Phylogeny and biogeography of Caribbean mammals

LILIANA M. DÁVALOS*

Department of Ecology, Evolution and Environmental Biology, Columbia University and Division of Vertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street New York, NY 10024–5192, USA

Received 28 February 2003; accepted for publication 7 August 2003

Vicariance and dispersal hypotheses have been proposed over the last two hundred years to explain the distribution, diversity, and faunal composition of the Caribbean biota. Despite great advances in understanding the geological history of the region, recent biogeographical reviews have not used historical biogeographical methods. In this paper I review the taxonomy, distribution and phylogeny of all Cenozoic Caribbean non-volant mammals and four bat lineages, and present reconciled trees for available phylogenies. Dates available from the fossil record and hypotheses of divergence based on molecular phylogenetic studies are also included in general assessments of fit between proposed geological models and Caribbean mammal diversification. The evidence posited in mammalian phylogenies does not add to the argument of dispersal vs. vicariance. One previously unidentified temporal pattern, the colonization of the Caribbean by South American mammals between the Paleocene and the Middle Miocene, accounts for the distribution and phylogeny of the majority of lineages studied. Choloepodine and megalocnine sloths, hystricognath rodents, and primates all arrived during this window of colonization. Of these, megalocnine sloths, hystricognath rodents, Brachyphylla and allied bats, Stenodermatina bats, and primates fit the pattern of divergence from the mainland implied by the Gaarlandia hypothesis. Sloths, rodents and primates also roughly fit the timing of arrival to the Caribbean implied by Gaarlandia. The remaining taxa show contradictory dates of divergence according to molecular clock estimates, and no taxa fit the predicted timing and pattern of divergence among Antillean landmasses under the Gaarlandia model. Choloepodine sloths, murid rodents, insectivorans, mormoopids, and natalids show patterns of divergence from the mainland that are inconsistent with the Gaarlandia hypothesis and seem to require taxon-specific biogeographical explanations. © 2004 The Linnean Society of London, Biological Journal of the Linnean Society, 2004, 81, 373–394.


INTRODUCTION

Explaining both the uniqueness and diversity of the fauna of the islands of the Caribbean Sea has been the objective of biologists for two centuries (Wallace, 1881; Woods, 2001). To this end, evidence from geology, phylogeny, and ecology has been accumulating at a particularly rapid rate over the last three decades (see papers in Woods, 1989a; Woods & Sergile, 2001). Despite these efforts the origins and patterns of diversification of the Caribbean biota are far from clear for most groups, and the debate on the historical biogeography of Caribbean vertebrates continues unabated (Williams, 1989; Woods, 2001).

The most contentious debate on the historical biogeography of the Caribbean concerns the relative roles of dispersal and vicariance in shaping its fauna. Hedges and colleagues (Hedges, Hass & Maxson, 1992, 1994; Hedges, 1996a,b, 2001) have argued that the fauna of the region shows a pattern of concordant dispersal from South America throughout the Cenozoic. Numerous others have argued that taxonomic, and more recently, phylogenetic congruence points toward a vicariant origin of the Caribbean fauna (Crother & Guyer, 1996; Rosen, 1975, 1985; Liebherr, 1988; Page & Lydeard, 1994; Guyer & Crother, 1996). While some vicariant models (e.g. Rosen, 1975) can be
rejected given the estimated timing of emergence of Caribbean islands, the vicariant model of Iturralde-Vinent & MacPhee (1999; MacPhee & Iturralde-Vinent, 1994, 1995, 2000) represents the most serious challenge to the dispersal hypothesis of Hedges and colleagues. According to the vicariance model of Iturralde-Vinent & MacPhee (1999), derived from geological hypotheses outlined below, a land bridge between the Greater Antilles and northern South America around the Early Oligocene allowed the continental South American fauna to reach the islands. Subsequent severance of the land bridge later resulted in vicariance of different lineages from their mainland relatives and among populations in Caribbean islands. This hypothetical land bridge has been called the Gaarlandia (Greater Antilles and Aves Ridge) land span.

The geology of the Caribbean region is complex, involving the Caribbean, Pacific (including Cocos and Nazca), South American, and North American tectonic plates (Meschede & Frisch, 1998: fig. 2). Pindell (1994) and Meschede & Frisch (1998) among others have recently reviewed the early history of the region. The Antilles were formed as a result of the subduction of the North American plate beneath the Caribbean plate in the Middle to Late Cretaceous, but the precise time of their emergence as subaerial entities is not known. At the time of the Cretaceous–Tertiary boundary, about 65 Mya, an asteroid penetrated the atmosphere and the resulting dust clouds disrupted photosynthesis worldwide (Alvarez et al., 1980). The Chicxulub crater in the Yucatán peninsula is considered the site of impact of this asteroid (Claeys et al., 1998). Massive earthquakes (Claeys et al., 1996), continental margin failures (Norris et al., 2000), ejecta and tsunamis (Grajales et al., 2000) followed the asteroid impact in the Caribbean. This led Hedges et al. (1992) to propose that the asteroid impact decimated the ancient Caribbean land biota, and to explain the current faunal assemblage as a result of repeated colonization from South America thereafter.

Iturralde-Vinent & MacPhee (1999) proposed that the Aves ridge connected the already emergent Greater Antilles (Cuba, Hispaniola, Puerto Rico) to northern South America during the Late Eocene/Early Oligocene transition (35–33 Mya). This hypothesis is based on the incidence of general uplift and major sea level drops at the beginning of the Oligocene (Haq, Hardenbol & Vail, 1993; Miller et al., 1996). The connection could have been an island chain (Perfit & Williams, 1989) or a dry land bridge (Iturralde-Vinent & MacPhee, 1999). By the Late Oligocene, sea level rose and land exposure declined. Emergent land areas including Cuba, Hispaniola, Puerto Rico, and the Aves ridge were further isolated as a consequence of active tectonic disruption of the northern and southern Caribean plate boundaries (Perfit & Williams, 1989; Iturralde-Vinent & MacPhee, 1999). Jamaica had been largely emergent during the Cretaceous/Eocene transition (Portell, Donovan & Domning, 2001), but was submerged during most of the Oligocene (Robinson, 1994). From the Miocene to the Early Pliocene (between 24 and 5 Mya), the Caribbean plate continued to move eastward in relation to the American plates causing uplift and emergence of most of the islands, including Jamaica (Perfit & Williams, 1989). In the Late Miocene (9 Mya), ‘stepping stone’ connections between North and South America first became available.

By the Pliocene, the general configuration of the Antilles, including the Lesser Antilles and Jamaica, resembled the present, with sea level changes associated with glaciations playing a larger role in shaping subaerial margins. The Bahamas, for instance, are thought to be the product of sea level changes in the Late Quaternary (Hearty, 1998). Sea level has peaked at or above present levels at least three times over the past 0.45 Myr (Hearty & Kaufman, 2000), with a similar number of drops exposing landmasses that could have served as stepping-stones for relatively vagile land organisms. A summary of area relationships expected from geological hypotheses beginning with the Late Eocene/Early Oligocene transition is shown in Figure 1.

Both the vicariance and dispersal approaches are based on current geological hypotheses. The geological history of the Caribbean only loosely constrains the interpretation of biogeographical patterns and is the subject of much debate (Williams, 1989). In this context, the Caribbean vicariance/dispersal debate misses a fundamental question in historical biogeography: does the observed biogeographical pattern correspond to a general pattern of area interconnections, and thus reflect the history of those areas (Platnick & Nelson, 1978)? If most Caribbean lineages are monophyletic, and the arrival of their ancestors is constrained to a particular time, then the search for a common geological cause is warranted. Conversely, if most of the Caribbean fauna consists of independent lineages that reached the islands at disparate times, then the particulars of each radiation become more relevant than the pattern of interconnections among areas.

Recent reviews of the biogeography of Caribbean vertebrates (Hedges, 1996a) and mammals (MacPhee & Iturralde-Vinent, 2000) have not presented compelling phylogenetic (i.e., biological history) evidence for the preferred modes of explaining faunal assemblages. To evaluate the connection between the geological and biological history of the Caribbean, I review the taxonomy, distribution, and phylogeny of all Cenozoic non-volant West Indian mammals and four bat lineages, and evaluate the congruence between
phylogeny and geological hypotheses by generating reconciled trees.

**METHODS**

**GEOGRAPHIC SCOPE**

In this paper 'West Indies' is used in a biogeographical sense following the classification of Hershkovitz (1958), Morgan & Woods (1986), and Morgan (2001). The West Indies include the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico), Bahamas, Cayman Islands, Swan Islands, Virgin Islands and the Lesser Antilles south to St. Vincent and Barbados. Grenada and the Grenadines, Trinidad, Tobago, Margarita, and Aruba, Bonaire and Curacao are excluded from this definition of the West Indies, as their biota is more characteristic of continental South America. The terms 'Antillean', 'Caribbean', and 'West Indian', used in a faunal sense, are intended to be synonyms, and thus encompass all the islands defined above as part of the West Indies (Morgan, 2001).

**GEOLOGICAL AREA CLADOGRAM**

The geological hypothesis of area relationships shown in Figure 1 was pruned to make it amenable to com-

---

Figure 1. Expected area relationships among areas of endemism relevant to the Caribbean beginning in the Early Oligocene. Length of branches and distances among branches are not proportional to approximate timing, or distance among areas of endemism. The composite geological origin of Jamaica and Hispaniola is not depicted. Composite origins involving more than one geological unit have been proposed for western and eastern Jamaica (Robinson, 1994; Iturralde-Vinent & MacPhee, 1999), and the northern and southern part of western Hispaniola (Perfit & Williams, 1989). The hypothesized interconnection between the Aves Ridge and the Lesser Antilles via the Grenada basin is not depicted. The geological hypotheses relevant to this study correspond to the Oligocene and after because most of the Antilles was submerged or evanescent before that time (Robinson, 1994; Iturralde-Vinent & MacPhee, 1999). Aves = Aves Ridge, Baha = Bahamas, CeAm = Central America, Hisp = Hispaniola, Jama = Jamaica, LeAn = Lesser Antilles, NoAm = North America, NoSA = northern South America, Puer = Puerto Rico. Dotted line indicates connection via stepping-stone islands, grey part of branches indicates time when landmass was mostly submerged. The grey box implies cycling of isolation and near-interconnection events among islands. The pattern of area relationships expected from the Plio-Pleistocene is not resolved in strictly dichotomous form, given the short branches and repeated separations and reconnections among areas.
parison with taxon-area cladograms, and modified to include two areas whose fauna is hypothesized to have arrived by dispersal given current geological evidence: Jamaica & the Lesser Antilles. Iturralde-Vinent & MacPhee (1999) proposed the Jamaican Blue Mountains were emergent and interconnected to Gaarlandia, but this hybrid geological origin is not included in the hypothesis of area relationships used hereafter (Fig. 2). In addition to the geological hypotheses presented in the Introduction, another assumption underlies the area relationships of Figure 2: that Jamaica and the Lesser Antilles were colonized by dispersal from the nearest Caribbean landmass, rather than from Central America or northern South America. All subsequent biogeographical analyses interpret these two nodes of the geological area cladogram in light of the choice described above, since there is some biological evidence for such patterns of area relationships (Griffiths & Klingener, 1988; Koopman, 1989).

TAXONOMIC SCOPE

There are c. 60 extant and 75 extinct species of non-introduced Caribbean land mammals from the Late Quaternary and Recent, classified in 14 families and 5 orders (Morgan & Woods, 1986). The extinction of 75 species of mammals, 67 of them non-volant, in two spasms around 10 000 and 4500 years ago (Morgan & Woods, 1986) has been attributed to climate change (Pregill & Olson, 1981), Pleistocene overkill by newly arrived humans (Martin, 1967), and/or the spread of particularly virulent diseases associated with humans and their commensals (MacPhee & Marx, 1997). The number and classification of genera and species of Cenozoic and Recent Caribbean mammals are presented in Table 1.

Taxon-area cladograms

I analysed the following taxon cladograms using a computer implementation of reconciled trees (Page, 1993): (1) the two taxon cladograms for Caribbean ground sloths resulting from a cladistic analysis of 69 skeletal characters by White & MacPhee (2001); (2) the cladogram resulting from analyses of 82 morphological characters by Woods, Borroto & Kilpatrick (2001) for Antillean hystricognaths in the families Capromyidae, Echimyidae, and Heptaxodontiidae (often referred to as West Indian Caviomorpha); (3) four different chiropteran cladograms: (a) congruent results of molecular and morphological characters analyses for the family Mormoopidae (Lewis-Oritt, Porter & Baker, 2001; Simmons & Conway, 2001; Jones et al., 2002; Van Den Bussche, Hooper & Simmons, 2002), (b) the cladogram of the Brachyphylla–Erophylla–Phyllonycteris phyllostomid clade (Jones et al., 2002), (c) the cladogram of the phyllostomid tribe Stenodermatina (Jones et al., 2002), and (d) results of morphological character analyses for the family Natalidae (Morgan & Czaplewski, 2003); (4) the cladogram from the morphological character analysis including three extinct species of Antillean atelid primates by Horovitz & MacPhee (1999).

Finally, the taxon cladograms used in chiropteran reconciled tree analyses were updated following recent publications: extinct species Pteronotus pristinus and Mormoops magna added as sister to P. parnellii and M. megalophylla (Simmons & Conway, 2001); Erophylla sezekorni and E. bombifrons recognized as separate, sister species (Simmons, in press), and Phyllonycteris major added as part of a trichotomy with other Phyllonycteris; extinct Phyllops vetus added as sister to Phyllops falcatus; and Natalus major (Simmons, in press) comprising an unresolved

![Figure 2](image-url). Simplified strictly dichotomous area relationships for Caribbean landmasses. Note the addition of Jamaica and the Lesser Antilles (nodes with grey circles) as dispersal interconnection based on distance to other Antillean areas. See ‘Geological area cladogram’ under Methods, for details.
trichotomy of the nominate *N. primus*, *N. major*, and *N. jamaicensis* (A. Tejedor, V. d. C. Tavares & G. Silva-Taboada, unpubl. data). The Caribbean distribution of many bat species (Table 1) that are widespread throughout the Americas is not analysed in this article, since reconciled tree analysis is designed to investigate association between areas and differentiated lineages.

Other sources of information
In two cases taxon cladograms for Caribbean groups were not available: (1) the relationships among the eight species of Caribbean sigmodontine murids *Oryzomys* and *Megalomys* are not resolved because they are part of the vast sigmodontine radiation (Table 1), and (2) there are no phylogenetic analyses including both lineages of Caribbean insectivores (Table 1) relevant to this biogeographical study.

Because previous hypotheses regarding these groups are relevant to this mammalian biogeographical analysis, they are discussed in a comparative context despite the lack of cladograms. The temporal context of taxon cladograms, inferred from

the age of available fossils, and/or the dating of nodes by molecular techniques, is also discussed in light of the reconciled tree analyses.

The Eocene fauna of Seven Rivers, Jamaica, comprising a ?primate petrosal (MacPhee et al., 1999) and the lower jaw of the perissodactyl Hyrachythys (Domning et al., 1997), is not analysed further because the island was inundated from Middle Eocene to Late Miocene (Robinson, 1994). Hyrachythys is found in the Eocene in Europe, Asia, and North America (McKenna & Bell, 1997), perhaps suggesting Holarctic affinities for this Jamaican fauna.

**RECONCILED TREE ANALYSIS: COMPONENT**

The taxon-area cladograms listed above were mapped onto the hypothesized area cladogram obtained from geological evidence (Fig. 2) using Component ver. 2.0 for Windows (Page, 1993). The key concept in tree mapping is reconciling a tree for the taxa with a tree for the areas, under the assumption that the relationship between taxa and areas is due to ‘association by descent’ (Brooks & McLennan, 1991), or that areas and taxa evolve together. The analysis provides a measure of fit between taxa and area cladograms that generates hypotheses about the relative ages of divergence events for both taxa and areas, and can also be tested statistically. The taxon and area cladograms can be reconciled so that observed relationships between areas and taxa can be explained solely by ‘association by descent.’ To accomplish this the observed taxon cladogram is postulated as a subtree of a larger tree, a **reconciled** tree. This reconciled tree represents the complete taxon cladogram, of which the actual taxon tree is hypothesized to be a subsample or relict, given that extinction or incompleteness might have restricted taxon sampling.

Component reconciles trees by mapping the taxon cladogram to the area cladogram. The map requires that each node in the taxon cladogram is assigned to the smallest cluster in the area cladogram that contains the set representing the distribution of the taxa for each node in the taxon tree. All the nodes in the reconciled tree (a taxon tree) are therefore clusters of the area cladogram. If each node in the taxon tree maps onto a different node in the area cladogram then the associate tree is either identical with the area cladogram, or a consistent subtree of the area cladogram. If more than one taxon node maps onto the same node in the area tree then a duplication is postulated. Two kinds of duplication are recognized: those required because of incongruence between taxon and area cladograms, and those required because the descendants of a given taxon have overlapping ranges in an area (redundant nodes sensu Page, 1988).

Component assumes that the incongruence between area cladograms derived from different sources is due to poor taxonomic sampling and/or extinction, an idea originally proposed for area relationships by Nelson & Platnick (1981), who also counted dispersal as a source of error. Component maps all taxa onto the area cladogram, equivalent to the treatment of widespread taxa under ‘Assumption 0’ (Zandee & Roos, 1987), while the option of not mapping widespread taxa in the analysis implements ‘Assumption 1’ (Nelson & Platnick, 1981).

Component computes three measures of fit between taxon and area cladograms: the number of duplications, the number of leaves added, and the number of independent losses. Duplications are explained above, the number of leaves added is half of the difference between the number of terms and components in the reconciled tree and the original taxon cladogram (items of error sensu Nelson & Platnick, 1981), and losses are number of branches hypothesized to be missing in the process of reconciling the trees.

Additionally, I compared the observed number of leaves added and losses postulated in the reconciled tree with a distribution generated by mapping each taxon cladogram to 1000 random area cladograms (generated using the ‘Random trees’ command of the ‘Generate’ menu in Component). Comparisons with these distributions assessed the fit between observed taxon and area cladograms and the fit expected by chance alone.

**RESULTS**

**RECONCILED TREES**

Reconciled trees for the eight mammalian lineages analysed using Component are shown in Figures 3–10. All reconciled trees shown were obtained by plotting widespread distributions and assuming that absence from an area means information is missing. Because both taxon and area cladograms have to be fully resolved to use Component, the unresolved nodes present in taxon cladograms were resolved arbitrarily and this is noted here for reference in later discussion. The taxon cladograms used to generate Figures 3 and 4 (reconciled trees for meganychids) were both fully resolved and have no known representatives in Jamaica or the Lesser Antilles (White & MacPhee, 2001). The cladogram for South American hystricognath rodents contained one Jamaican representative (Geocapromys brownii) and numerous unresolved nodes (Fig. 5). The cladogram of mormoopids contained five Jamaican species and two unresolved nodes (Fig. 6). The cladogram of Brachyphylla–Phyllonycteris–Erophylla contained
three Jamaican species and one unresolved node (Fig. 7). The cladogram of the Stenodermatina has three unresolved nodes and a representative each in Jamaica and the Lesser Antilles (Fig. 8). The cladogram of the Natalidae has only one unresolved node, plus two species in Jamaica, and one in the Lesser Antilles (Fig. 9). Finally, the cladogram of Caribbean atelids shows one Jamaican species and no unresolved nodes (Fig. 10).

**Measures of fit**

Table 2 summarizes the measures of fit and statistical significance of the reconciled trees. The number of duplications caused by incongruence between taxon and area cladograms is highest in the *Brachyphylla–Phyllonycteris–Erophylla* clade, and lowest in mor-mopids, sloths, caviomorphs, and primates. In nearly every case interpreting ‘missing’ taxa as primitively
absent increases the number of losses and leaves added to reconcile taxon cladograms with the hypothesis of area relationships of Figure 2. For those groups including widespread taxa, removing them from analyses generally increased the fit between cladograms and area relationships. Choloepodine sloths, caviomorphs and bats showed significant measures of fit, while for other taxa the measures of fit observed were obtained by random chance between 5.3 and 35.9% of the time. The number of leaves in the reconciled area cladogram limits the measure of significance, i.e. in some cases the fit will not be significant simply because there are less than 20 permutations that reconciled the observed area with random taxon cladograms. Information on dates relevant to the reconciled cladograms (Figs 3–10) is summarized in Table 3. No molecular estimates of the divergence of relevant bats were found, and available Caribbean fossils were too recent (Pleistocene, if at all dated) to include in Table 3.

**Congruence between taxon and area cladograms**

Congruence varies among the taxa examined: of the non-volant mammals choloepodine sloths (Fig. 3) and

### Table 2. Mammalian lineages, biogeographical assumptions, and measures of fit for reconciled trees. Taxonomy follows McKenna & Bell (1997); taxonomy of bats follows Simmons (in press) unless otherwise noted. The interpretation of ‘missing’ taxa or absence of a clade from a particular area: ‘missing data’ = considered missing due to lack of data, ‘prim. absence’ = considered primitively absent. See Methods for explanation on measures of fit and obtaining significance values. I = duplication due to incongruence between taxon and area cladogram, O = duplication due to overlap among taxa. Total nodes includes all nodes seen in the figures except any CeAm-NoSA node among outgroups, codivergent nodes excludes nodes supported by taxa widespread across a node. *P < 0.05, **P < 0.01

<table>
<thead>
<tr>
<th>Lineage</th>
<th>Widespread taxa</th>
<th>Interpretation of missing taxa</th>
<th>Duplications</th>
<th>Measures of fit</th>
<th>Measures of codivergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td>I</td>
<td>O</td>
</tr>
<tr>
<td>Xenarthra</td>
<td></td>
<td></td>
<td>6</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Choloepodinae</td>
<td>Included</td>
<td>Missing data</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Prim. absence</td>
<td>6</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Megalocninae</td>
<td>Included</td>
<td>Missing data</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Rodentia</td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Antillean</td>
<td>Included</td>
<td>Missing data</td>
<td>11</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Hystercoptera</td>
<td>Included</td>
<td>Prim. absence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chiroptera</td>
<td></td>
<td></td>
<td>11</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Mormoopidae</td>
<td>Included</td>
<td>Missing data</td>
<td>8</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Prim. absence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Missing data</td>
<td>8</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Excluded</td>
<td>Missing data</td>
<td>8</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Excluded</td>
<td>Prim. absence</td>
<td>8</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Brachypilnia–</td>
<td>Included</td>
<td>Missing data</td>
<td>5</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Phylontycetes–</td>
<td>Included</td>
<td>Prim. absence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erophylla</td>
<td>Excluded</td>
<td>Missing data</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Excluded</td>
<td>Prim. absence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stenodermatina</td>
<td>Included</td>
<td>Missing data</td>
<td>6</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Prim. absence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Missing data</td>
<td>6</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Excluded</td>
<td>Missing data</td>
<td>6</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Excluded</td>
<td>Prim. absence</td>
<td>6</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Natalidae</td>
<td>Included</td>
<td>Missing data</td>
<td>7</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Prim. absence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Missing data</td>
<td>7</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Excluded</td>
<td>Missing data</td>
<td>6</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Excluded</td>
<td>Prim. absence</td>
<td>6</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Primates</td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Atelidae</td>
<td>Included</td>
<td>Missing data</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Included</td>
<td>Prim. absence</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3. Estimates of oldest age and latest possible date of arrival of Caribbean non-volant mammals, excluding the Eocene fauna of Jamaica (see ‘Other sources of information’ under Methods). Taxonomy follows McKenna & Bell (1997), unless otherwise noted.

<table>
<thead>
<tr>
<th>Clade</th>
<th>Previous dated node (Mya)</th>
<th>Location of node</th>
<th>Source</th>
<th>Latest possible date of arrival (Mya)</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choloepodinae</td>
<td>16–21</td>
<td>Bradypus–Choloepus</td>
<td>Delsuc et al., 2001</td>
<td>29–34&lt;sup&gt;2&lt;/sup&gt;</td>
<td>Puerto Rico</td>
<td>MacPhee &amp; Iturralde-Vinent, 1995</td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>Bradypus–Choloepus</td>
<td>Hoss et al., 1996</td>
<td></td>
<td>Puerto Rico</td>
<td>MacPhee &amp; Iturralde-Vinent, 1995</td>
</tr>
<tr>
<td></td>
<td>73–88</td>
<td>Cingulata–Pilosa</td>
<td>Hoss et al., 1996</td>
<td>12–15</td>
<td>Cuba</td>
<td>MacPhee et al., 2003</td>
</tr>
<tr>
<td>Caviomorpha</td>
<td>c. 16</td>
<td>Octodon–Other Octodontoidae</td>
<td>Huchon &amp; Douzery, 2001</td>
<td>12–15</td>
<td>Cuba</td>
<td>MacPhee et al., 2003</td>
</tr>
<tr>
<td></td>
<td>31 ± 7</td>
<td>SA Hystricognathi radiation</td>
<td>Huchon, Catzeflis &amp; Douzery, 2000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA Hystricognathi fossil remains</td>
<td>Vucetich, Verzi &amp; Hartenberger, 1999</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>33–49</td>
<td>SA–African Hystricognathi</td>
<td>Nedbal, Allard &amp; Honeycutt, 1994</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insectivora</td>
<td>None</td>
<td>Callicebus radiation</td>
<td>Purvis, 1995</td>
<td>12–15&lt;sup&gt;3&lt;/sup&gt;</td>
<td>Cuba</td>
<td>MacPhee et al., 2003</td>
</tr>
<tr>
<td>Atelid primates</td>
<td>7</td>
<td>Callicebus–extant sister taxon</td>
<td>Schneider et al., 1993</td>
<td></td>
<td>Cuba</td>
<td>MacPhee et al., 2003</td>
</tr>
<tr>
<td></td>
<td>13–16</td>
<td>Callicebus–extant sister taxon</td>
<td>Purvis, 1995</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>29 ± 5</td>
<td>Cebidae–Callitrichidae&lt;sup&gt;3&lt;/sup&gt;</td>
<td>Purvis, 1995</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>1</sup>Cebidae = Pithecia, Cacajao, Chiropotes, Alouatta, Ateles, Lagothrix, Brachyteles.

<sup>2</sup>A megalonychid fossil from Puerto Rico, unnamed genus and species B (MacPhee & Iturralde-Vinent, 1995: 12) not assigned to either subfamily would constrain the arrival of sloths to before the Early Oligocene (White & MacPhee, 2001: 211), but it cannot simultaneously represent both groups unless a Caribbean origin for the clade containing extant sloths is postulated.

<sup>3</sup>An Eocene ?primate petrosal from Jamaica (MacPhee et al., 1999) is not included here because this fauna has no continuity till the present. See ‘Taxonomic scope’ under Methods, for other sources of information.
rodents (Fig. 4) show no duplications due to incongruence among cladograms (Table 2, note that incongruence in rodents corresponds to artificially resolved node 1). Surprisingly for bats, the mormoopid phylogeny is, using the duplication criterion only, fully compatible with a geological hypothesis of (mostly) vicariant landmasses (Figs 1, 2). Megalocnine sloths (Fig. 4), the remaining bats (Figs 7–9) and primates (Fig. 10) show incongruence between phylogenies and the area cladogram, although the number of duplications is inflated by arbitrarily resolved nodes in Brachyphylla–Phyllonycteris–Erophylla (Fig. 7: node 1), Stenodermatina (Fig. 8: node 1), and natalids (Fig. 9: node 1).

**DISCUSSION**

**HISTORICAL ASSOCIATION**

It is clear that there is some historical association between taxon and area cladograms. This is a necessary but not sufficient condition to postulate cospeciation between areas and taxa because any two trees can be reconciled given an unlimited number of duplications (Page, 1994). The question would then revolve around how much of the diversification among taxa can be ascribed to the geological history. In effect, how many codivergent nodes (i.e. not redundant and not conflicting) are there in each reconciled tree? For the Caribbean, this question involves at least two steps:
Megalocnine sloths (Fig. 4), rodents (Fig. 5), Brachyphylla–Phyllonycteris–Erophylla (Fig. 7), and primates (Fig. 10) each show a unique basal nonarbitrary node connecting a monophyletic Caribbean taxon to the mainland (nodes marked C in the figures). All other groups show a mainland-Caribbean component somewhere higher in the reconciled tree (nodes marked c in the figures). There are three inter-island codivergent nodes: the first and most common is the Cuba–Jamaica dispersal node, a hypothesized dispersal, supported by widespread distributions of mormoopid, Erophylla, Brachyphylla, Natalus, and Nyctiellus. The Puerto Rico–Hispaniola node, and the third is the Cuba–Jamaica dispersal node, both seen in rodents (marked PH and CJ in Fig. 5). Note that arbitrarily resolved nodes (marked with numerals in the figures), and taxa widespread across the node examined were excluded from this discussion. The Cuba–Jamaica node, a hypothesized dispersal, is also supported by widespread distributions of mormoopid, Erophylla, Brachyphylla, and Chilonatalus bats. One node inferred from geological studies finds support only among bats: the Cuba–Bahamas relationship seems characterized by the widespread distribution of Pteronotus, Mormoops, Phyllonycteris, Brachyphylla, Natalus, and Nyctiellus. The Puerto Rico–Hispaniola node.
Rico–Lesser Antilles node, another hypothesized dispersal, is only seen among bats in the widespread distribution of *Pteronotus parnellii, Mormoops blainvillii*, *Phyllonycteris major*, and *Brachyphylla cavernarum*. The last three species would have followed a dispersal route south from Puerto Rico, as hypothesized in the area cladogram of Figure 2, since the remainder of their populations is exclusively Antillean (Figs 6, 7). In contrast, *Natalus stramineus* shows a relationship between the continent and the Lesser Antilles pointing to dispersal from northern South America (Fig. 9), more in agreement with the biogeographical hypothesis of Hedges and colleagues.

For primates the position of *Xenothrix* as sister to other Caribbean primates contradicts the dispersal Cuba–Jamaica node proposed in Figure 2. Rather, the phylogeny (Fig. 10) implies a common ancestor present in Cuba, Hispaniola, and Jamaica, potentially compatible with the hypothesis of interconnection between the Blue Mountains (see ‘Geological area cladograms’ under Methods) and other Caribbean landmasses.

An overall comparison of total nodes vs. codivergent nodes shows that the highest proportion of the latter is found among non-volant mammals, between 25% and 75%. The proportion among bats only ranges from 6% to 20%, although excluding widespread taxa generally increases it (see Table 2).

For non-volant taxa, the lowest codivergence is among rodents, whose poorly resolved phylogeny may obscure greater incongruence or codivergence, particularly given the effects of outgroup choice on a clade.

---

**Figure 6.** Reconciled tree of the distribution of mormoopids. See Methods for sources of the phylogeny.
with many other taxa to choose from (see Woods et al., 2001: 346–347). The choice of Proechimys is logical, but a rigorous test of the monophyly of the Caribbean group would require denser sampling from among the hystricognath rodents of South America, including the extant families Myocastoridae, Octodontidae, and Ctenomyidae, in addition to Echimyidae (Nedbal et al., 1994). Only one heptaxodontid, Elasmodontomys obliquus, was included so the monophyly of the giant hutias was not tested in the analyses of Woods et al. (2001), although Flemming & MacPhee (1996) present evidence for the monophyly of the group (but see Pas- cual, Vucetich & Scillato-Yané, 1990) for a dissenting view regarding Clidomys).

Although there is greater resolution, the phylogeny of choloepodine sloths (Fig. 3) is also unstable since there are almost 100 genera of mostly South American extinct sloths (McKenna & Bell, 1997), so taxon sampling will probably modify this phylogeny (White & MacPhee, 2001). Gaudin’s (1995) cladistic analysis for 21 genera, for instance, is consistent with White & MacPhee’s (2001) hypothesized sister relationship between Choloepus and Acratocnus but conflicts in every other respect with their phylogeny. Finally, the phylogeny of Antillean primates is also fluid: the description of Paralouatta marianae from Cuba (MacPhee, Iturralde-Vinent & Gaffney, 2003) already brings the proportion of codivergent nodes from 67% down to 50%.

For bats the proportion of codivergence is low, particularly among mormoopids, a group whose phylogeny is supported by morphological (Simmons & Conway, 2001), mitochondrial, and nuclear DNA character analyses (Lewis-Oritt et al., 2001; Van Den

Figure 7. Reconciled tree of the distribution of Brachyphylla, Phyllonycteris, and Erophylla, obtained from Jones et al. (2002). See Discussion for alternative phylogenetic hypotheses.
Bussche, Hoofr & Simmons, 2002). Natalids show only a marginally better proportion of codivergence, despite the artefact of placing Primonatalus prattae in Central America rather than Florida, where it was found (Morgan & Czaplewski, 2003). This artefact is used solely to fit the cladogram to the test of the Gaarlandia geological hypothesis, because the Early Oligocene natalid remains from Florida (Morgan & Czaplewski, 2003) suggest a North American origin for the group.

The two phyllostomid clades analysed will probably be revised in the future: the taxon cladograms used to generate Figures 7 and 8 were taken from a matrix representation with parsimony supertree by Jones et al. (2002). The supertree analysis placed the endemic Antillean genera Brachyphylla, Erophylla, and Phyllonycteris within a single radiation. Recent (mostly) morphological (Wetterer, Rockman & Simmons, 2000) and molecular (Baker et al., 2000) phylogenetic hypotheses did not independently recover this topology. For the Stenodermatina, a monophyletic Antillean clade (Jones et al., 2002) was consistent with Wetterer et al.’s (2000) morphological hypotheses, but was not supported by Baker et al.’s (2000) molecular analysis (which excluded Phyllops).

Among all lineages the inclusion of fossils contributed to the resolution of area relationships, not only when all Antillean representatives are extinct as with sloths and primates, but also when most species are extinct, i.e. hystricognath rodents. Among bats, the inclusion of fossils alters the interpretation of missing areas substantially: mormoopids are extinct from the

---

**Figure 8.** Reconciled tree of the distribution of the phyllostomid tribe Stenodermatina (sensu Wetterer, Rockman & Simmons 2000), obtained from Jones et al. (2002). See Discussion for alternative phylogenetic hypotheses.
Bahamas and Lesser Antilles, Phyllonycteris from the Lesser Antilles, and Natalus from the Bahamas. Without these remains their absence would be interpreted as primitive (for an example of primitive absence given current knowledge see Puerto Rico in Fig. 9).

TEMPORAL COMPATIBILITY
The evaluation of congruence has hitherto focused on spatial and speciation patterns, with no regard for the temporal frame for Caribbean diversification. The geological hypotheses outlined in the Introduction, however, constrain the interconnection among landmasses as summarized in Figure 1.

The timing of divergence between Bradypus and Choloepus has been estimated (Table 3) at 16–21 Mya (Delsuc et al., 2001), or >40 Mya (Hoss et al., 1996). The former estimate would not be compatible with the Early Oligocene interconnection postulated in Figure 1, but the latter would. Delsuc et al. (2001) attributed the difference among age estimations to poor taxonomic sampling in previous studies, although a similar case could be made for poor taxon sampling of extinct groups altering estimations of phylogeny and divergence dates within this recent xenarthran molecular phylogeny. If megalonychid B of MacPhee & Iturralde-Vinent (1995) is a choloepodine, given the phylogeny in Figure 3, the estimate of Delsuc et al. (2001) must be wrong. Conversely, if megalonychid B is a megalocnine, there is no conflict between molecular divergence dates and Caribbean fossil evidence. The older limit of the divergence between Antillean megalocnines and their South American relatives, given the phylogeny of White &
MacPhee (2001), would be given by the estimates of divergence among major xenarthran lineages (Table 3).

For rodents there are several, sometimes contradictory, estimates of divergence relevant to the Caribbean clade (Table 3). Huchon, Catzeflis & Douzery (2000) dated the caviomorph radiation to the Early Oligocene (Table 3), around the same time as the hypothesized Oligocene Caribbean–South American interconnection of Figure 1. This estimate is based on a single nuclear gene and well supported by cross-calibration with higher-level mammalian divergences (Huchon et al., 2000), but incompatible with dating estimates from one additional nuclear and one mitochondrial gene (Honeycutt, Rowe & Gallardo, 2003). Because Honeycutt et al. (2003) obtain a radically different topology from that of Huchon and colleagues, estimates by the former cannot be directly compared to those of the latter and are not included in Table 3.

The Early Oligocene date for the caviomorph radiation is compatible with an Early to Middle Eocene divergence between African and South American hystriocnaths (Huchon & Douzery, 2001). Other molecular estimations push the intercontinental hystriocnath divergence back to the Cretaceous (Table 3, Mouchaty et al., 2001; but see Huchon et al., 2002), opening the possibility of an even earlier South American hystriocnath radiation and perhaps indicating that the debate surrounding the topology and age of the diversification will continue.

The extinct Caribbean murids Megalomyx and Oryzomys are thought to have reached the Lesser Antilles from South America (for a recent dispersalist argument see McFarlane & Lundberg, 2002), except for the Jamaican Oryzomys antillarum, a presumed Central American disperser (Woods, 1989b; McFarlane, Lundberg & Fincham, 2002). Since murids are unknown from northern South America until the Early Pliocene, their entry into the Antilles is presumed to have occurred after this time (Morgan & Woods, 1986). Until their relationships are resolved, however, the number and age of colonization events associated with these taxa remains untested.

The only recent phylogenetic analysis to include both Antillean insectivorans – Solenodon and Nesophontes – concluded that ‘[a]dditional data are necessary to better resolve Caribbean lioppythlan phylogeny’ (Asher, 1999: 239). This, and the ever-growing controversy over insectivoran phylogeny (Springer et al., 1997; Stanhope et al., 1998a, b; Emerson et al., 1999; Liu & Miyamoto, 1999; Mouchaty et al., 2000; Murphy et al., 2001; Malia, Adkins & Allard, 2002), precluded a reconciled tree analysis. There have been no attempts to date the divergence of Solenodon or Nesophontes from other insectivorans. An insectivoran fossil preserved in amber traces the occurrence of insectivores on the Antilles minimally to the Late Oligocene/Early Miocene of Hispaniola (Table 3).

Whidden & Asher (2001) reviewed the phylogenetic and biogeographical data on insectivorans, concluding that four biogeographical hypotheses are still viable: (1) overwater dispersal of an Early Tertiary North American insectivore related to Apternodus or the geolabidid Centetodon; (2) vicariance of an Early Tertiary North American insectivoran on the Western Jamaica Block with subsequent dispersal to the Greater Antilles; (3) dispersal of a Gondwanan insectivoran from Africa, and (4) dispersal of a Gondwanan insectivoran from Africa via South America.

The viability of hypothesis 2 rests exclusively on the Seven Rivers Eocene fauna of Jamaica (Domning et al., 1997; MacPhee et al., 1999). This mammal fauna has no continuity until the present (see ‘Other sources of information’ under Methods, above). The phylogenetic hypotheses of Liu et al. (2001) and Stanhope et al. (1998a) favour hypothesis 3 over hypothesis 4 because insectivoran remains appear in South America only after the faunal exchange linked to the closing of the Panamanian landbridge. Since the latter
phylogenies did not include extinct taxa, hypothesis 1 also remains viable.

Among bats, the dearth of Tertiary fossils and limited taxon sampling in higher-level phylogenies aimed at dating nodes have limited the dates available for analysis. For *Brachyphylla–Erophylla–Phyllonycteris* the single radiation hypothesis would imply that the ancestor of the Antillean clade and the ancestor of New World nectar-feeding bats (glossophagines and lonchophyllines) are the same age (South American glossophagines are at least 11–13 My old according to Czaplewski, 1997). Morphological (Wetterer et al., 2000: fig. 49) studies show the ancestor of *Phyllonycteris* and *Erophylla* to be as old as the New World nectar-feeding bats, while the unresolved position of *Brachyphylla* precludes any estimation of age for this clade. Molecular analyses (Baker et al., 2000: fig. 2) recover a different topology and are therefore incompatible with this date estimation. The oldest natalid is an unnamed Early Oligocene fossil from Florida, although only the Early Miocene *Primonatalus pratiae* is included in phylogenetic analyses (Morgan & Czaplewski, 2003: fig. 9). The Early Oligocene natalid remains in Florida, together with the relatively novel hypothesis of phylogenetic relationships linking the Natalidae to Vespertilionidae and Molossidae (see Morgan & Czaplewski, 2003: 746 for a complete review), suggest a North American origin for this group.

Among primates, the older limit for the Caribbean radiation would be given by the Cebidae–Callitrichidae divergence (Table 3), estimated to have occurred around or after the proposed Caribbean–South America interconnection of Figure 1. Because the phylogenetic hypothesis in Figure 10 conflicts with the supertree of Purvis (1995) this date estimation might not be informative on the age of the Caribbean primate clade. In contrast, the phylogeny of Schneider et al. (1993) is compatible with the taxon cladogram of Figure 10, but the estimate of divergence (Table 3) is too recent to be compatible with the Gaarlandia hypothesis.

**DISPERSAL VS. VICARIANCE?**

The evidence posited in mammalian phylogenies does not add to the argument of dispersal vs. vicariance. One pattern, the entry into the Caribbean from South America between the Palaeocene and the Middle Miocene, accounts for the distribution and phylogeny of the majority of lineages studied. Of these, few lineages fit the predictions of the Gaarlandia hypothesis in timing, and none regarding the divergence among Antillean landmasses. The remaining lineages show patterns that are inconsistent with the Gaarlandia hypothesis and require taxon-specific hypotheses.

The distribution of more than half of the groups studied – megalocnine sloths (Fig. 4), hystricognath rodents (Fig. 5), *Brachyphylla–Phyllonycteris–Erophylla* (Fig. 7), *Stenodermatina* (Fig. 8), and primates (Fig. 10) – can be explained by a single ancestral colonization of the Antilles from South America. In one case, megalocnine sloths, molecular divergence estimates are also consistent with the Gaarlandia hypothesis (Fig. 1). For hystricognath rodents and primates, molecular dating is not completely consistent, but could fall within the range of the Gaarlandia land bridge (Table 3). Finally, the phylogenetic instability and absence of Tertiary fossils for *Brachyphylla–Phyllonycteris–Erophylla* and Stenodermatina inhibit speculation on their time of arrival in the West Indies.

Choloepodine sloths (Fig. 3), mormoopids (Fig. 6), and natalids (Fig. 9) all show patterns that can only be partially reconciled (e.g. *Acratocnus*, Fig. 3), if at all, with the geological hypotheses underpinning Figure 1. The most recent molecular divergence estimates would make an Early Oligocene entry to the Caribbean by choloepodine sloths impossible (Table 3). The history of mormoopids (Fig. 6) points to repeated dispersal (at least twice in the *Pteronotus* clade) to the Caribbean from Central America or South America, e.g., *Pteronotus parnelli, Mormoops megalophylla*. Natalids invert the pattern of entry into the Caribbean: the current phylogeny points to a tropical North American ancestor whose range included Cuba and from there dispersed south to northern South America (Fig. 9).

The Cuba–Hispaniola divergence of Figure 1 dates back to the Late Oligocene, and has been suggested to be a common cause for speciation in bats (Griffiths & Klingener, 1988). This pattern of area relationships is seen in *Acratocnus* and *Neocnus* (Fig. 3), *Megalocnus* and *Parocnus* (Fig. 4), *Boromys* (Fig. 5), *Erophylla* (Fig. 7), and primates (Fig. 10), and may correspond to the resolution of Greater Antillean *Natalus* (Fig. 9). A Late Oligocene divergence, however, cannot be reconciled with the species or generic-level differentiation observed in the phylogenies and hence cannot account for this pattern. Concordant dispersal in all these taxa, or a more recent history of interconnection and separation, are more suitable explanations for this pattern.

With the exception of murid rodents, all non-volant lineages (including insectivorans: Table 3) reached the Caribbean before the Middle Miocene (MacPhee et al., 2003), and sloths arrived as early as the Early Oligocene (MacPhee & Iturralde-Vinent, 1995). Assuming the Chicxulub impact effectively wiped out a previous fauna, the arrival of non-volant mammals in the Antilles would be restricted to the period between the Palaeocene and the Middle Miocene. This limited window of opportunity for non-volant mammalian
lineages to colonize the Caribbean requires an explanation.

The Gaarlandia land interconnection proposed by Iturralde-Vinent & MacPhee (1999) can account for the pattern of speciation of megalocnine sloths, hystricognath rodents, two bat lineages and primates, as well as the timing of divergence from the mainland of these groups, with the exceptions of bats and perhaps hystricognath rodents and primates. The distribution of choloepodine sloths, murid rodents, insectivorans, and natalid bats has to be explained by different hypotheses: dispersal or other land interconnections, including the probable North American origin of insectivorans and natalids.

In principle, a mechanism that facilitated dispersal over the colonization period could explain the cluster of arrivals. This differs from the hypothesis of Hedges and colleagues because they have proposed numerous dispersal events into the Greater Antilles from South America throughout the Cenozoic following prevailing oceanic currents. An alternative explanation might be to accept the core of their dispersal hypothesis but find additional hypotheses to account for the lack of successful dispersal of non-volant mammals to the Caribbean between the Middle Miocene and the Present.

CONCLUSIONS

An analysis of current phylogenetic evidence finds that the geological hypotheses of Iturralde-Vinent & MacPhee (1999) can in principle account for the relationships between the mainland and the Caribbean species of megalocnine sloths, hystricognath rodents, Brachyphylla and allies, Stenodermatina, and primates. However, the distribution and/or proposed phylogenies of choloepodine sloths, insectivorans, mormoopids, and natalids cannot be reconciled with this model and require a different explanation for their distribution. Higher-level phylogenies for all the former groups also reveal contradictory evidence regarding the time of arrival to the Caribbean. As calibration of different molecular clocks converges, the evidence for the hypothesized Gaarlandia as an explanation of mammalian distribution will have to be reassessed.

The robustness of these biogeographical inferences is highly sensitive to the phylogenetic information, which remains incomplete for all groups examined. More taxon sampling is necessary among sloths and hystricognath rodents, and Caribbean murids and insectivorans both require species-level phylogenies. The stability of phyllostomid phylogenies seems to require further character sampling across many lineages, while the reconstruction of biogeographical history for mormoopids and natalids could benefit from population-level analyses to clarify routes of dispersal.

Among primates, the examination of all available fossil remains is necessary to clarify the status of numerous lineages not included in current analyses.

The inter-island patterns of speciation, evaluated by measuring codivergent nodes, do not conform to the geological hypotheses of Iturralde-Vinent & MacPhee (1999) although improvements in phylogenetic inference (see above) will probably reveal patterns currently obscured by poor character and taxon sampling. The search for Antillean and tropical American Tertiary mammal fossils over the last decade has shown that most non-volant Caribbean mammalian lineages arrived in the West Indies before the Middle Miocene. With the interconnection hypothesis of Iturralde-Vinent & MacPhee (1999) only accounting for part of the window of colonization that seems to have existed, other hypotheses—facilitated dispersal or other means of interconnection—remain viable as explanations for this hitherto unnoticed pattern.

ACKNOWLEDGEMENTS

This paper is a contribution from the Monell Molecular Laboratory and the Cullman Research Facility in the Department of Ornithology, American Museum of Natural History, and has received generous support from the Lewis B. and Dorothy Cullman Program for Molecular Systematics Studies, a joint initiative of The New York Botanical Garden and The American Museum of Natural History. This research is supported by the Department of Mammalogy of the American Museum of Natural History, the NASA grant no. NAG5-8543 to the Center for Biodiversity and Conservation at the American Museum of Natural History, the NSF grant DEB-0206336 to N. B. Simmons, R. DeSalle and the author, and the Department of Ecology, Evolution and Environmental Biology at Columbia University. I thank an anonymous reviewer, F. K. Barker, J. L. Cracraft, R. D. E. MacPhee, J. C. Morales, A. L. Porzecanski, C. Raxworthy, and N. B. Simmons for comments on earlier versions of the manuscript. For sharing their unpublished manuscripts I thank N. Czaplewski, E. S. Gaffney, M. A. Iturralde-Vinent, R. D. E. McPhee, G. Morgan, G. Silva-Taboada, N. B. Simmons, V. Tavares, and A. Tejedor.

REFERENCES


Wallace AR. 1881. Island life; or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates. New York: Harper & Brothers.


