer and activator of 5A gene or *stat5a*, as well as the autosomal exons brain-derived neurotrophic factor or *bdnf*, titin 6 or *ttn6*, and the X chromosome exon ATPase-7A or *atp7a*. The resulting phylogenies were similar to previous molecular analyses in defining new subfamilies but changed the positions of Micronycterinae and Lonchorhininae relative to other lineages (cf. figs. 6.2 and 6.3). The low support for defining the placement of Micronycterinae is also evident in the difference between the undated phylogeny of Dávalos et al. (2014) and the relaxed molecular clock, node-dated phylogeny of Rojas et al. (2016).

Although based on the same set of markers, Rojas et al. (2016) expanded taxonomic sampling using both new and published sequences and specifically set out to evaluate rates of taxonomic diversification across the phylogeny. Rojas et al. (2016) was the first to apply Bayesian mixture models of diversification to phyllostomids and close relatives, confirming Stenodermatinae as the clade with the highest rates of diversification both among phyllostomids (Dumont et al. 2012) and across all bats (Shi and Rabosky 2015). This well-corroborated result raises the question, discussed in detail in the next chapter, of what traits differentiate stenodermatines from other phyllostomids and how these traits might contribute to their elevated rates of diversification.

Historical Biogeography

Although several analyses with biogeographic implications (e.g., Stevens 2006), as well as historical biogeographic analyses of genera or certain groups had been published before (e.g., Velazco and Patterson 2013), the first comprehensive historical biogeographic analyses of phyllostomids were conducted by Rojas et al. (2016). There are three sets of results relevant to biogeography. First, Rojas et al. (2016) evaluated if Quaternary climate change disproportionately contributed to speciation across the radiation. The Pleistocene refugia hypothesis

has often been invoked to explain the diversity of species in the lowland forests of the Amazon (e.g., Haffer 1969; Hooghiemstra and van der Hammen 1998, but see Colinvaux et al. 2000; Lessa et al. 2003), where phyllostomids reach their highest richness. Since its inception, the refugia hypothesis has been extended to all Neotropical lowland forests, including the Brazilian Atlantic forests and the forests of Mesoamerica (Carnaval and Moritz 2008; Willis and Whittaker 2000). Unsurprisingly, studies of phyllostomid biogeography have applied this general framework to explain divergences, finding some genetic evidence for geographic structuring within species linked to such refugia for *Desmodus* in the Atlantic forests and the Pantanal (Martins et al. 2009), *Chrotopterus* in the Amazon (Clare 2011), and *Carollia brevicauda* and *Artibeus obscurus*, both in Brazil (Ferreira et al. 2014; Pavan et al. 2011). In contrast, no such patterns were obtained in earlier surveys of genetic diversity in the Atlantic forest for *Artibeus lituratus*, *Carollia perspicillata*, *Sturnira lilium*, or *Glossophaga soricina* (Ditchfield 2000), as well as Amazonian populations of *Desmodus*, *Micronycteris megalotis*, *Trachops*, *Uroderma bilobatum*, and small *Platyrrhinus* species (Clare 2011).

Nevertheless, testing Quaternary glacial refugia as centers of speciation requires examining both the pattern of geographic structure and the timing for divergence. To this end, Rojas et al. (2016) estimated divergence times between sister species. If Quaternary climate change had played a role in isolating populations ultimately resulting in speciation, then divergence times between sister species should cluster during this period. Analyses of speciation events did not support a Quaternary origin for the extant diversity of phyllostomids and, instead, indicated most of the sister species diverged much earlier. Additionally, because the number of divergence events across a phylogeny depends on the number of branches present at a given time, an excess of divergences between sister species (e.g., Garzón-Orduña et al. 2014) is not enough to demonstrate that a particular period disproportionately contributed to speciation. Therefore, Rojas et al. (2016) analyzed diversification rates, or the net difference between speciation and extinction rates, across the phylogeny. If the Quaternary disproportionately contributed to speciation and background extinction rates had remained more or less constant, this period would show elevated diversification rates compared to previous eras. This prediction was refuted. Instead, the largest change in diversification rates occurred in the ancestor to Stenodermatinae and was not concentrated in any particular period. In short, predictions from the hypothesis that Quaternary climate change played a substantial role in generating species-level diversity across phyllostomids were rejected.

The second contribution to the historical biogeography of phyllostomids by Rojas et al. (2016) is the model-based inference of ancestral areas for the entire family (fig. 6.4). Unlike earlier biogeographic analyses (e.g., Dávalos 2010), which tended to rely on equating areas with characters and optimizing using phylogenies, probabilistic model-based analyses explicitly include biogeographic processes that have no equivalent in character analyses and that account for branch lengths contributing to the probability of biogeographic events (Matzke 2013). Using one recently developed method called BioGeoBEARS, Rojas et al. (2016) encoded the three large and distinct areas of North and Central America, South America, and the Antilles. These analyses inferred South America as the ancestral area of most phyllostomid subfamilies (fig.6.4).

Although these analyses were not designed to differentiate among habitats or between tropical and subtropical regions within continents, the South American—and specifically tropical Andean or lowland forest—origin of most subfamilies contributes to the latitudinal gradient of diversity in phyllostomids (Stevens 2006). Two historical mechanisms were proposed to explain the gradient: tropical niche conservatism and time for speciation (Stevens 2011). In the former, the high heritability of climate niche traits leads to speciation in areas with similar climate, with reduced dispersal to, and species accumulation in, climatically distinct areas resulting in fewer, shallower lineages (Buckley et al. 2010). Time for speciation, in contrast, results from the greater species accumulation in older areas (Wiens et al. 2006). Predictions for each of these mechanisms can only be distinguished by separating spatial and hence biogeographic gradients from climate/environmental variation. Unfortunately, biogeographic and climate variation within the range of phyllostomids is confounded, leading to inconclusive results and only a slight explanatory advantage for niche conservatism in regressions of phylogenetic characteristics as a function of spatial and environmental variables (Ramos Pereira and Palmeirim 2013; Stevens 2011).

Analyses of latitudinal gradients sometimes include

phylogenetic characteristics (e.g., branch lengths, genus to species ratios) (Arita et al. 2014; Ramos Pereira and Palmeirim 2013; Stevens 2006, 2011), without fully integrating the phylogeny. By directly integrating phylogenies with patterns of species coexistence, Villalobos et al. (2013) found support for the niche conservatism hypothesis to explain the phyllostomid diversity gradient. The disproportionate coexistence of phyllostomid species with close relatives across multiple phylogenetic scales is consistent with environmental niche conservation within the radiation. The gradient itself would result from the combination of conserved climate preferences coupled with higher speciation rates in the area of origin (Villalobos et al. 2013), although these rates were not modeled. Diversification analyses by Rojas et al. (2016) support the conclusions of Stevens (2011) and Villalobos et al. (2013) because increased speciation or decreased extinction rates are concentrated in stenodermatines, whose climate niche—along with biotic preferences—appear to be highly conserved (Dumont et al. 2014).

While South America has been the main center of diversification for most phyllostomids, North and Central America were both important for a few early divergences, as well as more recent divergences within subfamilies (fig. 6.4). The first finding is consistent with fossils showing early noctilinonoids (Czaplewski and Morgan 2012), as well as an undescribed mormoopid (Morgan and Czaplewski 2012) from the Oligocene of Florida. Oligocene fossils in North America suggest that the ancestors of the family were present on this continent early on, well before any fossils found in South America (where the earliest findings correspond to the Miocene). The hypothesis of an early North American divergence or origin including both sets of Tertiary fossils, however, remains to be tested using model-based biogeographic methods. Additionally, the within-subfamily divergences are in line with analyses by Arita et al. (2014) who, based on latitudinal patterns of endemism and diversity across genera, identified the two continental landmasses as independent centers of diversification for phyllostomids. Additionally, Arita et al. (2014) proposed the absence of continuous desert and tropical dry forest habitats from Central America since the Miocene as the main ecological factor preventing *Macrotus*, *Choeronycteris*, and *Musonycteris* (but not *Leptonycteris*) from reaching South America from the north and the lonchophyllines *Dryadonycteris*, *Platalina*, and *Xeronycteris* from reaching Central and North America from the south. This distinctly historical hypothesis also needs to be tested, for example, by combining phyllostomid phylogenies with inferred ancestral climate niche envelopes in phyloclimatic analyses (e.g., Yesson and Culham 2006).

The third important set of findings on phyllostomid biogeography from Rojas et al. (2016) centers on the role of the Antilles in the history of the clade. The descendants of the most recent common ancestor of *Glossophaga* and *Brachyphylla* (tribes Glossophagini and Brachyphyllini (Cirranello et al. 2016), along with the short-faced bats or Stenodermatina, have proposed origins in the Caribbean islands with subsequent colonization of the continent (Dávalos 2007, 2010). The biogeographic models supported reverse colonization only for the glossophagines (fig. 6.4), and not for the short-faced bats. This rejection of the Caribbean-origin hypothesis for short-faced bats, however, remains to be tested by including *Cubanycteris*, an extinct species from Cuba whose primitive morphology suggests it is an early branch in the subtribe (Mancina and Garcia-Rivera 2005), in character-based analyses and subsequent biogeographic models. Finally, dating analyses also supported a potential role for Miocene sea-level changes in facilitating colonization to and from the Antilles (Rojas et al. 2016).

Within phyllostomids, the historical biogeography of only four of the more than 50 phyllostomid genera has been analyzed to date (*Carollia*, *Platyrrhinus*, *Sturnira*, and *Uroderma*), all but one member of the subfamily Stenodermatinae (Cuadrado-Ríos and Mantilla-Meluk 2016; Hoffmann and Baker 2001; Velazco and Patterson 2008, 2013; table 6.2). But these genera are not all equally diverse. With 21 species each, *Platyrrhinus* and *Sturnira* are two of the most diverse phyllostomid genera, contributing to the high diversity of stenodermatines, with five species analyzed for *Carollia* (Hoffmann and Baker 2003), and the most liberal estimates of *Uroderma* diversity include only five species (Cuadrado-Ríos and Mantilla-Meluk 2016). Analyses of the only genus outside the subfamily Stenodermatinae, *Carollia*, included three species distributed in both Central and South America and two Central American endemics (Hoffmann and Baker 2003). Three biogeographic patterns were identified: (1) genetic continuity between the Chocó biodiversity hotspot west of the Andes in northern South America and Central America,

Table 6.2. Annotated historical biogeography analyses including phyllostomids.

Biogeographic method	Taxonomic scope	Source
Comparative phylogeography	*Carollia*	Hoffmann and Baker 2003
Reconciled area analyses	Caribbean mammals	Dávalos 2004
Polynomial regressions of richness, divergence, variance of divergence, clade age, and variance of clade age as functions of latitudinal gradient	Phyllostomidae	Stevens 2006
Shimodaira-Hasegawa tests of alternative phylogenies	Stenodermatina	Dávalos 2007
Regressions of richness against environmental variables	Lonchophyllinae	Mantilla-Meluk 2007
Dispersal-vicariance analysis, Lagrange	*Platyrrhinus*	Velazco and Patterson 2008
Analyses of assemblage composition and nestedness as functions of island characteristics	Caribbean chiroptera	Presley and Willig 2008
Parsimony optimizations of geographic distributions	Caribbean chiroptera	Dávalos 2010
Phylogenetic regressions	New World Noctilionoidea	Rojas et al. 2012
Generalized additive models of mean root distance as a function of latitude	New World chiroptera	Ramos Pereira and Palmeirim 2013
Dispersal-vicariance analyses, Lagrange	*Sturnira*	Velazco and Patterson 2013
Phylogenetic species variability, phylogenetic species clustering	Phyllostomidae	Villalobos et al. 2013
Phylogenetic distance, phylogenetic species variability, phylogenetic species clustering, and covariation among these	New World Noctilionoidea	Stevens and Tello 2014
Species/genus ratios, latitudinal richness analyses	New World chiroptera	Arita et al. 2014
Likelihood model comparisons	New World Noctilionoidea	Rojas et al. 2016
Dispersal-vicariance analysis and Bayesian binary MCMC method	*Uroderma*	Cuadrado-Ríos and Mantilla-Meluk 2016

(2) deep divergences within Amazonian populations of *brevicauda* and *castanea*, and (3) a very recent expansion of *perspicillata* and *sowelli* into the northwesternmost extent of the range in Yucatán. The similarities in faunas west of the Andes extending north into Central America was originally highlighted for birds (Chapman 1917; Haffer 1967), but few studies with bats have highlighted it, especially within species. The remaining patterns remain to be tested more generally, both in Amazonia and Mesoamerica.

The broad distribution of *Platyrrhinus* and *Sturnira* and radiation into a range of Neotropical biomes makes them great examples for testing biogeographic mechanisms at much finer scales. Current *Platyrrhinus* and *Sturnira* phylogenies include both mitochondrial and nuclear sequences (the mitochondrial *cytb*, NADH dehydrogenase subunit 2 *nd2* genes and the D-loop regulatory region and the nuclear *rag2* for both genera, and the recombination-activating protein 1 *rag1* for *Sturnira*), reducing the probability of inferring particular resolutions based on a single gene tree.

By defining several biogeographic areas within continents, analyses for both *Platyrrhinus* and *Sturnira* were able to test biogeographic hypotheses within South America (Velazco and Patterson 2008, 2013), and not just at the continental scale. Velazco and Patterson (2008) inferred the Brazilian Shield as the biogeographic area of origin for *Platyrrhinus* by applying model-based biogeographic analyses of dispersal, local extinction, and cladogenesis using Lagrange (Ree and Smith 2008). Ancestors of multiple species dispersed from the area of origin to the Amazon lowlands (most recent common ancestor of *P. brachycephalus* and *P. matapalensis*) and to the Andes (most recent common ancestor *P. albericoi* and *P. infuscus*), giving rise to the current distribution of species concentrated in the Andes. Individual lineages dispersed from the Andes to the Chocó or Pacific lowlands and then to Central America, explaining the distribution of *P. helleri*. Finally, dispersal from the Amazon to the Guianan Shield would be responsible for the widespread distribution of *P. aurarius* and *P. infuscus*. In summary, the results support dispersal as the primary biogeographic mechanism leading to the present-day distribution of *Platyrrhinus*

and suggest that the Andes have been crucial for the diversification of the group, as was first proposed by Karl Koopman based on distributional analyses (Koopman 1978). This finding is also in line with previous studies for birds (Smith et al. 2014; Weir 2006), amphibians (Santos et al. 2009), and clearwing butterflies (Elias et al. 2009).

Velazco and Patterson (2013) applied the dispersal, local extinction, and cladogenesis model to infer the biogeographic history of *Sturnira*, crucially including endemic Antillean species. In contrast to *Platyrrhinus* and its colonization of the Andes, earliest-diverging lineages of *Sturnira* have exclusively Andean distributions, inferring the Andes as the area of origin for the genus. From the Andes, *Sturnira* lineages repeatedly dispersed to the Chocó and then to Central America. A single lineage dispersed to the Lesser Antilles and could have originated in one of several areas in northern South America (Chocó, northern Andes, or Caribbean lowlands). The timing of these events illuminates the links between earth history and the biogeography of phyllostomids. Dispersal into Central America followed the closing of the Isthmus of Panama, contributing to the Great American Biotic Interchange (GABI), a biogeographic mechanism first proposed by A. R. Wallace himself (Wallace 1876a, 1876b), with paleontological evidence accumulating throughout the twentieth century (Marshall 1988; Simpson 1980). More recent analyses grounded on phylogenetics have shown that *Sturnira* bats joined birds (Weir et al. 2009) and didelphid marsupials (Jansa et al. 2014) in the unusual south-to-north colonization associated with GABI. Arita et al. (2014) highlighted the main ecological factor contributing to GABI dispersal for *Sturnira* as well as for other frugivorous phyllostomids: continuous corridors of tropical wet forests connecting South America to southern Mexico. Similarly, the colonization of the Antilles dates to the Pleistocene (Velazco and Patterson 2013), when glaciations exposed large banks linking Grenada to Saint Vincent (Dávalos and Turvey 2012), facilitating dispersal from northern South America. Compared to dispersal to Central America or the Antilles, out-of-the-Andes dispersal to other regions of South America has been the norm, giving rise to sympatric assemblages of both early and recently diverging species in the Andes.

Phylogenetic analyses for *Uroderma* have been restricted to sequences of the mitochondrial *cytb* originally published by Hoffmann et al. (2003) to uncover the genetic diversity and divergence between chromosomal races in the genus. Given the known history of secondary hybridization in populations of *Uroderma bilobatum* (Baker 1981; Greenbaum 1981), using this exclusively matrilineal marker has the potential to produce a gene tree discordant with the species tree because of introgression. Nevertheless, Cuadrado-Ríos and Mantilla-Meluk (2016) used this best estimate of phylogeny to infer its biogeographic history by applying a statistical implementation of dispersal-vicariance analysis (Yu et al. 2015). As dispersal-vicariance analysis imposes no cost for vicariance (Ronquist 1997) and as no constraint was placed on the number of areas inferred for any node, all early nodes were inferred to be composites of multiple and sometimes discontinuous areas. Despite methodological challenges, a general pattern is evident in the biogeographic history of *Uroderma*. Both the Central Andes and Central America played important roles in the diversification of the genus since first emerging in the Miocene, with the northern Andes acting as a link between these two regions but not as a center of diversification.

Conclusions

Phylogenies based on molecular markers have the upended traditional understanding of evolutionary relationships among phyllostomids, and current phylogenies—whether based on several independent loci or entire mitochondrial genomes—differ from the original analyses of two loci by Baker et al. (2003) only in minor details. Although the monophyly of subfamilies is now settled, relationships among subfamilies—in particular, the phylogenetic positions of Micronycterinae relative to Desmodontinae (fig. 6.3)—and Lonchorhininae (cf. figs. 6.1 and 6.3) remain outstanding. Likewise, while phyllostomid Miocene fossils have been included in character-based analyses (fig. 6.3), support for those relationships is low, and future analyses should benefit from including several Oligocene close relatives of phyllostomids (Czaplewski and Morgan 2012; Morgan and Czaplewski 2012). Relaxed clock analyses accounting for the instability of the nodes offer a potential route forward (e.g., Herrera and Dávalos 2016) but have yet to be implemented, despite the publication of several new data sets (table 6.1).

Biogeographic analyses for the entire family have

rejected Quaternary glaciations as a primary species pump and have demonstrated many instances of dispersal at a continental scale (fig. 6.4). But analyses of individual genera have uncovered critical ecological factors necessary for both cladogenesis and dispersal, such as the continuity of habitats across continents, and have revealed direct connections between biogeographic events and earth history. The three genera analyzed to date have demonstrated the crucial role of the Andes in phyllostomid cladogenesis, as well as the importance of lowland rainforests in the long-term diversity of these stenodermatines. As family-wide analyses are forced to examine only large biogeographic regions, it is essential to extend genus or subfamily analyses to other clades to test these emerging patterns across the whole radiation. Much work remains to be completed to understand the historical biogeography of phyllostomids and the relative importance of geoclimatic events relative to adaptations to particular climatic niches in this family.

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