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Fossils, Molecules and Morphology

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Chapter

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11

Molecular time scale of diversification of feeding strategy and morphology in New World Leaf-Nosed Bats (Phyllostomidae): a phylogenetic perspective

ROBERT J. BAKER, OLAF R. P. BININDA-EMONDS, HUGO MANTILLA-MELUK, CALVIN A. PORTER AND RONALD A. VAN DEN BUSSCHE

11.1 Introduction

Diversification of feeding strategies within each of the 19 chiropteran families (Hoofer and Van Den Bussche, 2003; Van Den Bussche and Hoofer, 2004; Simmons, 2005) typically is limited to one (13 families) or two (five families) food sources. The family Phyllostomidae, however, represents an exception to this pattern with six distinct feeding strategies: sanguivory, insectivory, frugivory, nectivory, carnivory (feeding on vertebrates) and omnivory.

Among families of bats, phyllostomids comprise the largest number of genera (56) and the third largest number of species (160+) (Simmons, 2005). They are distributed throughout tropical and subtropical regions of North and South America and have been highly successful in exploiting a diverse array of life-history strategies. Included among its members are three species of obligate sanguivores, a feeding strategy unknown in vertebrates other than fish (Figure 11.1). Among phyllostomids additional examples of feeding specialization exist, including subsisting exclusively on insects, as well as primarily on fruit, nectar, frogs, rodents and other vertebrates. Such specializations are remarkable when viewed in the context of the concomitant suite of adaptations associated with the sensory apparatus, locomotion, digestion, dentition, kidney function and reproduction, among others (Griffiths, 1982; Greenhall and Schmidt, 1988: Fleming *et al.*, 2005) that must be favored by directional natural selection for successful exploitation of new ecological opportunities. No other clade of mammals with roots in the Eocene displays such radical evolutionary modifications.

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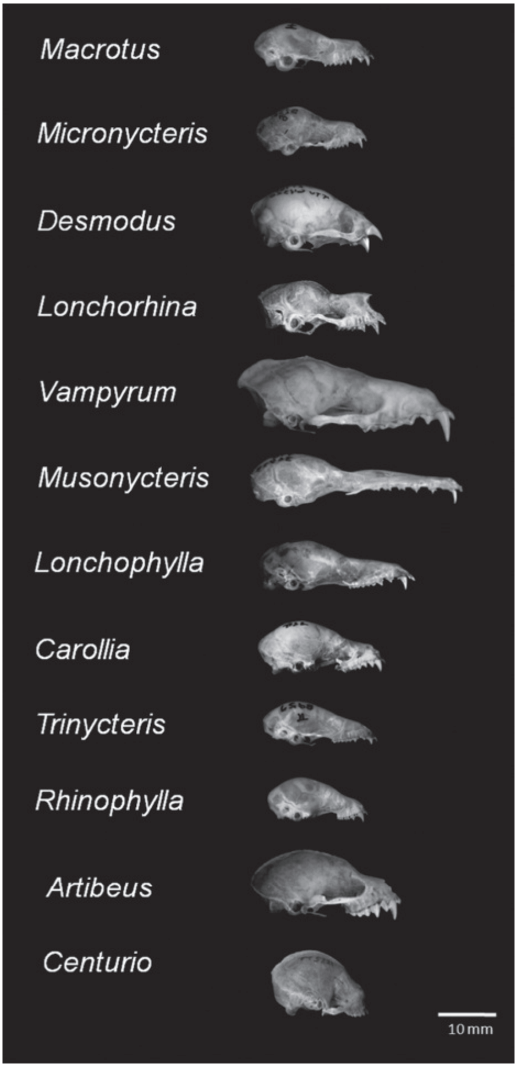

Figure 11.1 Crania of 12 genera representing the 11 subfamilies of Phyllostomidae (see Baker *et al.*, 2003). Shape and morphology of crania provide a perspective of the magnitude of variation present in this family. *Macrotus, Micronycteris, Lonchorhina* and *Trinycteris* are primarily insectivores, but take some fruit. *Desmodus* feeds on blood. *Phyllostomus* and *Carollia* are omnivores and primarily eat fruit, but also insects and nectar. *Musonycteris* and *Lonchophylla* are primarily nectivores; *Rhinophylla* and *Artibeus* are primarily frugivores, but take some insects; *Centurio* is an obligate frugivore.

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Understanding the inter-relationships of genomics, ecosystem dynamics, and morphological and physiological adaptation associated with different feeding strategies in phyllostomid bats has implications to furthering our understanding of the mode and tempo of the evolution of adaptive radiation. For example, there has been a series of proposals on the genetic mechanisms that drive morphological and physiological change. Proposed mechanisms (modified from Sutter *et al.*, 2007) include demographic features producing inbreeding resulting in fixation of chromosomal rearrangements (Wilson *et al.*, 1975); mobile DNA altering gene expression patterns (Pascale *et al.*, 1993; Furano *et al.*, 1994); increased recombination or mutation rates (Thompson, 1917; Eldredge and Gould, 1972; Wilson *et al.*, 1974); a unique role of short repeat loci near genes (Eldredge and Gould, 1972); expansion of specific interspersed nuclear elements (Carroll, 2000); timing variation in regulatory genes (Kirschner and Gerhart, 1998; Wren *et al.*, 2000); readily altered developmental programs (Darwin, 1859; Kirschner and Gerhart, 1998); gene duplication (Kawasaki *et al.*, 2007; Ohno *et al.*, 1968); gene recruitment to new tissues/cell expression sites (Phillips *et al.*, 1993); gene sharing (Phillips *et al.*, 1993; Phillips, 1996). This research focus has seen increasing attention of late, especially with regard to the relative importance of mutational vs. regulatory changes, as the main driving force behind evolutionary change (Hoekstra and Coyne, 2007).

Most of the experimental studies of rapid morphological evolution are based on cultivars, lab animals or human pets that have been analyzed in the context of artificial selection, where genetic mutations have a disproportionate probability of survival, reproduction (Fondon and Garner, 2004, 2007; Sutter *et al.*, 2007) and relative fitness. Artificial selection has been valuable in understanding the potential for genetic change and has been a common theme since Darwin's *The Origin of Species* (Darwin, 1859). However, to better understand the evolution of biodiversity and adaptive radiation, more model systems are needed to study the significance of the above proposed mechanisms for facilitating rapid morphological and physiological change under the constraints and rigors of natural selection. With the advent of genome sequencing, phylogenetic comparative methods and measures of magnitude of morphological and physiological change, the significance of these proposed mechanisms can be tested by mapping the presence-absence of each of their expected genetic footprints onto a phylogenetic tree, together with multiple examples of character stasis and change. We propose that phyllostomid bats represent such a model system.

The ever-increasing application of whole-genome sequencing, bioinformatics, candidate gene identification etc. will make it increasingly likely to determine what genes or combination of genes dictate specific adaptations and how genome organization can facilitate the extreme examples of adaptational

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change. Furthermore, a perspective of geological time will provide insight into the temporal requirements for transformation (e.g., of a generalized insectivorous bat into respective lineages of bats specialized for frugivory, carnivory or sanguivory), as well as providing insights into past ecological and environmental conditions and events that existed at the time the feeding strategies evolved.

The study of when and where evolutionary change occurred can only be accomplished within a robust phylogenetic framework, providing a priori knowledge of the evolutionary relationships of the group in question and thus the order of diversification of the focal trait(s). Numerous studies (reviewed in Wetterer *et al.*, 2000) inferred phyllostomid relationships for more than a century. However, prior to the molecular studies, trees derived from external and skeletal morphology showed either little agreement among studies and/or a lack of resolution. Two studies examined the origin and diversification of feeding strategies in phyllostomid bats within a phylogenetic context (Ferrarezzi and Gimenez, 1996; Wetterer *et al.*, 2000). Although these studies utilized the most robust hypotheses of phyllostomid phylogeny known at that time, both were limited by a lack of statistically supported resolution for the deep branching order within the family.

Since then, two studies have examined variation in DNA sequences of the nuclear protein-coding *RAG2* gene (1.3 kilobases; Baker *et al.*, 2000) and mitochondrial ribosomal genes (2.6 kilobases; Baker *et al.*, 2003). Results from separate analysis of these two unlinked data sets were highly congruent, yet radically different from all previous morphologically based estimates of phyllostomid relationships. Furthermore, these genetic data provide well-supported resolution to the primary divergences within the family, and thus to the order of diversification among phyllostomid feeding strategies. A study by Datzmann *et al.* (2010) using sequences involving ten 396 base pairs from an additional set of genes (von Willebrand factor (*vwf*), recombination activating gene 2 (*rag2*), axon11 of the breast cancer susceptibility gene (*brca1*), non-coating nuclear loci of the phospholipase C beta 4 gene (*plbc4*) and short intron of the phospheonopyruvate carbonxykinase gene (*pepck*), a mitochondrial fragment of NADH (*nd1*) and tRNA Valin, plus published sequences of five mitochondrial loci (CO1, Cytb, 12S rRNA, 16S rRNA and tRNA Valin), produced a phylogenetic tree for 37 species of 29 genera. The focus of their paper was the origin of nectar feeding, but their analysis supported the general branching order of clades in phyllostomid bats shown in Figure 11.2.

In this chapter, we use the molecular phylogenetic hypothesis of Baker *et al.* (2003): (i) to estimate geologic time of shared ancestry within phyllostomid clades and (ii) to re-examine the origin and diversification from strict insectivory to omnivory, carnivory, nectivory, frugivory and sanguivory. Our

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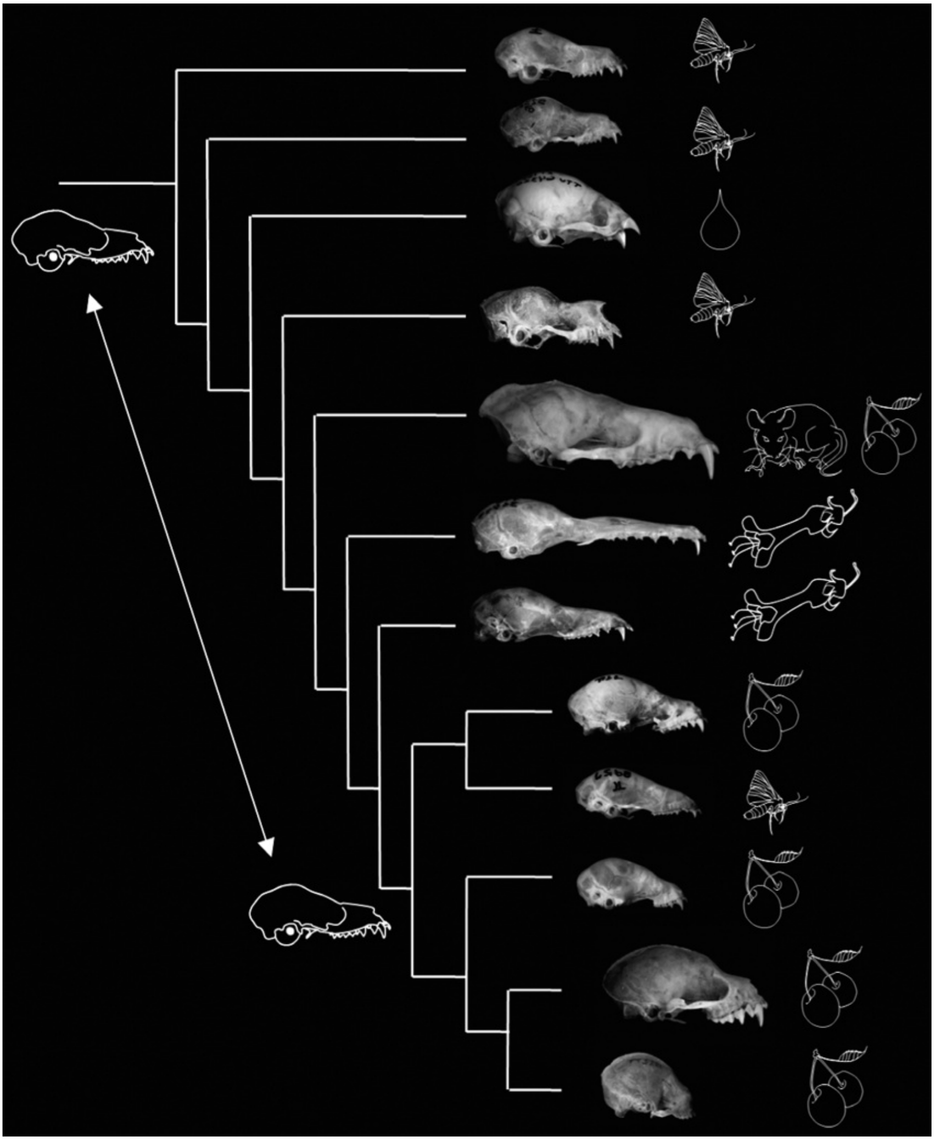

Figure 11.2 A phylogenetic perspective of cranial variation in extant species at the terminal branches of the tree and a stylized image of a *Macrotus-Micronycteris-Glyphonycteris*-like common ancestor for nodes 1–8. That a *Macrotus-Micronycteris-Glyphonycteris*-like bat that was primarily insectivorous, but took some plant material gave origin to the highly derived respective feeding strategies in the Phyllostomidae is hypothesized based on parsimony. Icons to the right of skulls represent the primary food of each extant genus depicted in the pictures: insectivory (moth); sanguivory (droplet); vertebrates (opossum); nectivory (flower); frugivory (fruit).

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format is (1) to estimate the primitive condition for ancestors at basal nodes, in a time order of establishment of clades that gave rise to stasis and change; (2) to establish the nature of clades that result in different specific feeding strategies; and (3) to describe the ecological conditions that existed during the origin of clades that exploited the different feeding strategies.

11.2 Methods and materials

In the following discussion, we follow the feeding habits based on Ferrarezzi and Gimenez (1996) as modified by Wetterer *et al.* (2000, pp. 164–165). Clades in Figure 11.3 are numbered using Baker *et al.* (2003: 9–10, table 1, and figure 5). Outgroup clades in Figure 11.3 are numbered with letters A–E. Specimens examined and Genbank sequences utilized are listed in the appendix of Baker *et al.* (2003). Divergence times were determined using the relDate procedure (Bininda-Emonds *et al.*, 2007), whereby sequence data for genes (nDNA: *ADRA2B, RAG1, RAG2* and *VWF*; mtDNA: *MT-CYB, MT-ND1, MT-TP* (tRNA-proline), and the ribosomal gene sequence 12S rRNA, MT-TV (tRNA-valine) and 16S rRNA) were fitted to the tree topology of Baker *et al.* (2003) under the assumption of a local molecular clock (see Purvis, 1995) and calibrated using the fossils employed by Jones *et al.* (2005) to estimate the geological times of divergence for the families of bats. Using the same priors as Jones *et al.* (2005), there is a link between the ages in their tree of bat families and dates in our tree of phyllostomid bats. Genetic data were derived from the data sets of Baker *et al.* (2003) and Bininda-Emonds *et al.* (2007).

The optimal model of evolution was inferred for all genes under the AIC as implemented in ModelTEST v3.6 (Posada and Crandall, 1998) in combination with PAUP* 4.0b10 (Swofford, 2002), with the reference tree being the Baker *et al.* (2003) topology pruned to the specific taxon set present for each gene (in place of the default NJ tree). At the same time, the applicability of a global molecular clock for each gene was investigated in PAUP* for the optimal model using a likelihood-ratio test. The relatively restricted taxonomic distribution meant that a global clock could not be rejected for most genes, the exceptions being *RAG2, VWF* and the ribosomal gene sequence.

Thereafter, the sequence data for each gene were fitted to the Baker *et al.* (2003) topology (again, pruned to only the relevant species) according to the optimal model of evolution under a maximum-likelihood criterion using PAUP*. Following Purvis (1995) and Bininda-Emonds *et al.* (2007), the relative branch lengths for each relevant branch on the Baker *et al.* (2003) topology were determined individually for each gene tree using the Perl script relDate v2.3.

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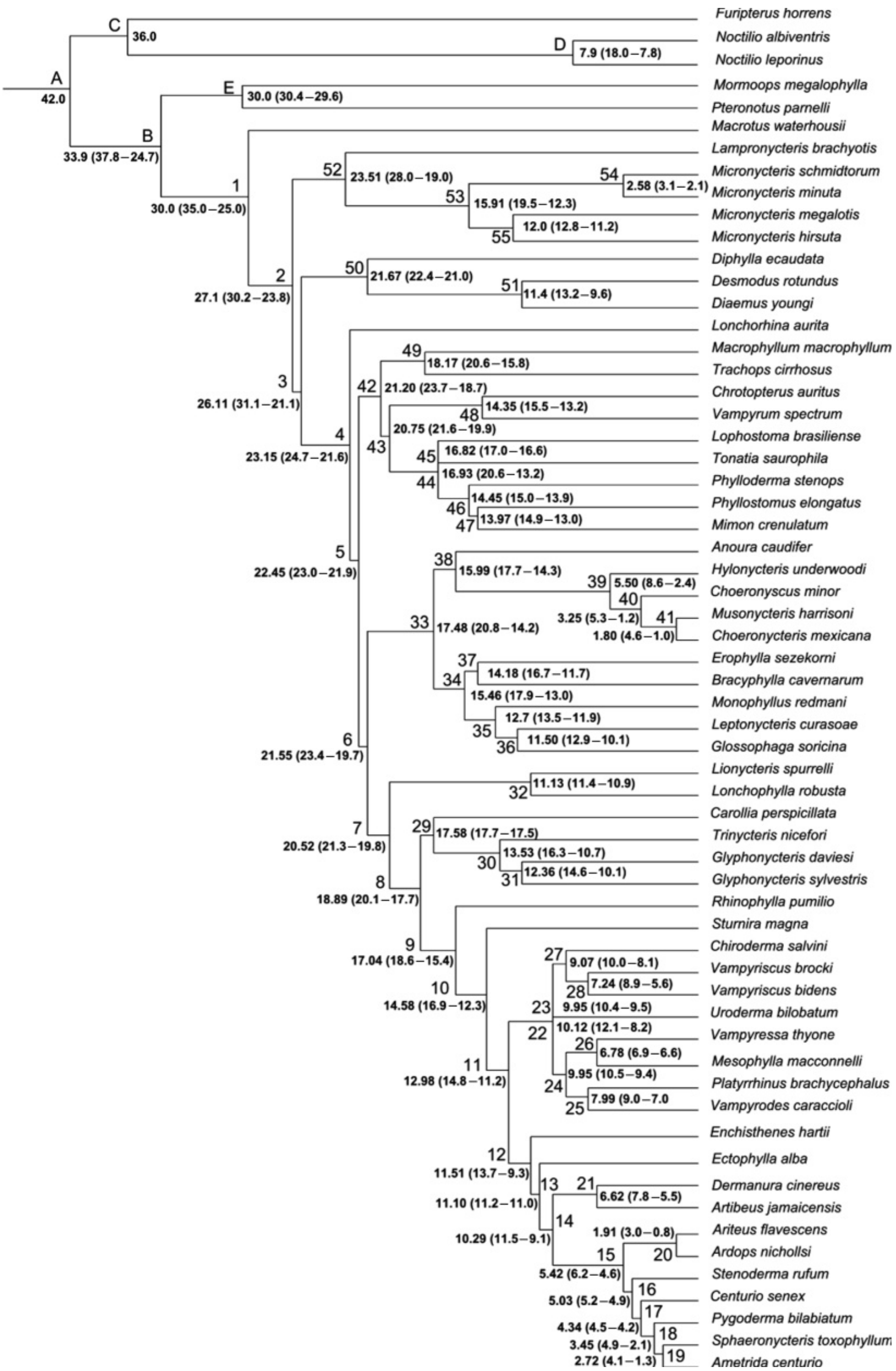

Figure 11.3 Estimates of geological age mapped on phylogenetic tree of mitochondrial and nuclear genes after Baker *et al.* (2003). Geological time-frame estimates are firsts with confidence lower and upper limits in the parenthesis. Outgroups (non-phyllostomids) are labeled A through E, and nodes (1–55) for phyllostomids follow the numbering system in figure 5a of Baker *et al.* (2003, p. 10). Branch lengths reflect genetic distance scores in Baker *et al.* (2003) rather than scores of the geological age. Confidence limits for nodes A and C are unavailable.

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Using this method, the age of a node is taken to be some percentage of the age of an ancestral node based on the height of the node relative to that of the ancestral node. Only the gene trees for the clock-like genes were considered to be rooted at this stage.

The relative branch lengths were then calibrated against a set of eight fossil dates with the initial divergence date for any given node being the maximum of either the fossil date or median of all fossil plus molecular date estimates (i.e., the fossil date acted as a minimum age constraint). Upper and lower bounds on these estimates were obtained from the 95% confidence intervals of all individual gene and/or fossil estimates for that node. Finally, any negative branch lengths arising through this procedure (e.g., due to conflict between date estimates from different genes) were corrected for, using the Perl script chronoGrapher v1.3.3.

More details regarding this dating procedure, including its strengths and weaknesses with respect to other relaxed molecular clock methods (recently reviewed in Renner, 2005) can be found in Bininda-Emonds *et al.* (2007).

11.3 Results

Estimates of geological time for each node are shown in Figure 11.3. Feeding strategies associated with various members of respective clades and other characteristics of diversification are reviewed in Table 11.1. Examples of differences in level in cranial shape in extant forms and proposed common ancestors are shown in Figure 11.2.

11.4 Geological time frame and development of feeding characteristics in respective clades

Teeling *et al.* (2005) used a phylogenetic tree generated from both nuclear and mitochondrial genes to establish the deep branching nodes with a molecular time scale for the evolution of bats. The origin of bats was estimated to be at the KT boundary, and diversification of families was in the Eocene (Simmons, 2005; Teeling *et al.*, 2005). The molecular gene tree was divided into four superfamilies, Rhinolophoidea, Emballonuroidea, Noctilionoidea and Vespertilionoidea. By contrast, the dated supertree of Bininda-Emonds *et al.* (2007), which is based on the bat supertree of Jones *et al.* (2002), pushes both the origin of bats (84.8 mya) and the first, basal split of the crown group (71.2 mya) well into the Cretaceous.

For this chapter, it is valuable to analyze the evolution of feeding habits in an explicit phylogenetic framework to better understand what feeding habits the

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Table 11.1 Characteristics of nine clades of phyllostomid bats that are hypothesized to have evolved from a common ancestor with *Micronycteris*-like characteristics as present in *Macrotus, Micronycteris* and *Glyphonycteris*. Clade numbers are from node numbers in Figure 11.2, where respective clades are separated from the remainder of the family. Intraclade age is defined as the time that the clade separated from all other phyllostomid bats until the initial divergence within that clade of extant genera present in that clade. Change from common ancestor is based on an overview of general knowledge of the bats of the clade.

Clade	Food Source	Age (mya)	Intraclade age (mya)	Time in common ancestor	No. of genera	No. of species	Change from ancestor
1	Primarily insects, some plant	29.5	n/a	n/a	1	2	Minimal
2	Primarily insects, some plant	26.7	23.2	3.5	2	8?	Minimal
3	Blood	25.9	21.7	4.2	3	3	Maximum
4	Primarily insects, some fruit	23.3	n/a	n/a	1	6	Moderate
5	Omnivores, vertebrates, insects	22.3	21.1	1.2	9	20	Moderate to High
6	Primarily nectar, pollen, some fruit, insects	21.4	17.4	4.0	13	31	High
7	Primarily nectar, pollen, some fruit, insects	18.5	11.0	7.5	4	10	High
8	Primarily insects, some fruit or primarily fruit, some insects	18.5	17.2	1.3	3	13	Minimal (*Trinycteris*) Moderate (*Carollia*)
9	Mostly fruit or obligate fruit	18.5	16.2	2.3	19	68	High
					55	**161**	

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common ancestor of the sister clade to the Phyllostomidae and the last common ancestor of all phyllostomid bats possessed. Establishing the latter in particular represents the first step in reconstructing the order and relationships of change of feeding habits in phyllostomids. Within the 19 families of bats, 13 are strict insectivores, four include strict insectivores and carnivores (Megadermatidae, Nycteridae, Noctilionidae, and Vespertilionidae), one includes fruit as well as nectar feeders (Pteropodidae) and one, the focus of this paper, includes species that are strict insectivores, omnivores, nectivores, carnivores, sanguivores, and frugivores.

The widespread occurrence of strict insectivory as a feeding strategy, together with its distribution, results in it being reconstructed as the primitive strategy for bats as a whole plus most major clades within bats, including all nodes connecting families within Noctilionoidea. Carnivory instead represents a derived state, usually within individual genera, with other members of the genus retaining the primitive state of strict insectivory. For instance, nearly all species of Vespertilionoidea are strict insectivores, and those that take fish (carnivores) are congeneric with strict insectivore species. Likewise, nearly all species of Emballonuroidea are strict insectivores with the exception of the genus *Nycteris*, where some species take some vertebrates but where others are strict insectivores. In the Rhinolophoidea, most species are strict insectivores except for the two carnivorous genera *Megaderma* and *Macroderma*. For Noctilionoidea, five families in this superfamily are strict insectivores, with the sixth family Noctilionidae comprising only two species; one is a strict insectivore and the other takes fish and insects. However, molecular data indicate that the fish-eater evolved within the last ten million years (Lewis-Oritt *et al.*, 2001; Bininda-Emonds *et al.*, 2007). Given this pattern and also that all extant members of the Mormoopidae, the sister family to Phyllostomidae, are strict insectivores, the most parsimonious explanation is that the ancestral condition for the last common ancestor of phyllostomid and mormoopid bats was a strict insectivore (Figure 11.3).

Molecular data calibrated against geologic estimates place the divergence of the last common ancestor for mormoopids and phyllostomids between 36 (42–32) mya (Teeling *et al.*, 2005) and 42.5 (46.7–38.3) mya (Bininda-Emonds *et al.*, 2007). Our estimates for this node are younger than both at 33.9 (37.8–24.7) mya. Both our estimate and that of Teeling *et al.* (2005) fall within the Oligocene, although the confidence limits for the latter overlap the boundaries of the Eocene. This brings into question whether the families Phyllostomidae and Mormoopidae existed in the Eocene as proposed by Simmons (2005) and supported by the dates of Bininda-Emonds *et al.* (2007).

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Using the information available in the molecular phylogenetic tree and the geological dates proposed for each node, we hypothesize that the successful diversification within Phyllostomidae is a result of the ancestral stock of the family shifting from strict insectivory to also including plant material in the diet. Such a shift in diet would have reduced competition with all other bat species known to be present in the New World from the Early Cenozoic forward. The transition from strict insectivory to a diet with plant material in extant bat families has been accomplished only twice (Phyllostomidae and Pteropodidae). However, given that plant material is abundantly available in all ecosystems exploited by bats, the logical conclusion is that the transition from insectivory to consuming plant material (or even other feeding habits) must be difficult, possibly requiring the availability of a series of ecological determinants and ancestral genetic variation that facilitate directional selection of appropriate characters. The benefits of making this transition are apparently exceptional if the diversity within phyllostomid and pteropodid bats are a reliable indicator. These two families account for over 350 species or 30% of the total number of bats in all 19 families.

Teeling *et al.*'s (2005) phylogeny is designed primarily to address evolution among the bat families and does not provide much detail within the Phyllostomidae where only four of the 56 recognized genera were examined. Hoffman *et al.* (2008) focused on the subfamily Phyllostominae (Baker *et al.*, 2003) to provide a geological time scale of 18 genera and 24 species. Despite the different taxonomic foci of the two studies and different underlying data sets (both in terms of the genes and outgroups used), their tree shows generally good agreement with the dates presented in this chapter. Topological differences tend to be present for the more poorly supported nodes in the respective trees. Importantly, there is also generally substantial overlap in the confidence limits for the date estimates for nodes shared between Hoffman *et al.* (2008) and our studies but see the variation in date estimates in table 2 of Datzmann *et al.* (2010, p. 34).

In the estimates of the geological time frame in Datzmann *et al.* (2010) their dates were substantially older in their figure 4. However, in their table 2 of model comparisons of alternative molecular clocks and priors their third molecular clock model (Datzmann *et al.*, 2010, p. 34) estimated the origin of phyllostomid bats to be 29.07 mya (23.4–37.0) as compared to the estimate in this chapter of 30.0 mya (35.0–25.0). Clearly the use of different priors and models give substantially different results. We note that our priors and use of fossils are the same as those reported in Jones *et al.* (2005). Therefore our dates as discussed below are most relevant to those shown in Jones *et al.* (2005) for other bat families.

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11.5 From insectivory to herbivory: prevailing trends in feeding diversification

An overview of the extent to which clades (Figure 11.3) within Phyllostomidae used plant material as a food source is outlined in Table 11.1. The first five extant lineages include no species that are obligate plant feeders and few that are predominantly plant feeders. Three lineages (1, 2 and 4, recognized as subfamilies Macrotinae, Micronycterinae and Lonchorhininae, respectively) do take some plant material, but are primarily insectivores. The fourth lineage (clade 3, subfamily, Desmodontinae) feeds entirely on animal tissue (blood), and it seems likely that the species in this lineage never took much plant material after its divergence from other phyllostomids. The final basal lineage contains species that are true omnivores, but also another that is a strict insectivore (*Macrophyllum*) as well as others that are carnivores (*Vampyrum* and *Trachops*). Therefore, we hypothesize that, up to this point, the ancestral condition for the first five clades was primarily an insectivore that took some plant material.

The origins for each of the first five clades is prior to the end of the Oligocene, and much, if not all, of the diversification in the fifth lineage (node 42 forward) occurred during the Miocene. The remainder of the diversification within these clades that are mostly dependent on plant material as a food source (nodes 6–15) also occurred during the Miocene (Table 11.1, Figures 11.2–11.3).

Each of the 31 and 14 extant species belonging to clades 6 and 7, respectively, are primarily consumers of plant material (Figure 11.2). Although each of these species are typically referred to as nectar feeders (Gardner, 1977; Ferrarezzi and Gimenez, 1996), the available data suggest that they probably all take pollen, fruit and insects as well. Thus, both of these clades have made the transition to feeding primarily on plant material, with several species showing extreme adaptations (Figure 11.1) for retrieving nectar from flowers such as *Musonycteris* (Phillips, 1971), *Anoura fistulata* (Muchhala, 2006) and *Lonchophylla* (Griffiths, 1982). In addition, both clades have coadapted as pollinators such that certain flowering plants and bats are symbiotic in a complex community structure (Fleming *et al.*, 2005).

Clade 8 comprises two lineages with different feeding strategies. One includes the genera *Glyphonycteris* and *Trinycteris*, which are so similar morphologically to members of *Micronycteris* (clade 2) and *Macrotus* (clade 1) that they have been held to be congeners (Jones *et al.*, 2002). We propose instead that the observed morphological similarities (Figure 11.2) represent shared primitive features present in *Macrotus* (clade 1), *Micronycteris* (clade 2) and *Glyphonycteris* and *Trinycteris* (clade 8) rather than evidence of a monophyletic

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group as implied in the supertree of Jones *et al.* (2002). All extant species resulting from nodes 1 and 2, and node 30, which is a subset of the diversity in node 8, share a feeding strategy (primarily insectivorous with some plant material) that was retained in the respective common ancestors of nodes 1–8 (Figure 11.2). If this hypothesis is true, then the primitive state for the respective common ancestors for nodes 1–8 was *Macrotus*-, *Micronycteris*- and *Glyphonycteris*-like, with this phenotype giving rise to all the specialized and unique feeding strategies and derived phenotypes found in the family Phyllostomidae (Figure 11.2) except for the obligate fruit feeding of node 15, the subtribe Stenodermatina which represents additional specialization of a primarily frugivore ancestor.

The other member of clade 8 is the genus *Carollia* whose species specialize on fruits (Fleming *et al.*, 2005), especially those of *Piper*, a plant that has coadapted its fruit presentation to provide easy access for bats. However, *Carollia* also employs a mixed feeding strategy, with the primary food source being insects for times when fruit availability is limited (Fleming, 1988).

The extant species that have evolved from clade 9 have a feeding strategy ranging from primary to obligate frugivores. This successful transition to fruit as the primary or sole food source has resulted in a clade with the greatest relative number of genera (20) and species (68) among phyllostomids (Baker *et al.*, 2003). Our results indicate that the final stage of the transition (node 15), obligate frugivory, occurred less than 10 mya with the lineage diversifying into eight monotypic genera in the last 5 mya (Dávalos, 2007; 5.9 (7.6–4.5) mya according to Bininda-Emonds *et al.*, 2007). The magnitude of morphological change and evolutionary plasticity that is present among the extant members of clade 8 suggests both that extensive vacant niches were present and that the respective genomes were exceptional at producing the morphological variation necessary to facilitate directional selection to exploit these new niches. This radiation to exploit obligate frugivory relative to the generic divergence within that observed in clades 1–7 is the most recent burst of diversification present in the family. The hypothesis that obligate frugivory evolved in the Antilles Islands and successfully invaded the competitive landscape of bats on the continental mainland of the New World Tropics (Dávalos, 2007) is also contra to most proposed scenarios of evolution on islands.

11.6 Evolution of unique feeding strategies

Many papers have presented hypotheses concerning the intermediate stages involved in the origin of the multiple feeding strategies present in Phyllostomidae (Gillete, 1975; Fenton, 1992; Ferrarezi and Gimenez, 1996).

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As proposed above, character evolution along the phylogeny shown in Baker *et al.* (2003) is that all derived feeding strategies evolved independently from a *Macrotus, Micronycteris, Glyphonycteris*-like morphology characterized by adaptations to an insectivorous diet that also allowed the consumption of some plant material. Gillete (1975) emphasized the role of the feeding habit duality in the process of evolution from primitive insectivory to some other kinds of feeding habit specialization, a hypothesis accepted by Ferrarezi and Gimenez (1996) for phyllostomids. Our scenarios of diversification of feeding strategies among phyllostomids are compatible with the feeding habit duality model of Gillette (1975). Our conclusion is that the basal ancestor for all derived feeding strategies and resulting evolutionary consequences was primarily insectivorous, but taking some fruit. No highly derived feeding strategy evolved from another highly derived feeding strategy, as proposed for the origin of vampires from nectar feeders (Baker, 1979; Straney *et al.*, 1979), from fruit eaters (Slaughter, 1970) or from omnivorous phyllostomines (Schutt, 1998). Feeding habit duality is present in all phyllostomid bats except vampires, *Macrophyllum* which is a strict insectivore and the obligate frugivores of the Stenodermatinae (node 15, Figure 11.3).

11.6.1 Sanguivory

Obligate blood feeding has evolved only once in tetrapods. The lineage that gave rise to the vampires diverged (node 3) from the remainder of the family about 26 (31.1–21.1) mya, and the three extant species in the clade are obligate vampires. As currently recognized, each is a distinct genus, with two being specialists on bird blood, and the third, the common vampire bat (*Desmodus rotundus*), feeding primarily on mammals. The most basal genus of vampire, *Diphylla* (node 50), diverged from the two remaining forms 21.67 (22.4–21.0) mya. Because bird blood contains nucleated red blood cells and a higher level of sugar content, it is probable that the first successful vampire activities involved feeding on birds (Schutt, 1998), which the current distribution of vampire prey would also support. During the transition period to sanguivory, it was probably important to provide food in quantities that were small enough to not kill the prey, suggesting possibly a preference for larger prey objects (e.g., large ratites or flying species weighing a kilo or more). Flight and the ability to search large areas for sources of blood meals would also be critically important. Similarly, nocturnal feeding would be advantageous because the high diurnal activity of birds would likely have resulted in avoidance behaviors of the activities that are typical of vampire bats during feeding.

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To address what types of birds were available for initial exploitation by the vampires requires knowledge of the avian fauna of the Neotropics from the geological time frame between 31.1 and 21.0 mya, when our study suggests that sanguivory presumably evolved (including outer 95% confidence intervals). A varied bird population has been documented for the middle to upper part of the Eocene, including a number of currently existing bird genera such as pelicans, ibises, marabous, ducks, cormorants and flamingos (Osborn, 1910). Many species in these genera are of a relatively large size and also form large migrating flocks that hypothetically could have populated the typical marshy environments that surrounded common inland water masses during the Aquitanian (23.03–20.43 mya), the narrower time frame during which our results suggest an evolutionary origin of sanguivory (26.11–21.67 mya).

We hypothesize that the common ancestor of the vampires was *Micronycteris*-like and in a window of a little more than four million years made the myriad of necessary changes to be a successful obligate blood feeder (e.g., the evolution of anticoagulants, changes in dentition necessary to obtain blood, adaptation to a highly specialized diet of blood cells and proteins, kidneys that can facilitate flight weight restriction by quickly reducing the amount of water in a blood meal, the anatomical changes necessary to be sufficiently agile in non-flight locomotion to obtain a blood meal from roosting birds and the sensor adaptation to find a blood meal). The evolution of this suite of traits undoubtedly involved many areas of the genome and changes in many single copy loci.

Indeed, the magnitude of evolution required to be a successful sanguivore (Greenhall and Schmidt, 1988) may be the greatest outlier from the shared features of all other bats. It is also a candidate to be the mammalian lineage that has undergone the largest magnitude of directional selection within a restricted time frame (4 mya) resulting in an extremely modified morphology, physiology, behavior and all the other unique features required to be a sanguivore.

11.6.2 Carnivory

Carnivory is defined herein as feeding on other vertebrates. The transition to vertebrates as food has occurred in bats independently at least six times. In addition to phyllostomids, examples of carnivory are present in megadermatids, noctilionids, nycterids and vespertilionids (at least twice in *Myotis*), *M. vivesi* and *M. macrodactylus*. Each of these four families is primarily insectivorous with isolated examples of carnivorous species (Simmons and Conway, 2003). Within phyllostomids, *Trachops* has evolved as a specialist for small frogs, and the sister clade to *Trachops/Macrophyllum* includes two other genera (*Vampyrum* and *Chrotopterus*) that take a variety of foods but are

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primarily specialists for feeding on vertebrates. The *Vampyrum/Chrotopterus* clade (node 43) diverged from the remainder of the phyllostomid bats 20.75 (21.6–19.9) mya in our tree and 19.5 (±2) mya according to Hoffmann *et al.* (2008), with the two genera diverging from each other (node 48) 14.35 (15.5–13.2) mya in our tree and 14.4 (+/–1.9) mya in Hoffmann *et al.* (2008). *Vampyrum* is the largest bat in the New World and feeds on other bats, rodents, birds and possibly also some fruit and insects (Gardner, 1977). It is known to take bats in flight, but probably also catches rodents by passive acoustic detection from sounds made by them on the forest floor (Siemers *et al.*, 2001). *Chrotopterus*, like *Vampyrum*, takes small vertebrates (e.g., geckos, opossums, birds and bats), but also takes insects and fruit.

11.6.3 Nectivory

Within our tree, there are 12 genera in the subfamily Glossophaginae (*sensu* Baker *et al.*, 2003; node 6) that are primarily nectar-feeding bats, with the morphological variation ranging from species with relatively short rostra (*Brachyphylla*) to those with rostra and tongues of extreme length, Figure 11.1 (*Musonycteris* and *Anoura fistulata*, Muchhala *et al.*, 2005). Glossophagines diverged from the other phyllostomid bats 21.55 (23.4–19.7) mya, with the last common ancestor of all 12 genera being present 17.48 (20.8–14.2) mya. Because all extant genera are primarily nectar feeders, it is parsimonious to assume that the last common ancestor for all members of node 33 was a nectar feeder as well. This results in a maximal estimate of nine million years to evolve from a primarily insectivorous omnivore (node 6) into a nectar feeder (node 33).

A second group of nectar-feeding bats (node 7) diverged from the remainder of Phyllostomidae about 1 mya after the divergence from those present in node 6, 20.52 (21.3–19.8) mya (although the confidence intervals for both clades overlap). Within our data set, the last common ancestor for *Lionycteris* and *Lonchophylla* diverged 11.13 (11.4–10.9) mya, yielding a similar maximal estimate (ten million years) of time as proposed for the Glossophaginae during which this clade would have evolved all the necessary adaptations to be a nectivore. However, not all genera within this clade have been sequenced and dated such that the date estimate of the last common ancestor for the extant members of the group may be nearer to the time of divergence than all other phyllostomids. In the Datzmann *et al.* (2010) estimates of the origin of the two nectar-feeding groups, more than two million years separate their independent origins.

There has been extensive debate concerning how many times nectar feeders have evolved within the phyllostomid assemblage, as well as a wide array of proposed monophyletic assemblages (Baker, 1967; Baker and Bass, 1979;

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Griffiths, 1982; Haiduk and Baker, 1982; Warner, 1983; Smith and Hood, 1984; Koopman, 1993; Wetterer *et al.*, 2000; Carstens *et al.*, 2002; Datzmann *et al.*, 2010). If there had been morphological canalization for nectar feeding, it is likely that all nectar feeders would have shared a substantial number of synapomorphies in the hyoid and lingual regions. However, Griffiths' (1982) substantial data set, concerning the morphology associated with lingual aspects of nectar feeding, documents two alternative modifications of these regions to facilitate nectar feeding. This result is compatible with the hypothesis derived from our molecular reconstructions and those of Datzmann *et al.* (2010) that there was independent evolution of the two lineages from a primarily insectivorous bat taking some fruit into highly derived nectar feeders.

The only nectar-feeding bat fossil known from the northern part of South America is *Palynephyllum antimaster*, a form intermediate between *Lonchophylla handleyi* and *Anoura caudifer* (Czaplewski *et al.*, 2003), recovered from the Miocene deposits of La Venta, Colombia and dated between 13 and 12 mya. This fossil, together with our proposed dates for the last common ancestor of nectivorous forms, ties the origin of nectivory with significant global climate changes that resulted in abrupt episodes of global cooling causally linked to major expansions of ice cover over Antarctica and accentuated due to a preceding interval of extreme global warmth in the latest Oligocene (Zachos *et al.*, 2001). Furthermore, the arid conditions associated with the cooler environments of the MI-1 Glaciation coincide with the appearance of the Neotropical endemic Cactaceae (Hershkovitz and Zimmer, 1997), a group typically pollinated by nectar-feeding bats. Morphological, physiological and behavioral changes in both bats and plants involved in pollination syndromes are not trivial and reflect a parallel evolutionary history (Heithaus, 1982).

11.6.4 Frugivory

Species that are primarily frugivorous rather than nectivorous or insectivorous first appeared in the tree at nodes 29 (*Carollia*), 9 (*Rhinophylla*) and 10 (*Sturnira*), and all other taxa derived from node 11. Obligate frugivory characterizes the species descended from node 15. Node 9 represents the most successful radiation in the family in number of genera (20) and number of species (67). Our date estimates suggest that predominant frugivory evolved towards the end of the Oligocene (17.58 (17.7–17.5) mya for *Carollia* and 18.89 (20.1–17.7) mya for the last common ancestor of all members of node 9) and, therefore, slightly later than the other bat family that also evolved frugivory and nectivory (Pteropodidae) (24 (29–20) mya, Teeling *et al.*, 2005; 25.1 (30.3–22.7) mya, Bininda-Emonds *et al.*, 2007). The relative congruence of the estimates

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for the origins of frugivory in phyllostomids and pteropodids suggests that a global transtropical floral shift facilitated the evolution of frugivory in bats. This hypothesis is supported by data from paleobotany, which suggest that the Neotropical rainforest appeared in North America in the Early Paleocene and in South America during the Early Eocene (Burnham and Johnson, 2004 and citations therein).

11.6.5 Strict insectivory

Strict insectivory is the *status quo* for essentially all other non-phyllostomid bats that were present in the Neotropics during the Oligocene/Miocene time frame. Therefore, it is not surprising that phyllostomid bats did not commonly revert to the highly competitive feeding strategy of strict insectivory, and then apparently only if they could occupy a unique niche that would avoid competition with other strictly insectivorous species.

The only species of phyllostomid bat that is a strict insectivore, *Macrophyllum macrophyllum* (clade 49), arose in the Early Miocene, 18.1 (19.3–16.8) mya, as part of a clade (42) comprising a broad array of omnivores. Unlike any other strict insectivorous bats present in the Neotropics, *Macrophyllum* feeds from the surface of the water by gleaning insects. Otherwise, *Macrophyllum* is morphologically a typical insectivorous as well as carnivorous bat, except that its hindlimbs are uniquely modified for gleaning from the surface of the water. We hypothesize that *Macrophyllum* was successful at becoming a strict insectivore because this method of collecting insects avoided competition with other strict insectivorous as well as other phyllostomid bats. There are two noteworthy observations relative to *Macrophyllum* competing as a strict insectivore. First, the sister taxon to *Macrophyllum* is *Trachops*, which feeds on frogs and frequently takes them from the water's surface while they are making mating calls (Gardner, 1977), and second, that gaffing insects from the surface of the water has not commonly evolved in other insectivorous bat assemblages. *Macrophyllum* is another example of a member of the phyllostomid complex exploiting a relatively unique unfilled niche.

11.7 Conclusion and implications for future work

We propose that phyllostomid bats present the most radical adaptive radiation of feeding strategies from a common ancestor for any monophyletic group of mammals. Further, the time frame for this radiation, and the evolution of the individual feeding strategies, has been relatively short when compared to other phylogenetically defined examples of diversification under the rigors of

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natural selection (Teeling *et al.*, 2005). An appropriate question is why did this level of diversification occur only in this group of bats? This is a difficult question. Rapid radiation is typically associated with short generation times, rapid sexual maturity and large numbers of offspring per breeding cycle. Relative to most mammals, however, bats do not embody these characteristics. Female bats typically reach sexual maturity after one year, the number of offspring is usually one per breeding cycle, and bats are notoriously long-lived relative to other groups in the mouse-to-elephant curve of mammalian life-history characteristics. Nonetheless, since the beginning of the Oligocene, phyllostomids have not only changed radically in a broad array of phenotypic character states, but have also successfully evolved adaptation to more feeding strategies, sanguivores, frugivores, nectivores, carnivores and omnivores, than are represented collectively in all other 19 families of bats. No other bat family has more than two feeding strategies. We propose that this successful radiation is a result of successfully including plant material in addition to insects in the diet in concert with the environmental opportunities present in the Oligocene/Miocene in the Neotropics. It is not obvious how these lineages have overcome their relatively long generation time and other life-history characteristics usually adjacent with slower rates of evolution to facilitate the extreme directional selection needed, but there must have been involvement of genetic and/or genomic mechanisms to allow expression of the broad array of phenotypes to be acted upon by natural selection.

In the Introduction, we proposed that mapping genetic changes onto the clades of a phylogenetic tree can be used to test which genetic mechanisms were active in accomplishing rapid morphological and physiological change. Assuming that the common ancestor for nodes 1–8 was morphologically and physiologically a relatively typical insectivorous bat that fed on some plant material, and that this ancestral phenotype, through multiple cladogenic events, gave rise to clades that ultimately evolved into the diversity of highly specialized feeding types (blood feeders, nectar feeders, fruit and foliage eaters, and carnivores), such a test should be possible.

Within our phylogenetic tree (Figures 11.2–11. 3) there are three independent examples of species (clades leading to *Macrotus* (node 1), *Micronycteris* (node 2) and *Glyphonycterinae*, node 30) that today are quite similar to the proposed ancestral conditions (Jones *et al.*, 2002). These lineages are examples of morphological stasis and the genomic comparisons of extant members of these three respective groups should reflect stabilizing selection for comparison to lineages that have undergone extensive directional selection. Seven other examples (lineages derived from clades 50, 42, 33, 32, 9 and those leading to *Carollia* and *Lonchorhina* (Figures 11.2–11.3) have undergone exceptional

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morphological and physiological evolution, which permits multiple tests to better understand the extent to which the proposed mechanisms (see Introduction, Fondon and Garner, 2004, 2007, and Sutter *et al.*, 2007 for reviews) of genetic change have been involved in these examples of substantial directional evolution as compared to minimal genetic change observed is the extant species comprising the subfamilies *Macrotinae, Micronycterinae* and *Glyphonycterinae*. Interestingly, the results from Bininda-Emonds (2007), who examined substitution rates across all mammals based on 18 nuclear and 26 mitochondrial genes would seem to rule out a global change in substitution rate across the genome for phyllostomids in that no branch or clade within the group showed a significant deviation from the mammalian average. This result, however, does not exclude the possibility of genetic mechanisms such as gene duplications, mutations in tandem repeats, bursts of transposable element activity, variation in mutation rates of single copy genes and timing of gene expression, which were not examined by Bininda-Edmonds (2007).

Finally, it is important to experimental design that there are multiple examples of stasis, as well as of independent clades whose members have different phenotypes. In initial studies of genetic mechanisms that potentially underlie rapid and extensive evolutionary change (Fondon and Garner, 2004, 2007; Sutter *et al.*, 2007), candidate genes or mechanisms of genomic rearrangement etc. have mostly been compared for single examples of change. In the phyllostomid model, by contrast, it will be possible to compare the variation present in each of the proposed mechanisms across multiple examples of independent evolution to different phenotypes. Thus, both this model system and the database it provides should be invaluable, providing a better understanding of how mechanisms that promote rapid evolution under the constraints of natural selection over a geological time frame successfully accomplish the directional evolution required to exploit a new feeding niche or evolutionary grade. Once patterns of change in different morphological evolution are revealed, such patterns can be explored for possible convergence in the context of the recent discovery of convergent sequence evolution between echolocating bats and dolphins (Li *et al.*, 2010; Lui *et al.*, 2010). Examples would include nectar-feeding mutations shared by members of the Glossophaginae and the Lonchophyllinae for presence in independently evolved Old World nectar feeders such as the genera *Eonycteris, Macroglossus, Megaloglossus* and *Syconycteris*. Rostral elongation and tongue feeding have evolved numerous times in the class Mammalia. It will be fascinating to determine commonality in the genetic basis of each of these events in the diversification of bats and other mammals for successful nectar feeding, as was proposed for echolocation across mammalian orders (Jones, 2010). Further, using these sequence alterations in

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genes to be transplanted for expression in the *Mus* model system will be quite an experiment to synthesize an understanding of the alternatives and diversity of how the genome can successfully function to facilitate evolutionary change.

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