

Edited by Theodore H. Fleming and Paul A. Racey

Island Bats

Evolution, Ecology, and Conservation

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The second largest order of mammals, Chiroptera comprises more than one thousand species of bats. Because of their mobility, bats are often the only native mammals on isolated oceanic islands, where more than half of all bat species live. These island bats represent an evolutionarily distinctive and ecologically significant part of the earth's biological diversity.

Island Bats is the first book to focus solely on the evolution, ecology, and conservation of bats living in the world's island ecosystems. Among other topics, the contributors to this volume examine how the earth's history has affected the evolution of island bats, investigate how bat populations are affected by volcanic eruptions and hurricanes, and explore the threat of extinction from human disturbance. Geographically diverse, the volume includes studies of the islands of the Caribbean, the Western Indian Ocean, Micronesia, Indonesia, the Philippines, and New Zealand.

With its wealth of information from long-term studies, Island Bats provides timely and valuable information about how this fauna has evolved and how it can be conserved.

Earth History and the Evolution of Caribbean Bats

Liliana M. Dávalos

Introduction

Bats are the most species-rich and abundant of Caribbean mammals, the survivors of a fauna that once included native sloths, monkeys, rodents, and insectivorans, all now extinct or nearly so (Morgan and Woods 1986). There are 64 Recent and late Quaternary species in 32 genera of 6 families (Dávalos 2005, 2006; Koopman 1989; Morgan 2001; Tejedor et al. 2004; Tejedor et al. 2005). The bat fauna of the Antilles is unique: about 50% of the species are endemic to the region, and the proportion of endemics rises when only considering the Greater Antilles (Baker and Genoways 1978; Koopman 1989). How can we explain the diversity and distribution of this fauna?

Two main biogeographic hypotheses have been proposed: a temporary land bridge connecting the Greater Antillean Ridge and northwestern South America through the Aves Ridge (Iturralde-Vinent and MacPhee 1999), and dispersal over ocean barriers sometimes mediated by prevailing ocean currents (Hedges 1996). The land-bridge—or Gaarlandia—hypothesis draws on stratigraphic sections and submarine samples that indicate that land exposure in the Caribbean was at a maximum during the Eocene/Oligocene transition (Haq et al. 1993; Iturralde-Vinent and MacPhee 1999). The dispersal hypothesis, in contrast, is based on the finding that estimates of divergence between Caribbean and continental amphibians and reptiles were scattered throughout the Cenozoic for 75 of 77 lineages studied (Hedges 1996). A third alternative, the interconnection of North America and South America through the proto-Antilles in the Cretaceous, has recently been revived by Mesozoic-age divergence estimates for the insectivoran mammal *Solenodon*, the frog genus *Eleutherodactylus*, and the xantusiid lizard *Cricosaura* (Roca et al. 2004). This alternative probably does not apply to bats, in light of the dust clouds, tsunamis, and earthquakes that followed the asteroid impact at nearby Chicxulub (Yucatán) 65 million years ago (Ma) (Alvarez et al. 1980; Grajales et al. 2000), and the subsidence of the West Indies in the Eocene (Iturralde-Vinent and MacPhee 1999).

The fossil record and phylogenies of a few Caribbean land mammals (e.g., megalonychid sloths, caviomorph rodents, primates, and one bat lineage) are com-

patible with the Gaarlandia hypothesis (Horovitz and MacPhee 1999; Wetterer et al. 2000; White and MacPhee 2001), but divergence estimates are available only for nonflying lineages, and their reliability is at best questionable (Dávalos 2004). To date, no analysis has combined the necessary taxonomic and molecular sampling to examine the land-bridge model, in part because most nonflying Caribbean mammals are extinct (Morgan and Woods 1986). As the most abundant and diverse of extant West Indian mammals (Griffiths and Klingener 1988), bats are ideally suited for such a study.

If the Gaarlandia land bridge enabled bats to reach the islands from the continent, the descendents of colonizing populations would share one common ancestor with mainland relatives as ancient as the Eocene/Oligocene boundary. Conversely, multiple divergences between continental and island species within each lineage, scattered across many different dates, would be consistent with the dispersal scenario. Here I conduct phylogenetic analyses of seven groups of Caribbean bats in the families Natalidae, Mormoopidae, and Phyllostomidae, representing about 40% of all bat species found in the West Indies, to test the Gaarlandia hypothesis. These taxa comprise all West Indian endemic bat genera and subgenera and represent >80% of extant endemic species. To test the monophyly of each lineage and estimate the timing of divergence between insular and continental species, continental taxa closely related to each Caribbean group were also included.

A Phylogenetic Approach to Caribbean Bat Biogeography

Geographic and Taxonomic Scope

In this chapter “West Indies,” “Antilles,” and “Caribbean” refer to the islands of the Caribbean Sea that have an insular biota (Morgan 2001; Morgan and Woods 1986). Special attention is devoted to the Greater Antilles: Cuba, Jamaica, Hispaniola, and Puerto Rico. The bat fauna of Grenada and the Grenadines, Trinidad, Tobago, Margarita, Aruba, Bonaire, and Curaçao is not discussed here because these islands are characterized by a South American biota.

A total of 64 extant and sub-Recent bats have been recorded in the West Indies, in about 30 separate groups. This study examines seven groups in detail: mormoopids (with four West Indian representatives), two phyllostomid groups, and natalids.

Phylogenetic Analyses of Caribbean Bat Lineages

DNA was extracted from frozen tissues of relevant taxa using the Qiagen DNeasy kit. DNA was amplified and sequenced to generate a data set of one nuclear gene fragment (*Rag2*) and one complete mitochondrial gene (cytochrome *b*). Amplification and sequencing used previously described protocols and primers (Dávalos 2005, 2007; Dávalos and Jansa 2004). ABI 3700 automated

sequencers (ABI) with Big Dye terminator chemistry (ABI) were used to collect sequences. Mitochondrial cytochrome *b* and *Rag2* sequences not generated as part of this study were obtained from Baker et al. 2000; Hooper et al. 2003; Lewis–Oritt et al. 2001; and Ruedi and Mayer 2001. The species names and GenBank accession numbers of sequences collected for this study are presented in table 4.1.

A data set obtained from GenBank including partial sequences of mitochondrial ribosomal subunits 12S and 16S, and the complete sequence of the tRNA^{Val} intervening gene, was included in analyses (Baker et al. 2003; Van Den Bussche and Hooper 2001; Van Den Bussche et al. 2002). These sequences were aligned using CLUSTAL W 1.83 (Thompson et al. 1994) with a gap opening penalty of 10 and a gap extension penalty of 5, transitions weighed 0.5 with respect to transversions. Alignments were examined and corrected manually to ensure the reliability of positional homology assessments. Concatenated data–set length was 5,175 bp for natalids and outgroups, and 5,219 bp for mormoopids, phyllostomids, and outgroup. Maximum likelihood (ML) analyses were performed with PAUP* 4.0b10 (Swofford 2002), using heuristic searches with a neighbor joining (NJ) starting tree and subtree pruning–regrafting (SPR) branch swapping. Nonparametric ML bootstrap analyses were performed using 100 heuristic replicates with SPR branch swapping. Settings for the GTR+ Γ +I model of DNA sequence evolution were estimated directly using PAUP* (Swofford 2002) and remained fixed in bootstrap analyses. Parameter settings for each of the two data sets are shown in table 4.2.

Bayesian phylogenetic analyses were conducted using the program MRBAYES 3.0b4 (Huelsenbeck and Ronquist 2001) with a GTR+ Γ +I model of DNA sequence evolution for each partition (mitochondrial ribosomal DNA [mtrDNA], mitochondrial cytochrome *b*, and nuclear *Rag2*), as described previously (Dávalos 2005). Model parameters were unconstrained and unlinked between partitions. Two independent runs of 1 million generations using four Markov chains were conducted for each data set. Trees were sampled every 100 generations, and the first 10,000 generations were discarded as burn-in. Bayesian posterior probabilities (BPP) for branches and parameter estimates were concordant in separate runs, with one exception (see below). Table 4.2 summarizes the parameters obtained through Bayesian analyses for each of the two data sets.

The majority–rule consensus trees obtained through Bayesian analyses were congruent with the ML trees, with the exception of the position of *Pteronotus psilotis* (sister to the *P. parnellii* lineage with 0.54 BPP; or sister to a clade formed by *P. quadridens–macleayii* and *P. davyi* with 0.53 BPP in a separate run). Figure 4.1 shows the phylogenetic relationships of (A) Natalidae and outgroups and (B) Mormoopidae, Phyllostomidae, and outgroup obtained through ML analysis of concatenated sequences using PAUP* (Swofford 2002). The ML trees are congruent with those obtained through Bayesian analysis using MRBAYES,

Table 4.1. Species, molecular sequences, and geographic distribution

Taxon	12S tRNA ^{val} 16S	cyt <i>b</i>	<i>Rag2</i>	Geographic distribution
<i>Molossus molossus</i>	AF263215	L19724	AY141017	CA, SA, GA, LA
<i>Myotis velifer</i>	AF263237	AF376870	AY141033	NA, CA
<i>Myotis riparius</i>	AF263236	AF376866	AY141032	CA, SA
<i>Nyctiellus lepidus</i>		AY621006 ^a	AY604463 ^a	GA
<i>Chilonatalus tumidifrons</i>		AY621027 ^a	AY604464 ^a	GA
<i>Chilonatalus micropus</i>	AF345925	AF345925	AY141023	GA
<i>Natalus mexicanus</i>		AY621013 ^a	AY604467 ^a	NA, CA
<i>Natalus jamaicensis</i>		AY621022 ^a	AY604466 ^a	GA
<i>Natalus major</i>		AY621020 ^a	AY604465 ^a	GA
<i>Natalus tumidirostris</i>		AY621008 ^a	AY604468 ^a	SA
<i>Natalus stramineus</i>	AF345924	AF345924	AY141024	LA
<i>Noctilio leporinus</i>	AF263224	AF330796	AF316477	CA, SA, GA, LA
<i>Pygoderma bilabiatum</i>	AY395826	AY604437 ^a	AF316483	SA
<i>Ametrida centurio</i>	AY395802	AY604446 ^a	AF316430	SA
<i>Sphaeronycteris toxophyllum</i>	AY395828	AY604451 ^a	AF316486	SA
<i>Centurio senex</i>	AF263227	AY604442 ^a	AF316438	CA, SA
<i>Ardops nichollsi</i>	AY395803	AY572336 ^a	AF316434	LA
<i>Ariteus flavescens</i>	AY395804	AY604436 ^a	AF316435	GA
<i>Stenoderma rufum</i>	AY395829	AY604431 ^a	AF316487	GA
<i>Phyllops falcatus</i>		AY604448 ^a	AY604453 ^a	GA
<i>Dermanura cinerea</i>	AY395810	ACU66511	AF316443	CA, SA
<i>Erophylla sezekorni</i> ^b	AY395839		AF316450	GA
<i>Erophylla bombifrons</i> ^b		AY620439 ^a		GA
<i>Phyllonycteris aphylla</i>		AF187033	AF316478	GA
<i>Brachyphylla cavernarum</i>	AY395806	AY572365	AF316436	GA, LA
<i>Glossophaga soricina</i>	AY395840	AF423081	AF316452	CA, SA
<i>Monophyllus redmani</i>	AY395824		AF316473	GA
<i>Anoura caudifer</i> ^b	AY395835	L19506		SA
<i>Anoura geoffroyi</i> ^b			AF316431	CA, SA
<i>Pteronotus portoricensis</i>		AF338665		GA
<i>Pteronotus pusillus</i>		AY604454 ^a		GA
<i>Pteronotus rubiginosus</i>	AF407180	AF330807	AF330817	SA ^c , EG
<i>Pteronotus ribiginosus</i>	AF407181	AF338667		NA, CA, SA ^c
<i>Pteronotus parnellii</i>		AY604456 ^a		GA
<i>Pteronotus davyi</i>	AF407176	AF338671	AF338692	NA, CA
<i>Pteronotus fulvus</i>		AF338672	AF338693	LA
<i>Pteronotus gymnotus</i>	AF407177	AF338674	AF338694	NA, CA, SA
<i>Pteronotus quadridens</i>	AF407179	AF338683	AF338695	GA
<i>Pteronotus macleayii</i>	AF407178	AF338700	AF338700	GA
<i>Pteronotus psilotis</i>	AF407182	AY604457	AY245416	NA, CA, SA ^c
<i>Mormoops megalophylla</i>	AF407174	AF330808	AF330818	NA, CA, SA
<i>Mormoops blainvillei</i>	AF407172	AF338685	AY028169	GA

Note: Geographic distribution obtained from Koopman 1994. GenBank accession numbers are given below the gene names. NA = North America; CA = Central America; EG = East Guianas (Surinam and French Guiana); SA = South America; GA = Greater Antilles (includes the Bahamas); LA = Lesser Antilles.

^aGenerated as part of this study.

^bConcatenated "hybrid" sequences.

^cDistribution of the lineage represented by this population, following Dávalos 2006.

Table 4.2. Maximum likelihood and Bayesian parameters using the GTR+ Γ +I model of nucleotide evolution

Data set	Method	R-matrix	Base frequencies	I	α
Natalidae and outgroups	ML	7.212, 12.307, 7.368, 0.735, 64.041, 1.000	0.349, 0.216, 0.172, 0.264	0.179	0.244
mtrDNA	Bayesian	10.065, 16.519, 13.068, 0.175, 71.157, 1.000	0.382, 0.192, 0.165, 0.258	0.200	0.453
<i>cyt b</i>	Bayesian	2.297, 9.016, 2.398, 0.111, 39.327, 1.000	0.316, 0.293, 0.118, 0.273	0.552	1.868
<i>Rag2</i>	Bayesian	4.242, 12.183, 2.265, 2.111, 15.136, 1.000	0.309, 0.214, 0.216, 0.261	0.484	21.089
Mormoopidae, Phyllostomidae, and outgroup	ML	4.017, 10.650, 3.531, 0.784, 40.551, 1.000	0.352, 0.261, 0.165, 0.221	0.456	0.469
mtrDNA	Bayesian	8.268, 15.766, 6.217, 0.140, 73.090, 1.000	0.384, 0.228, 0.164, 0.224	0.449	0.577
<i>cyt b</i>	Bayesian	0.686, 21.762, 1.780, 1.614, 31.353, 1.000	0.363, 0.378, 0.067, 0.191	0.497	0.735
<i>Rag2</i>	Bayesian	1.147, 5.172, 0.407, 1.330, 8.173, 1.000	0.298, 0.226, 0.220, 0.256	0.531	3.24

Note: I = proportion of invariant sites; α = shape parameter of the Γ distribution.

with the exception of the position of *Pteronotus psilotis*, as explained above. Maximum parsimony analyses using PAUP* (Swofford 2002) were conducted as described previously (Dávalos 2005), and the results were consistent with the trees obtained through ML and Bayesian analyses. Because of conflict surrounding the position of *P. psilotis*, and the resolution among *P. davyi*, *P. gymnonotus*, and *P. fulvus*, the branches resolving these relationships were collapsed for subsequent analyses of geographic distribution and divergence time.

Optimization of Geographic Distribution

Geographic distributions for each lineage were coded as a five-state character as shown in table 4.1. Taxa distributed across more than one region were coded as polymorphic for this character. Geographic distributions were mapped onto the ML phylogenies using MacClade 4.0 (Maddison and Maddison 2003). The phylogeny of mormoopids was modified to reflect the uncertain relationships of *Pteronotus psilotis* and *P. davyi*, and close relatives, as discussed above. Both accelerated transformation (acctran) and delayed transformation (deltran) were implemented; if results conflicted, the branch was coded as equivocal.

Estimation of Divergence Times

The Thorne and Kishino method (Kishino et al. 2001; Thorne et al. 1998) was applied to estimate divergence times. This method accounts for constraints based on unconnected data sources such as the fossil record, while allowing for independent rates of molecular evolution along tree branches. The ML tree topology for each data set (modified slightly for mormoopids) was used to estimate parameters of sequence evolution using PAML 3.14 (Yang 1997). The model of sequence evolution used was F84 (Felsenstein 1984), which allows for a transition/transversion parameter with a gamma rate distribution in four discrete categories. Branch lengths were estimated with the *estbranches* program of Thorne et al. (1998) for each of the two data sets. Divergence times were estimated using the program *multidivtime* (Kishino et al. 2001; Thorne et al. 1998). Markov chain Monte Carlo analyses ran for 1 million generations with a 100,000-generation burn-in, and chains were sampled every 100 generations.

The mean of the prior distribution of the root of the ingroup tree of natalids and their sister group (Vespertilionoidea) was set at 50 Ma, accounting for middle Eocene molossid and vespertilionid fossils (McKenna and Bell 1997), with a standard deviation of half the mean. The mean of the prior distribution of the root of the ingroup tree of Mormoopidae and Phyllostomidae was set at 36 Ma, in accordance with the recent discovery of Oligocene mormoopid remains in Florida (Czaplewski and Morgan 2003), with a standard deviation of half the mean. Each of these mean priors matches the node age estimated from 17 nuclear gene sequences, and calibrated with other fossil constraints, for the tree of all bat families (Teeling et al. 2005). The rate of molecular evolution

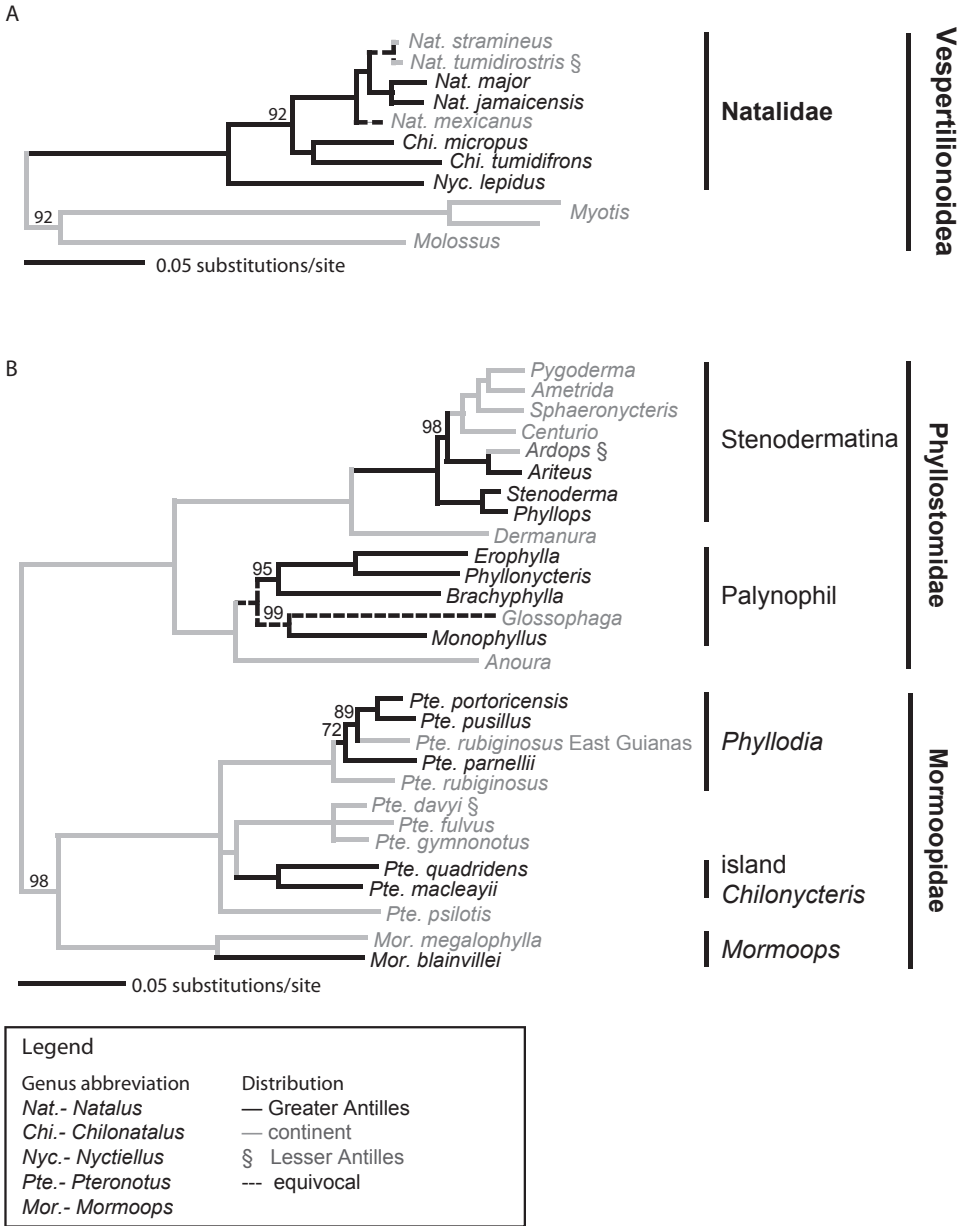


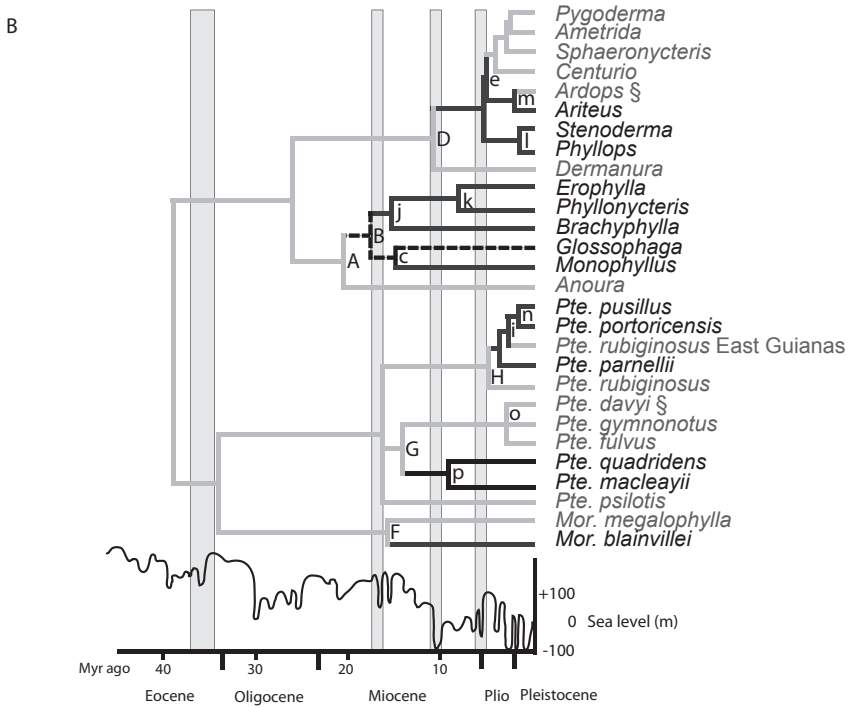
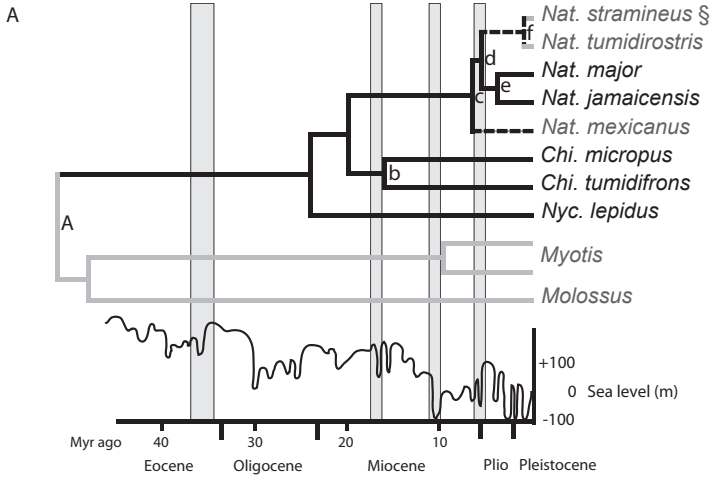
Figure 4.1. Phylogenies and optimization of geographic distribution for endemic Caribbean bats. Nodes are labeled with Bayesian posterior probability expressed as a percentage, when different from 1.00. Relationships depicted were also consistent with maximum parsimony and maximum likelihood analyses. The descendants of the most recent common ancestor of *Erophylla* and *Monophyllus* are herein named Palynophil (Chiroptera: Phyllostomidae), in reference to their love of pollen. *A*, Phylogeny of Natalidae and close relatives (superfamily Vespertilionoidea). *B*, Phylogeny of Mormoopidae and relevant Phyllostomidae.

Table 4.3. Ninety-five percent confidence intervals around time estimates for selected nodes in figure 4.2.

Node	Divergence time estimate (Ma) if $sd_{rate} = mean_{rate}$	Divergence time estimate (Ma) if $sd_{rate} = mean_{rate}/2$
Natalidae and outgroups (A)		
a	50.9 (31.1–89.0)	54.9 (33.2–88.6)
b	15.7 (7.4–32.5)	17.0 (7.6–33.3)
c	6.3 (2.5–14.6)	7.0 (2.6–15.7)
d	5.3 (2.1–12.4)	5.9 (2.2–13.2)
e	3.6 (1.3–8.6)	3.9 (1.4–9.0)
f	0.7 (0.1–2.1)	0.8 (0.1–2.3)
Mormoopidae and Phyllostomidae (B)		
a	19.9 (14.6–30.6)	18.9 (14.4–26.9)
b	17.0 (12.3–26.2)	16.2 (12.1–23.3)
c	14.5 (10.2–22.9)	13.8 (10.1–20.1)
d	10.6 (7.2–16.7)	10.0 (7.1–14.9)
e	4.9 (3.2–7.8)	4.7 (3.2–7.0)
f	15.3 (10.7–24.0)	14.7 (10.6–21.5)
g	13.6 (9.5–21.4)	13.1 (9.5–19.2)
h	4.7 (3.0–7.7)	4.5 (3.0–7.0)
i	2.7 (1.5–4.7)	2.6 (1.4–4.3)
j	14.9 (10.5–23.1)	14.2 (10.4–20.7)
k	7.8 (4.7–12.8)	7.4 (4.6–11.6)
l	1.5 (0.8–2.6)	1.4 (0.8–2.4)
m	2.0 (1.2–3.3)	1.9 (1.2–3.0)
n	1.5 (0.8–2.7)	1.5 (0.8–2.5)
o	2.8 (1.8–4.7)	2.7 (1.8–4.3)
p	8.9 (5.9–14.4)	8.6 (5.9–12.8)

was estimated as the median of tip-to-root branch lengths over the mean of the prior distribution of the root. The median of the three partitions corresponded to the rate of evolution of mitochondrial ribosomal DNA (12S, tRNA^{val}, and 16S). The standard deviation of the rate of molecular evolution was set to half the rate itself. To compare the effects of prior selection, parallel analyses using a standard deviation equal to the molecular evolution rate were conducted, assuming minimal prior knowledge. The differences between estimates of the mean divergence time were generally on the order of 50,000–500,000 years for the mormoopid and phyllostomid data set, and (exceptionally) up to 5 million years for the oldest divergence in the vespertilionoid data set (table 4.3).

The following fossil constraints applied to the data set of natalids and outgroups: (1) minimum 37 Ma for Molossidae to Vespertilionidae, assuming an end of the middle Eocene date for molossid and vespertilionid fossils (McKenna and Bell 1997); (2) minimum 30 Ma for Natalidae to Molossidae/Vespertilionidae (Morgan and Czaplewski 2003); and (3) minimum of 0.01 Ma for *Chilonatalus micropus* to *Chilonatalus tumidifrons* (Morgan 1993). The following fossil constraints applied to the data set of Mormoopidae and Phyllostomidae:



Legend

Genus abbreviation	Distribution
<i>Nat.</i> - <i>Natalus</i>	— Greater Antilles
<i>Chi.</i> - <i>Chilonatalus</i>	— continent
<i>Nyc.</i> - <i>Nyctiellus</i>	§ Lesser Antilles
<i>Pte.</i> - <i>Pteronotus</i>	--- equivocal
<i>Mor.</i> - <i>Mormoops</i>	

(1) minimum of 36 Ma for Mormoopidae to Phyllostomidae (Czaplewski and Morgan 2003); (2) minimum of 12 Ma for *Anoura* to *Dermanura* (Czaplewski et al. 2003); and (3) minimum of 0.01 Ma for *Phyllops* to *Stenoderma* (Morgan 2001). To compare the effects of phylogenetic uncertainty surrounding the nectar-feeding fossil *Palynephyllum antimaster* (Czaplewski and Morgan 2003), parallel analyses without constraint number 2 were conducted. Differences between estimates of the mean divergence time were on the order of 10,000–100,000 years. Figure 4.2 shows the timing of divergences in (A) Natalidae and outgroups and (B) Mormoopidae, Phyllostomidae, and outgroup.

The History of Caribbean Endemic Bats

How Did Bats Reach the Antilles?

To facilitate discussion, the descendants of the most recent common ancestor of *Erophylla* and *Monophyllus* are hereafter called Palynophil after the Greek *palyin*, “pollen,” and *phil*, “love.” The monophyly of each of the groups analyzed here—*Mormoops*, the subgenus *Phyllodia* (*Pteronotus parnellii* sensu lato), the insular species of the subgenus *Chilonycteris* (*Pteronotus macleayii* and *P. quadridens*), Palynophil, Stenodermatina, and Natalidae—was supported with Bayesian posterior probability (BPP) of 1.00 and maximum likelihood bootstrap (MLB) of 100% (except Palynophil, MLB = 73%). These phylogenies fit the branching pattern expected if a single ancestor had used a land bridge to reach the islands. The divergence dates corresponding to primary dispersal from the continent to the West Indies, however, reject the Oligocene land-bridge hypothesis (nodes in uppercase in fig. 4.2). Five out of six divergences—all but the Natalidae—have 95% confidence intervals (CI) that exclude the period when the land bridge would have existed (table 4.3). The divergence time between natalids and relatives is compatible with the land bridge, but Eocene-age fossils of the two closest extant relatives of natalids (Molossidae and Vespertilionidae) in Europe and North America, and one Oligocene natalid fossil from Florida, imply a northern origin for this West Indian lineage (McKenna and Bell 1997; Morgan and Czaplewski 2003). The South America–West Indies land bridge could not have played a role in the dispersal of natalids to the islands. Fossil evidence, though fragmentary, is also consistent with a post-Oligocene origin

Figure 4.2. Phylogeny and molecular timescale, with eustatic sea-level curve of Haq et al. 1993. Branch lengths are calibrated to match divergence times estimated using the Thorne and Kishino method, and each calibrated with three fossil constraints (McKenna and Bell 1997). Geological events indicated by *shading* include the period when Gaarlandia was exposed around the Eocene/Oligocene transition (Iturralde-Vinent and MacPhee 1999), and transitions that were marked by relatively low sea levels from the early to middle Miocene (~16 Ma), middle to late Miocene (~11 Ma), and Miocene to Pliocene (~5 Ma). *A*, Phylogeny of Natalidae and close relatives (superfamily Vespertilionoidea). *B*, Phylogeny of Mormoopidae and relevant Phyllostomidae.

for the remaining five bat groups. The oldest West Indian bat fossils in all lineages are from the Pleistocene and Holocene epoch (<2 million years old) (McKenna and Bell 1997; Morgan 2001).

These results suggest an alternative to the land–bridge model based on the exposure of submerged landmasses during periods of exceptionally low sea level in the Miocene. Four of six continent–to–Caribbean shifts coincide with Miocene transitions marked by exceptionally low sea levels (the average age of each *A* node in fig. 4.2 is older than the earliest Miocene transition). The 95% CI of a fifth divergence includes the early/middle Miocene boundary (node *A* in fig. 4.2A, table 4.3). Miocene transitions also mark Antillean–to–continent and geographically ambiguous shifts (fig. 4.1): three of five divergences correspond to eustatic lows, and the remaining two are compatible with them (*d* or *f* in fig. 4.2A; the 95% CI of *i* in fig. 4.2B spans the Miocene/Pliocene boundary). The effect of the Miocene transitions can also be seen in the speciation of ancient Caribbean lineages such as *Chilonatalus*, the divergence of *Brachyphylla* from *Erophylla* (fig. 4.2), and, possibly, speciation in *Chilonycteris* and the divergence of *Erophylla* from *Phyllonycteris* (table 4.3, fig. 4.2).

The Caribbean Sea Is a Two-Way Street

We take for granted that insular populations must have a continental origin, and not the other way around. The distinction between “islands” that acquire their biota from a larger “source” supports this notion. There is, however, no fundamental mechanism in the equilibrium theory of island biogeography to preclude island species from colonizing the mainland (MacArthur and Wilson 1963, 1967). The belief in one-way biogeographic traffic has only begun to erode as phylogenetic analyses have revealed insular origins for continental passerines, rodents, and lizards (Barker et al. 2002; Filardi and Moyle 2005; Glor et al. 2005; Jansa et al. 1999; Nicholson et al. 2005). Among plants, the genus *Exostema* has successfully diversified in the continental Neotropics, while two populations in the angiosperm genus *Erithalis* have colonized Florida (Santiago–Valentin and Olmstead 2004). At least two Neotropical bat lineages must now be added to the growing list of island–to–continent colonizers.

It is generally assumed that *Mormoops* reached the Caribbean several times, once for *blainvillei*, a second time for the Greater Antillean fossils assigned to *megalophylla*, and perhaps a third time for *magna* (Baker and Genoways 1978; Griffiths and Klingener 1988; Koopman 1989). Species limits and relationships among these populations are unresolved because *M. magna* is only known from scattered humeri, and the fossil range of *M. megalophylla* has not been thoroughly studied (Morgan 2001; Silva Taboada 1979). The extant diversity by itself would result in a simple scenario whereby a continental lineage reached the Antilles in a single colonization from the continent (fig. 4.1). The distribution of the *M. megalophylla* and *M. magna* fossils in Cuba and, to a lesser extent, the deep molecular divergence between extant taxa point to the northern Neo-

tropics as the ancestral area of *Mormoops* (Dávalos 2006). Barring the discovery of ancient mainland fossils, a West Indian origin for the genus seems more likely than not.

Each of the three Antillean lineages of *Pteronotus* descended from mainland ancestors, but one lineage of *Phyllodia*—the unnamed east Guianan populations currently assigned to *rubiginosus*—might be a colonist from the Antilles (fig. 4.1). Relationships within *Phyllodia* are among the least supported in the phylogeny (fig. 4.1), making this result tentative. Two Caribbean fossil species, the Hispaniolan *Pteronotus* sp. and the Cuban *P. pristinus*, are thought to be part of the *Phyllodia* lineage (Morgan 2001; Simmons and Conway 2001). The similarities in size between *Pteronotus* sp. and continental *Phyllodia* (Morgan 2001), and the possible insular ancestry of east Guianan *Pteronotus rubiginosus*, suggest a complex geographic history of colonization to and from the Caribbean for this subgenus (Dávalos 2006).

There is phylogenetic evidence for one Caribbean radiation in the phyllostomid family (Dávalos 2007), the subtribe Stenodermatina or short-faced bats, with a single continental lineage descended from West Indian ancestors (fig. 4.1). An alternative interpretation would be to code the continent as a single area (here it is coded as three areas; see table 4.1), whereby primary dispersal to the Caribbean followed by back-colonization to the continent would be as parsimonious as two dispersals to the islands by a “continental” ancestor. The first biogeographic interpretation is adopted in this chapter based on the primitive features of the recently described extinct short-faced bat *Cubanycteris*, as well as the separation of continental landmasses at the time of dispersal (fig. 4.2, although see Duque-Caro 1990 for an alternative scenario). The possibility that *Cubanycteris* constitutes a third independent and early-branching West Indian short-faced lineage will have to be evaluated with phylogenetic analyses of morphology to further support this interpretation.

The Palynophil might constitute another Antillean radiation, but the optimization of geographic distributions could correspond to the continent, the islands, or both (fig. 4.1). A middle Miocene fossil from La Venta (Colombia) places primitive nectar-feeding bats in northern South America (Czaplewski et al. 2003), but relationships to extant species are unclear. The fossil could be most closely related to (1) the Palynophil and place the early distribution of this group on the continent; (2) the sister to Palynophil and leave the basal distribution of the radiation ambiguous; (3) an extinct lineage older than the split between Palynophil and its sister and again lead to ambiguity; or (4) an entirely unrelated lineage, and have no bearing on the issue (fig. 4.3). If the Palynophil were Caribbean, the *Glossophaga–Leptonycteris* lineage would be one more example of island-continent colonization (fig. 4.1; *Leptonycteris* is not shown but is sister to *Glossophaga* with 1.00 BPP and 87% MLB support).

One family of insectivorous bats, the Natalidae, has been endemic to the West Indies, probably since the beginning of its evolutionary history (Dávalos

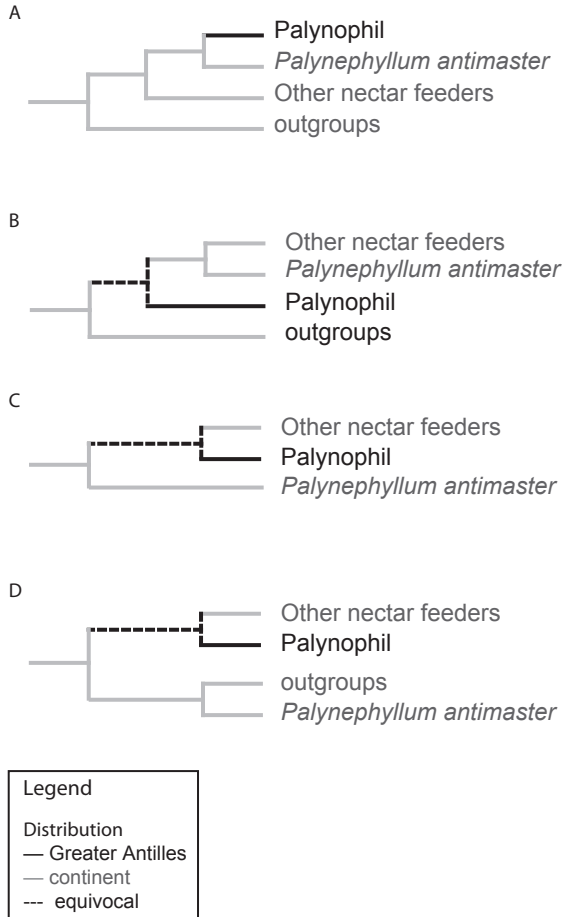


Figure 4.3. Four possible relationships of the middle Miocene fossil *Palynephyllum antimaster* (Czaplewski et al. 2003). A, As sister to Palynophil. B, As sister to the extant sister of Palynophil. C, As sister to the ancestor of Palynophil. D, As sister to an outgroup (e.g., Lonchophyllini).

2005). Two independent lineages of *Natalus* have reached the mainland (fig. 4.1), and several continental populations remain to be sampled.

In short, there is some phylogenetic and fossil evidence to suggest that *Mormoops* and *Phyllodia* are Antillean radiations whose descendants have reached the mainland once or twice. Current data are ambiguous about the geographic origin of Palynophil. The phylogenies of short-faced bats and natalids also indicate their continental species are derived from Caribbean ancestors. In all, between three and six lineages ranging from Sonora, Mexico (natalids) to Para-

guay (*Pygoderma*) most likely trace their history back to the West Indies. The Caribbean origin of these lineages might help explain some of their ecological characteristics: for example, cave roosting among natalids (Dávalos 2005). From a mechanistic perspective, an upper limit in tolerance to interspecific competition has been thought to restrict endemic Caribbean birds to the islands (Terborgh and Faaborg 1980). The distribution of continental bats of Caribbean ancestry belies this ecological restriction. *Centurio*, *Ametrida*, *Sphaeronycteris*, and *Natalus* are known from lowland Central American and Amazonian forests whose species richness is >50 species (Simmons and Voss 1998), and *Pygoderma* is known from the Atlantic forest and Cerrado of Paraguay and Brazil, again in sympatry with >50 species (Marinho-Filho 1996a, 1996b; Willig et al. 2000).

Only two vertebrate groups—bats and anoles—have phylogenies that strongly support West Indian origin for extant continental species. Phylogenetic analyses have revealed that dispersal from the Caribbean likely gave rise to an evolutionary radiation of anoles in Central America and South America (Nicholson et al. 2005), and at least one instance of dispersal out of Cuba coincides with the Miocene/Pliocene transition (Glor et al. 2005). Until now no single overarching hypothesis has been advanced to explain how these Caribbean endemics reached the continent, or how their ancestors reached the West Indies in the first place. The results presented here show that sea-level changes in the Miocene constitute a viable mechanism for facilitating dispersal between landmasses in the Caribbean.

The Deep Roots of Caribbean Bat History

The Caribbean bat community has been structured, at least in part, by geological changes that allowed short bursts of biotic exchange with other islands and with the mainland. During the early Miocene, Cuba, Hispaniola, and Puerto Rico were emergent, and western Cuba was separated by the Havana–Matanzas channel from the block formed by eastern Cuba, northern Hispaniola, and Puerto Rico (Graham 2003; Iturralde-Vinent and MacPhee 1999). The rise in sea level following the early/middle Miocene transition (Haq et al. 1993; Miller et al. 1996), probably in combination with the definitive separation of Cuba from northern Hispaniola and Puerto Rico, isolated populations of *Chilonatalus*, and *Brachyphylla* from the ancestor of *Erophylla*–*Phyllonycteris* (fig. 4.2). Abrupt changes in the benthic fauna signal uplift along the Isthmus of Panama, and perhaps a temporary closure of the isthmus, during the middle/late Miocene transition (Duque-Caro 1990; Roth et al. 2000). This might explain how the South American ancestors of the Stenodermatina reached Central America, and through it, the Greater Antilles (fig. 4.2). At the closing of the Miocene, Jamaica had reemerged, the Havana–Matanzas channel had disappeared, and northern and southern Hispaniola were united, matching the modern Greater Antillean contours (Iturralde-Vinent and MacPhee 1999). By the early Pliocene

the Stenodermatina reached Jamaica (*Ariteus*), the Lesser Antilles (*Ardops*), and the Neotropical mainland, mirroring the expansion of natalids to Jamaica (*Natalus jamaicensis*), the Lesser Antilles (*N. stramineus*), and Central America (*N. mexicanus*) and in synchrony with another eustatic decline. As the Miocene ended, *Phyllodia* was the last of the mormoopids to colonize the Greater Antilles (fig. 4.2).

By the Pliocene frugivores (Stenodermatina), pollen/nectar feeders (Palinophil), and three lineages of mormoopid insectivores were already part of the Caribbean bat community. Griffiths and Klingener (1988) suggested that eustatic minima caused by glacial cycles in the Pleistocene could help explain West Indian bat biogeography. Only one of the island-to-continent dispersal nodes (*i* in fig. 4.2B) might be compatible with this mechanism, and even the most recent primary dispersal node (*H* in fig. 4.2B) is too old to fit the Pleistocene hypothesis (table 4.3). Several island-island diversification events, however, are potentially compatible with a Pleistocene isolation model, suggesting a more localized role for this mechanism than previously believed (*i* in fig. 4.2A; and *m*, *l*, *i*, and *n* in fig. 4.2B). Because this study has narrowly focused on endemic genera and subgenera, the role of Plio-Pleistocene sea-level changes in the dispersal and diversification of nonendemic groups remains to be evaluated.

Conclusions

Dispersal events in West Indian vertebrates were constrained to narrow windows of time, even among flying organisms that presumably need no raft to breach ocean barriers. In fact, the flying abilities of bats do not mean they can disperse across oceanic barriers easily: most West Indian bats hardly tolerate hunger, and are highly susceptible to desiccation (Silva Taboada 1979). Periods of exceptionally low sea level have facilitated dispersal by decreasing the separation between landmasses, leading to congruent temporal divergences that should be common to many other organisms. This mechanism is an alternative hypothesis to land bridges or pure dispersal, and can readily be tested at other locations and for other groups (see, for example, Mercer and Roth 2003). The striking congruence across multiple bat groups found here underscores the influence of geological history in all biogeographic scenarios, including dispersal.

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