CHAPTER THREE

The Biogeographic History of Mesoamerican Primates

Susan M. Ford

INTRODUCTION

New World monkeys ranged into Mesoamerica along with the mass migration of South American fauna (and flora) northward during the Great American Interchange (Marshall *et al.*, 1982; Marshall, 1988; Stehli and Webb, 1985; Webb, 1991, 1999), as a result of the emergence of the Panamanian isthmus around 3.5 mya (Coates *et al.*, 2003; Cronin and Dowsett, 1996). This interchange involved a major influx of previously unrepresented southern taxa into Mesoamerica, and an even larger movement of northern (North American) groups into South America. However, uncertainty remains about the number of independent invasions of Mesoamerica by New World monkeys and other fauna, the timing of these invasions, and the speed and direction of movement into various Mesoamerican regions. In addition, the degree of isolation and eventual genetic separation of various groups into distinctive subspecies or even species remains controversial; this last question is addressed in other

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contributions to this volume, particularly Rylands *et al.* (this volume; see also Groves, 2001).

Here, the modern distribution of primates in Mesoamerica is interpreted against the backdrop of the geographic landscape across the region (including mountain ranges, lowlands, and habitats), the geologic history of the formation of the isthmian connection, and the phylogenetic ties of Mesoamerican primates to their South American relatives.

GEOGRAPHIC AND GEOLOGIC BACKGROUND

Key to this analysis is an understanding of the basic geography of the Central or Mesoamerican isthmus. It is a single, very long, narrow strip of land marked by Pacific and Atlantic coastal lowlands separated by high mountain ranges down the middle for much of its length (see Figure 1). In several places, these highlands reach nearly to the coast (especially in northwestern Costa Rica and across Honduras and El Salvador). These central mountains

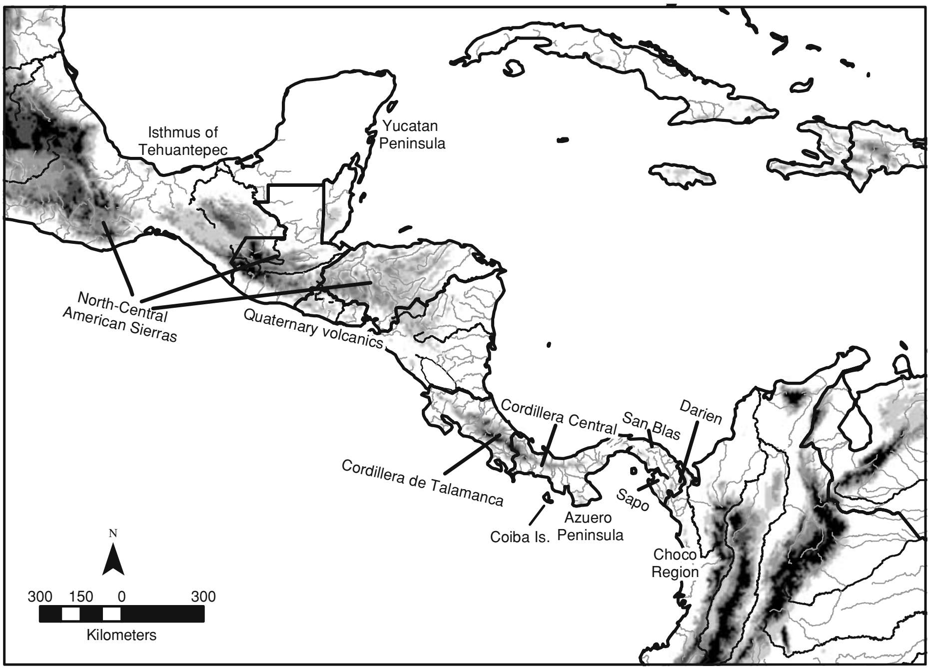

Figure 1. Map of Mesoamerican landscape, showing major topographic features.

Table 1. Approximate maximum elevation limits for Mesoamerican primates (from Reid, 1997)

Taxon	Max. elevation
Alouatta palliata	2500 m
Alouatta pigra	<500 m
Aotus zonalis	650+ m
Ateles geoffroyi	1800 m
Ateles fusciceps	>2000 m
Cebus capucinus	2000 m
Saguinus geoffroyi	900 m
Saimiri oerstedii	<500 m

are of varying age (de Cserna, 1989; Savage, 2002; Weyl, 1980): the North Central American Sierras, from southern Mexico through Guatemala and Honduras into northern Nicaragua, originated pre-Cenozoic but have experienced some additional Pliocene uplift. West of these, the Central American Tertiary Volcanics (Guatemala through Nicaragua) resulted from uplift and volcanism from the Miocene through Pliocene. This time frame also saw the uplift of the central mountains of Costa Rica (the Cordillera de Talamanca) and western Panama (the Cordillera Central). In the Quaternary and continuing today, active volcanic ridges have developed along the Pacific from southernmost Mexico through central Costa Rica. Most of these ranges include areas of high elevation that preclude habitation by modern monkeys except along forest river valleys. Mesoamerican primates are lowland fauna, with maximum elevations reported for *Alouatta palliata* at 2500 m and the others significantly lower (see Table 1 and reviews in Reid, 1997; Rylands *et al.*, this volume).

The Pacific coast tends to be drier than the Atlantic, as in South America, but there often remain areas of forest with continuous canopy (Savage, 2002). The presence of subhumid–semiarid forested corridors along both the coasts was likely the case through much of the Pleistocene (Colinvaux, 1993, 1996), despite arguments for periodic more arid conditions by others (e.g., Webb and Rancy, 1996; Whitmore and Prance, 1987). However, these have been divided by the central uplands throughout the late Cenozoic, and there may have been intermittent breaks in the corridors during particular cold–dry cycles (Savage, 2002) or during rises in sea-level flooding the coastal regions (Nores, 1999; Eberhard and Bermingham, 2004). Currently, major grass and shrub areas exist in the Azuero Peninsula, the Pacific coast of northwest Costa Rica and Nicaragua, and the northeastern corner of the Yucatan Peninsula.

There are three major areas of coast-to-coast lowlands: the Isthmus of Tehuantepec in southern Mexico; lowlands angling across from southwestern Nicaragua to northeastern Costa Rica (and now partly filled with Lake Nicaragua); and the Gatún region of Panama, the location of the modern Panama Canal. These represent areas for easy exchange of lowland fauna from the east and west coasts (including monkeys). A fourth, extra-isthmus lowland connection between the Atlantic and Pacific coasts occurs across extreme northwestern Colombia, in the Chocó/Atrato River region.

The exception to this pattern (of coastal lowlands separated by central highlands) is in eastern Panama, at the southeastern terminus of the isthmus. Here, the Serranía Darién now ranges across the entire isthmian terminus, at the border with Colombia, rising up to 2000 m in elevation and forming a formidable barrier to faunal exchange of lowland taxa. In eastern Panama, the highlands separate to form Atlantic (Serranía San Blas) and Pacific (Serranía Sapo-Baudo) coastal ranges separated by a central lowland region, with the coastal ranges diminishing as they reach the central Gatún lowland region. This narrowest part of the isthmus, which was an important corridor for transit of lowland fauna in the past, is now disrupted by the Panama Canal and various large lakes formed early in the 20th century.

Just west of this lowland region, the central ranges begin and the Pacific coast has a large peninsula, the Azuero Peninsula, one of the most arid regions of Mesoamerica and covered by grassland and shrub forest. Offshore, Isla de Coiba shares a similar habitat. It is separated by about 50 km, and was likely last connected to the mainland from about 24,000 to 15,000 yBP (Bartlett and Barghoorn, 1973; Froehlich and Froehlich, 1987). The peninsula was likely separated from the mainland as well, as the northern end is much lower than the southern and currently covered by arid grasslands (Bennett, 1968; Froehlich and Froehlich, 1987; see below). Both the Azuero Peninsula and especially Isla de Coiba have a markedly depauperate mammalian fauna, suggesting filtered migration and isolation (*Ibid.*), probably from both periodic flooding of the lowland regions and extensive grasslands when emergent.

None of the rivers of this narrow landform attain great size or length. Therefore, none of the isthmian rivers appears to represent a significant barrier to the movement of primates. The modern exception to this would be the recent addition of the Panama Canal to the landscape.

Platyrrhine primates have been able to move from South America to Mesoamerica only since the Pliocene connection of the two land areas. The geologic history of the southern isthmus has been recently reviewed in Gregory-Wodzicki (2000) and Ford (in prep.) and of the entire isthmus in Savage (2002); key aspects are presented here. Although the lower Central American region was largely under water for much of the Cenozoic (Pindell and Barrett, 1990), by the Mid Miocene (around 10 mya), the southern portion corresponding to modern Costa Rica and western Panama became an "extensively emergent archipelago" of volcanic islands associated with the uplift of the central mountains, while eastern Panama in the region of the Darién and the Chocó remained under deep water (Coates *et al.*, 2003: 271; also Coates, 1999; Collins *et al.*, 1996a). On the South American mainland, ongoing uplift of the Andean chain from the Miocene resulted in the increasing isolation of northwestern Colombia and western Ecuador, particularly of the modern Magdalena, Cauca, and Chocó/Atrato River basins and the Maracaibo Basin in northwestern Venezuela from the Amazon/Orinoco basins, although the individual northwestern basins continued to be forested tropical lowlands (Rull, 1998). By 9 mya, the freshwater fish of the Atrato Basin of far northwestern Colombia (which directly borders the Mesoamerican isthmus) became isolated from those in the other Colombian basins (Martin and Bermingham, 2000), suggesting that at least parts of the Chocó remained emergent (with freshwater) from then on. Late Miocene (8–5 mya) saw a general subsidence of the lower isthmus region under deepening water (Aubry and Berggren, 1999; Coates *et al.*, 2003; Collins *et al.*, 1996a). Most of the lower isthmus/contact region, including Costa Rica (Collins *et al.*, 1995; McNeill *et al.*, 1999), the Darién of southern Panama (Collins *et al.*, 1998), and the Atrato Basin of northwestern Colombia (Duque-Caro, 1990; Coates *et al.*, 2003), remained under deep water through this period. Although land migrations into Mesoamerica are unlikely this early, Collins *et al.* (1996b) suggest there may have been emergence sufficient to disrupt gene flow between Atlantic and Pacific marine foraminiferans around 8 mya. Based on molecular dating estimates, Salazar-Bravo *et al.* (2001) suggest possible migration south of northern field mice of the genus *Calomys* and Engel *et al.* (1998) for sigmodontine rodents in general into South America in an early pulse of exchange, and Perdices *et al.* (2002) use molecular dates to suggest a northern dispersal of *Rhamdia* freshwater fish around 6 mya.

The Early Pliocene (5–3 mya) saw significant shallowing and ocean regression in Costa Rica (McNeill *et al.*, 1999) and reef formation in Panama (Coates and Obando, 1996; Coates *et al.*, 2003; Collins and Coates, 1999). By the Late Pliocene, *ca.* 3.5–2.0 mya, there was complete emergence of the isthmus

(Coates *et al.*, 2003), with sea level 100 m lower than today around 3.4 mya (Vail and Hardenbol, 1979). This allowed the Great American Interchange to proceed in both northward and southward directions, involving terrestrial fauna (Eisenberg, 1989; Marshall *et al.*, 1982; Marshall, 1988; Savage, 2002; Simpson, 1980; Stehli and Webb, 1985; Webb, 1999), aerial forms (Eberhard and Bermingham, 2004; Hoffman and Baker, 2003), and freshwater fish (Martin and Bermingham, 2000; Perdices *et al.*, 2002). However, there is increasing evidence that this initial connection and exchange was transitory in nature. It is now apparent that between 2.8 and 2.5 mya there was a major exchange of Atlantic and Pacific marine fauna (Cronin and Dowsett, 1996) with subsidence of the lower isthmus, followed by a second wave of terrestrial dispersals around 2.0 mya (Savage, 2002). Mounting evidence of at least two separate periods of freshwater fish dispersals since 3.5 mya exists as well, but Martin and Bermingham (2000) suggest that the later dispersal was as late as 1.0 mya. Taken together, these strongly indicate at least two and perhaps as many as four separate and distinct periods of faunal migrations across the Darién region (filtered dispersal 8–6 mya, major exchange 3.5–3.0 mya, later exchanges 2.0 mya and perhaps 1.0 mya). In addition, there appears to be filtered exchange across the Darién today, along with probable recent (Pleistocene-Recent) introductions of Amazonian-based primates into the northwestern Colombian basins (Ford, in prep., for *Ateles fusciceps* and *Alouatta seniculus*, at least; see also Hoffman and Baker, 2003, on complex history of short-tailed bats in this region).

MODERN DISTRIBUTIONS OF MESOAMERICAN PRIMATES

I follow the species and subspecies usage of Rylands *et al.* (this volume). Figures 2–7 show the distribution of primate genera in Mesoamerica, superimposed on the topography of the region. These distributions are based on two major sources. They are drawn primarily from the literature as reviewed and presented in Rylands *et al.* (this volume; see also Henderson and Adams, 2002; Reid, 1997). Where my maps differ, I offer range expansions based on museum catalog records. The locality datapoints represent collecting localities (in Colombia, Panama, Costa Rica, and Nicaragua) associated with all primate specimens from four of the world's major museum collections of Neotropical primates: the Smithsonian Institution, Washington, D.C. (USNM), the American Museum of Natural History in New York (AMNH), the Field Museum of

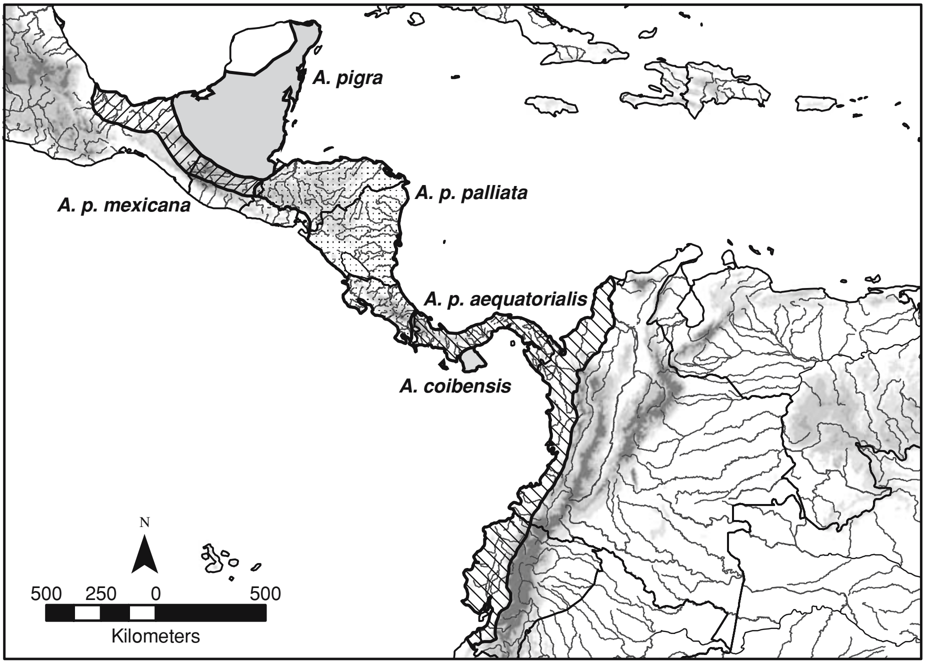

Figure 2. Map of distribution of *Alouatta coibensis*, *Alouatta palliata*, and *Alouatta pigra*. Changes in elevation shadings correspond to 500, 1000, 2000, and >2500 m.

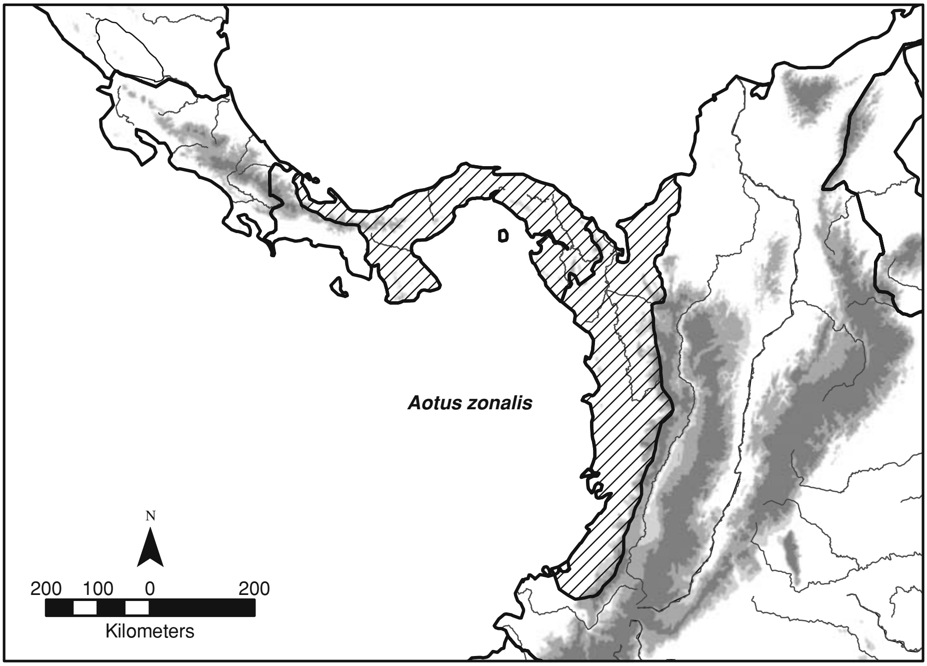

Figure 3. Map of distribution of *Aotus zonalis*. Changes in elevation shadings correspond to 650, 1000, and >2000 m.

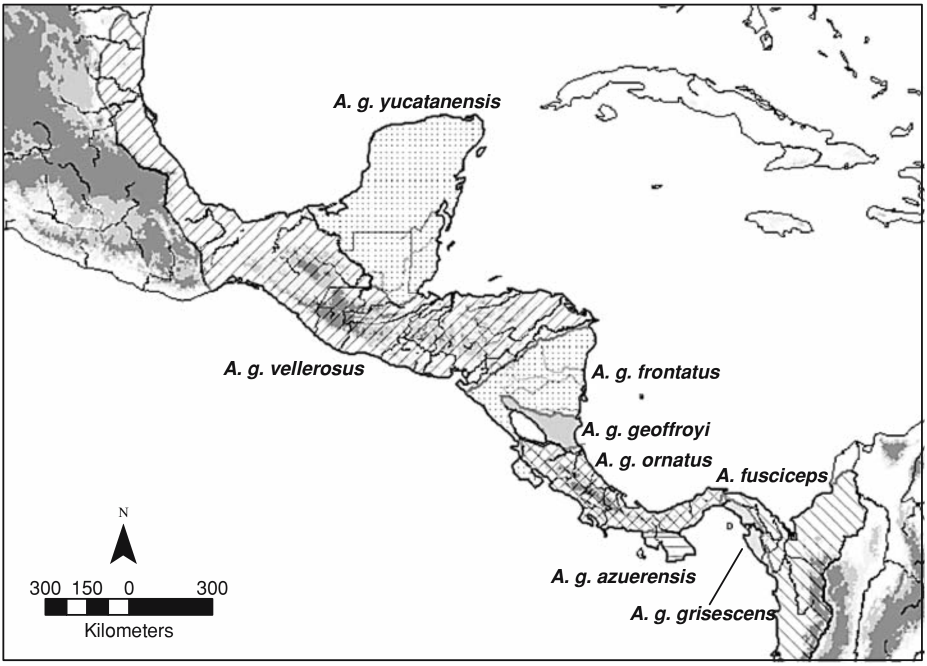

Figure 4. Map of distribution of *Ateles geoffroyi* and *Ateles fusciceps*. Changes in elevation shadings correspond to 500, 1000, and >1800 m.

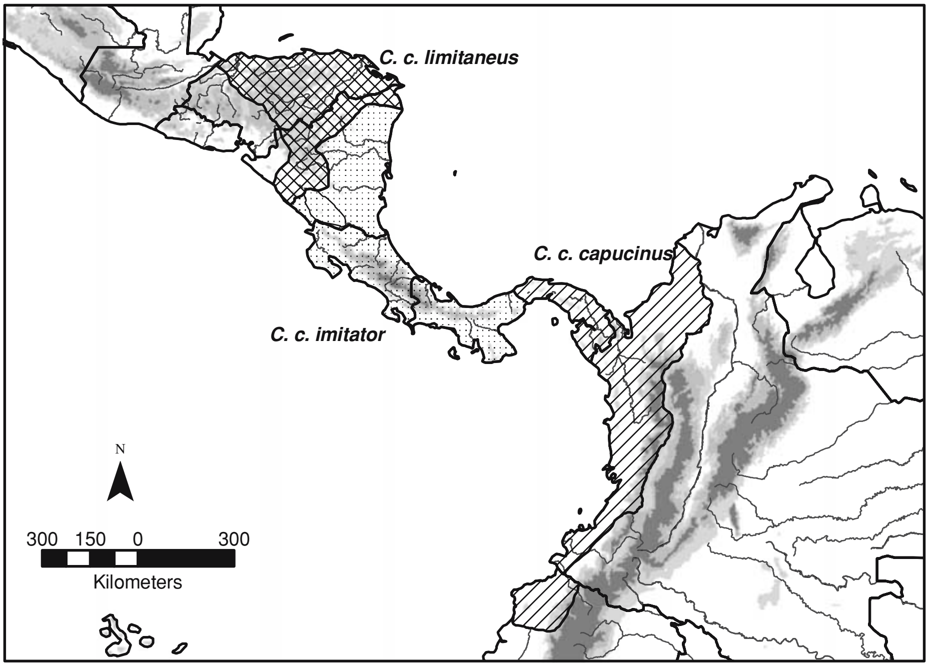

Figure 5. Map of distribution of *Cebus capucinus*. Changes in elevation shadings correspond to 500, 1000, and >2000 m.

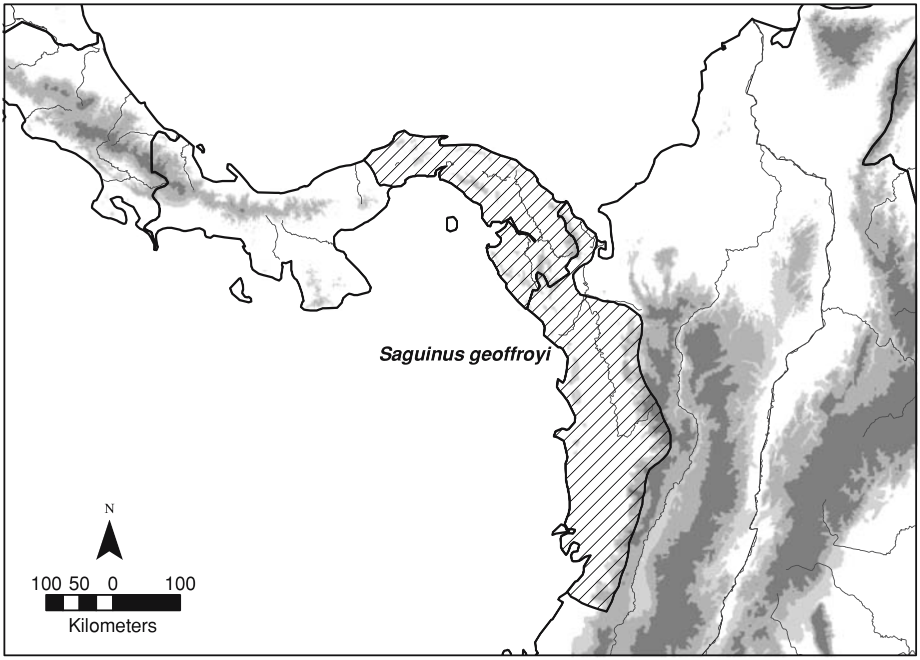

Figure 6. Map of distribution of *Saguinus geoffroyi*. Changes in elevation shadings correspond to 500, 1000, and >2000 m.

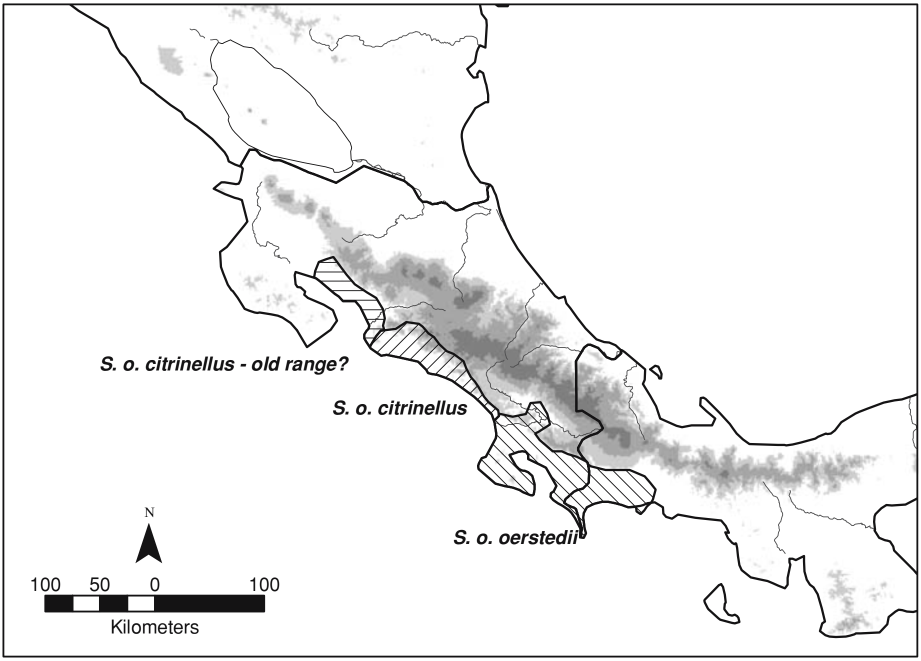

Figure 7. Map of distribution of *Saimiri oerstedii*. Changes in elevation shadings correspond to 500, 1000, and >2000 m.

Natural History in Chicago (FMNH), and the British Museum of Natural History in London (BM(NH)). These data were used to supplement the published range information that forms the basis of the maps in Rylands *et al.* (this volume). As part of a study of the biogeographic patterns of primates in northern South America, I have determined latitude and longitude values for these localities using a variety of gazetteers (Burt and Stirton, 1961; Goodwin, 1942, 1946; Hershkovitz, 1977; Paynter, 1982, 1993, 1997; United States, Geographic Names Division, gazetteers for each country, 1957–1985) and maps (*Ecuador—Atlas Histórico-Geográfico*, 1942; *General Map of Nicaragua Canal Region*, 1899; *Nicaragua*, 1979; *Panama*, 1981; *República de Panamá—Mapa Físico y Mapa Político*, 1993; *Republic of Panama*, 1967; *South America North West 4th Ed.*, 2000; *Travel Map of Ecuador*). All localities for which a latitude and longitude were determined (or the nearest landmark/community) were located on one or more maps of the area. In many cases, there is more than one place with the same name; use of this database covering multiple museum collections which could be sorted by collector and of the Harvard bird gazetteers (Paynter, 1982, 1993, 1997) allowed quite detailed information on the travels and locations of individual collectors, so that information on collector and date could aid in identifying localities. Also, maps from different time periods were used when possible, since some localities given by early collectors no longer exist.

These museum records and differing interpretations of published information did result in several differences from Rylands *et al.*'s (this volume) distributions. I expand the range of *Cebus capucinus* westward in Nicaragua and the range of *Saguinus geoffroyi* slightly farther westward in Panama, based on actual collecting records. *Saimiri oerstedii citrinellus* was collected north of its current range in 1902; I indicate this likely historical extension of its range separately in Figure 7. In the Brooks Parsimony Analysis described below, I also allow for the possibility that *Aotus zonalis* ranged into southeastern Costa Rica, following Timm (1994), but this possible range expansion is not indicated on the map in Figure 3. However, as will be seen, should this extension of the owl monkey's range be incorrect, the deletion has little effect on the overall scenario of primate biogeography in Mesoamerica. Last, the range maps of Rylands *et al.* cover broad areas that almost certainly include regions from which the monkeys are absent due to habitat or elevation restrictions. My map boundaries are slightly altered to accommodate presumed elevation limits; microhabitat effects will require more detailed data.

BROOKS PARSIMONY ANALYSIS

Methods

Using ArcView 8.2 GIS software (ESRI, 2002), distributions of primates are mapped and overlain on both topographic (Figure 1) and ecozone/habitat maps (not figured). The topographic map is provided by ESRI within ArcView, as is the ecozone map, which is based on data from the World Wildlife Fund.

As one means of exploring various historical biogeographic reconstructions, possible scenarios were tested using Brooks Parsimony Analysis (BPA) (Brooks and McLennan, 2001, 2002; Brooks *et al.*, 2001). In BPA, individual geographic areas become the operational taxa, and the presence or absence of individual species and their "ancestors" (from a known phylogenetic tree) become the characters for each area. Each species and each ancestral node for the phylogenetic trees are numbered; if a species is found in an area, then each of its ancestral nodes is coded as present as well. Repeated parsimony analyses are performed, duplicating areas to indicate independent occupations, until little or no homoplasy remains (ideally). These duplicate occupations of areas indicate separate vicariance events, dispersals, extinctions, or other modes of speciation or biogeographic processes beyond a simple unfolding of vicariance events associated with the original area cladogram.

Here, BPA was compromised by the fact that there are many species and subspecies of *Alouatta, Cebus*, and *Ateles* identified across the region, with no good phylogenies within each genus. For the subspecies of *Alouatta palliata* and *C. capucinus*, which are well dispersed ranging up the isthmus, assumptions were made that those farther from Colombia were more recently connected phylogenetically than those closest to Colombia. However, for the many subspecies of *Ateles geoffroyi*, scattered all over the isthmus, no such assumptions could be reasonably made (Collins, 2004; Collins and Dubach, 2000a,b, 2001; Madeiros *et al.*, 1997; Silva-Lópes *et al.*, 1996), leading to a large multichotomy. As a result, the trees produced in the BPA also never could be fully resolved, leading to ambiguity and limiting its usefulness. The phylogenetic tree for Mesoamerican platyrrhines used as a base for BPA is shown in Figure 8 and is derived in part from Collins (2004; Collins and Dubach, 2000a,b, 2001) and Cortés-Ortiz *et al.* (2003).

Sixteen distinct biogeographic zones within the isthmus, as well as two external but neighboring zones, were identified and used as the basis of discussion and analysis. While defining zones is a critical part of any BPA study, the

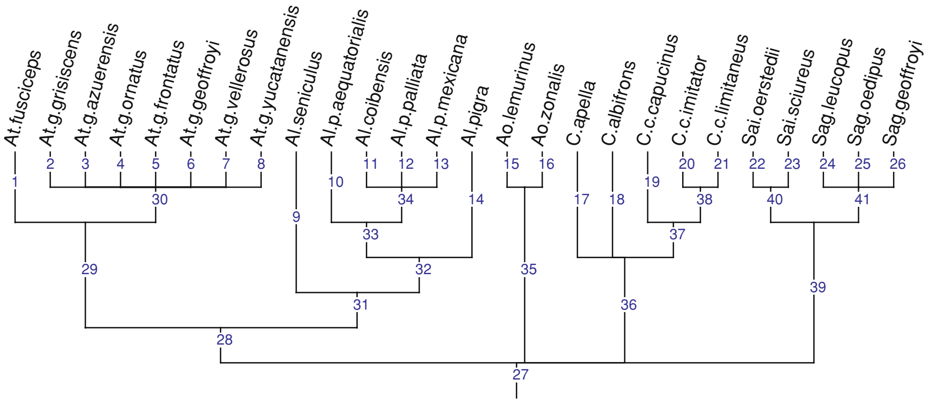

Figure 8. Cladogram of Mesoamerican primates, derived in part from Collins (2004; Collins and Dubach, 2000a,b, 2001) and Cortés-Ortiz *et al.* (2003). Numbered nodes indicate terminal taxa and "ancestors" as coded in the Brooks Parsimony Analysis.

geologic, geographic, and biologic history of Mesoamerica remains poorly understood. Therefore, the boundaries of the zones used here should not be interpreted as absolute but as hypotheses of "meaningful" biogeographic areas. The two mainland zones represent the Chocó/Atrato region, corresponding to a well-defined refuge area west of the Andean rise (Haffer, 1969, 1982), and the northern Colombian area between the Cordillera Occidental and Cordillera Oriental of the Andean area. The Andean uplift effectively isolated many trans-Andean faunal and floral elements from the Amazonian/Orinoco region (cis-Andean) to the east and south of this intra-Andean region around 8 mya (Díaz de Gamero, 1996; Haq *et al.*, 1987; Hoorn, 1993; Hoorn *et al.*, 1995; Lovejoy *et al.,* 1998; Martin and Bermingham, 2000; Montoya-Burgos, 2003; Reis, 1997; Rull, 1998; Sivasundar *et al.*, 2001; Van der Hammen, 1989; Vari, 1988).

The zones within the Mesoamerican isthmus were based on several criteria. Primary was a general consideration of the apparent boundaries for the modern distributions of subspecies of Mesoamerican primates. The distributions of the most supspeciose taxa, particularly *Ateles* and *Alouatta*, and the most restricted taxa (*Saguinus* and *Saimiri*) were given high consideration in drawing zone boundaries. In addition, Nores (1999) has suggested a 100 m rise in sea level during periods in the Pleistocene. Figures 9a and 9b show what the Mesoamerican landscape would look like, with all areas below 100 m elevation under water. It is apparent that such an event would entirely isolate the Azuero Peninsula, break the isthmus at the Gatún and Costa Rica/Nicaragua areas, and create

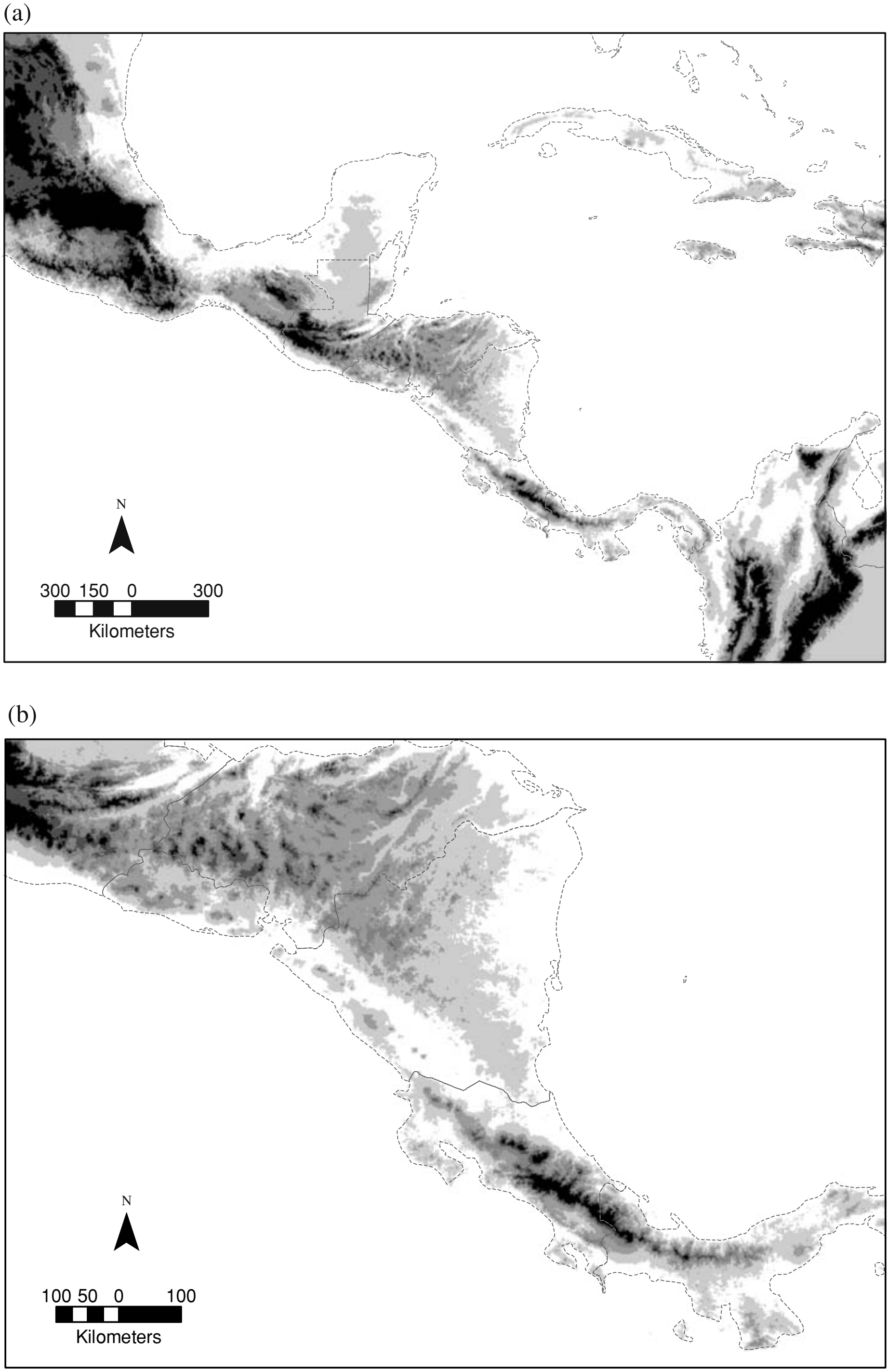

Figure 9. Map of Mesoamerica as it would appear with a 100 m rise in sea level. (a) lower Mesoamerica; (b) close-up of western Panama through Honduras. Only the shaded areas would be emergent.

major barriers to dispersal along the Pacific coast of Nicaragua and the Atlantic coast at the Honduras/Guatemala border. These gaps in land contact were also considered in defining biogeographic zones. Where central mountain ranges exist (much of the isthmus), the boundaries were drawn along the continental divide; this also conformed extremely well to posited boundaries for many individual subspecies in Rylands *et al.* (this volume; see Figures 2–7) and the divide is often of higher elevation than the reported elevational limits of most Mesoamerican primates. Finally, marked contrasts in ecozone which currently restrict primate taxa were also considered, although ecozones are more labile and changing over the last 3 my than geography.

The resulting zones should be interpreted as initial hypotheses of meaningful biogeographic zones in Mesoamerica, to be refined through this analysis and as more data become available on faunal and floral ranges across the region. The 18 zones are shown in Figure 10, and include: OUT—the Colombian northern areas west of the Cordillera Oriental, including the Magdalena and Cauca valleys; A—the Chocó/Atrato region of northwest Colombia and

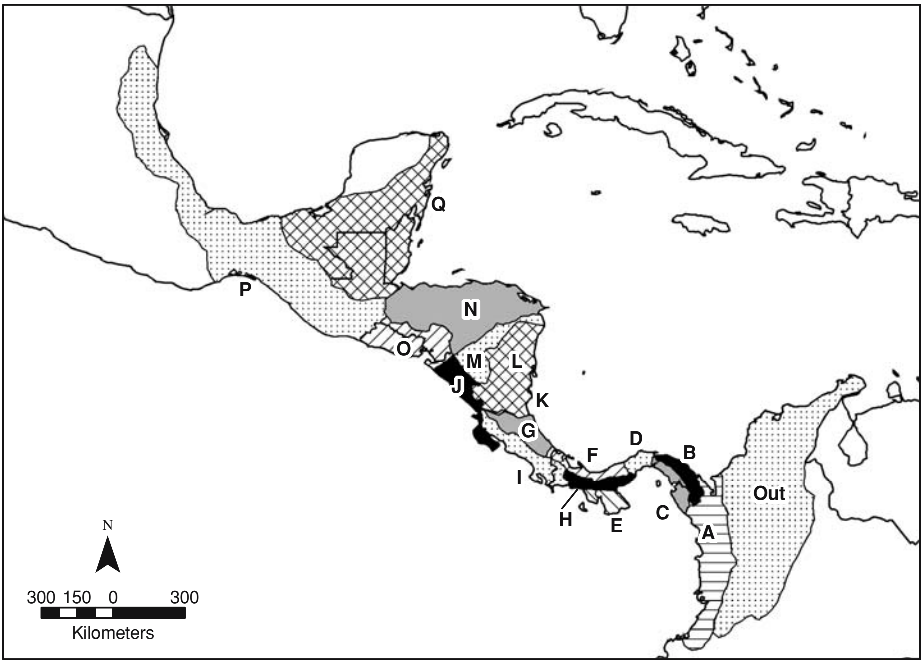

Figure 10. Map of seventeen distinct biogeographic zones plus "out" zone used for Brooks Parsimony Analysis of Mesoamerican platyrrhines. Zones are based on distributions of primate taxa and topographic features, as defined in text and used in Table 2.

western Ecuador; B—Atlantic and central region of the Darién of Panama; C—Pacific coast of the eastern Darién; D—central lowlands of Panama, including current Canal Zone; E—Azuero Peninsula and Isla de Coiba; F—Atlantic coast of Panama just into Costa Rica; G—Atlantic coast of Costa Rica and central lowlands to Lake Nicaragua; H—Pacific coast of western Panama almost to Costa Rica; I—far southwestern Panama and Pacific coast of southern Costa Rica (lusher woodlands, ends where drier forests begin); J—Pacific coast of northern Costa Rica and Nicaragua (more arid wood/shrublands), and including Ometepe Island; K—Atlantic Coast of southern Nicaragua, to Lake Nicaragua; L—highlands of northeastern and northern Nicaragua; M—northeastern and central borderland of Nicaragua; N—Atlantic Honduras and southeastern Guatemala; O—Pacific Honduras and extreme northwestern Nicaragua, El Salvador, and western Guatemala; P—southern Mexico and northeastern Guatemala; Q—prehistorically forested regions of the Yucatan, Belize, and northeastern Guatemala. The distribution of monkeys in these areas is given in Table 2.

The data (consisting of 18 geographic zones as taxa and the presence or absence of taxa and their ancestral nodes in a zone as characters) were entered and final trees produced with MacClade 4.0 (Maddison and Maddison, 2000). All parsimony analyses were done with PAUP* 4.10 (Swofford, 2002), with the goal of reducing homoplasy (Homoplasy Index), raising consistency (Consistency Index), and improving retention (Retention Index). All analyses were heuristic searches, with random addition of taxa, ACCTRAN, and retention of all shortest trees. Bootstrap analyses (600 replicates) were also performed, to produce a consensus tree (generally identical to the Strict Consensus Tree resulting from the heuristic search). Multiple analyses were run, from an initial exploration of a common inhabitation of each zone by all constituents to various separate migrations up the isthmus by different combinations of primate genera, following protocol in Brooks and McLennan (2001, 2002).

Results

As expected, given the poorly resolved phylogenies of Mesoamerican primate species, the Brooks Parsimony analytical runs never achieved zero homoplasy, or anything approaching it. The best run, duplicating nearly every area at least once, resulted in a consistency index of only 0.64, with a homoplasy index of 0.36, similar to the original analysis with only 18 zones, but it raised the

Table 2. Mesoamerican primate distributions by zone

	ZONE																	
	OUT	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
Ateles																		
A. fusciceps	×	×	×	×														
A.g. grisescens		×		×														
A.g. ornatus					×		×	×	×	×								
A.g. azuerensis						×												
A.g. frontatus											×		×	×				
A.g. geoffroyi												×						
A.g. vellerosus															×	×	×	
A.g. yucatanensis																		×
Alouatta																		
A. seniculus	×	×																
A.p. aequatorialis	×	×	×	×	×		×		×									
A.p. palliata								×		×	×	×	×	×	×			
A.p. mexicana																	×	
A. coibensis						×												
A. pigra																		×
Aotus																		
A. lemurinus	×	×																
A. zonalis	×	×	×	×	×	×	×		×									

Cebus																		
C. apella	×																	
C. albifrons	×	×																
C.c. capucinus	×	×	×	×	×													
C.c. imitator						×	×	×	×	×	×	×	×					
C.c. limitaneus											×			×	×			
Saguinus																		
S. leucopus	×																	
S. oedipus	×	×																
S. geoffroyi		×	×	×	×													
Saimiri																		
S. oerstedii										×								

The biogeographic zones are defined in the text and illustrated in Figure 10. They include: OUT—the Colombian northern areas west of the Cordillera Oriental, including the Magdalena and Cauca valleys; A—the Chocó/Atrato region of northwest Colombia and western Ecuador; B—Atlantic and central region of the Darién of Panama; C—Pacific coast of the eastern Darién; D—central lowlands of Panama, including current Canal Zone; E-Azuero Peninsula and Isla de Coiba; F—Atlantic coast of Panama just into Costa Rica; G—Atlantic coast of Costa Rica and central lowlands to Lake Nicaragua; H—Pacific coast of western Panama almost to Costa Rica; I—far southwestern Panama and Pacific coast of southern Costa Rica (lusher woodlands, ends where dry forest begins); J—Pacific coast of northern Costa Rica and Nicaragua (more arid wood/shrublands), and including Ometepe Island; K—Atlantic Coast of southern Nicaragua, to Lake Nicaragua; L—highlands of northeastern and northern Nicaragua; M—northeastern and central borderland of Nicaragua; N—Atlantic Honduras and southeastern Guatemala; O—Pacific Honduras and extreme northwestern Nicaragua, El Salvador, and western Guatemala; P—southern Mexico and northeastern Guatemala; Q—prehistorically forested regions of the Yucatan, Belize, and northeastern Guatemala.

retention index markedly to 0.86, suggesting a stronger hypothesis of the connections between areas. This run included separate codings of the areas inhabited by *Alouatta pigra* and *Saimiri oerstedii* from all others, separate dispersal events by *Alouatta palliata/coibensis*, *Ateles geoffroyi*, plus *Cebus capucinus* from that of *Aotus zonalis* and *Saguinus geoffroyi,* and separate from *Ateles fusciceps.* This suggests a total of four to five (if *A. pigra* and *S. oerstedii* dispersed in separate events) distinct invasions into the isthmus region from the Chocó.

When branches with less than 70% bootstrap support are collapsed in this final run, the separate isthmian invasions remain, but most branchings within these Mesoamerican biogeographic zones disappear. A few but important patterns remain, however. The areas with *Alouatta palliata*, *Alouatta coibensis*, *Ateles geoffroyi*, and *Cebus* form a single, large, almost entirely unresolved bush. Nested within this is an area clade for zones defined by the presence of *Saguinus* and *Aotus.* All analyses, including this preferred one, indicate close ties between zones B and D (especially) and C, identity of zones F and H, and ties between zones G, L, J, and M, with I (not including the presence of *Saimiri*) nearly as close. These suggest that within each major dispersal, there was broad exchange and similarity across eastern Panama through the central lowlands, continued broad exchange between Atlantic and Pacific coastal regions of Panama near the start of the central range, and across northern and central Nicaragua along with Pacific coastal Nicaragua/Costa Rica. While these zones were defined based on individual range boundaries of primate species, they are probably not meaningfully different biogeographic areas.

The largest differences (with most changes in faunal elements) are between Colombian Area A and the clade of all Mesoamerican regions (bootstrap of 94), a break between elsewhere and the zones for *Saimiri oerstedii* (bootstrap of 86) and for *Alouatta pigra* (bootstrap of 70), and between the zones including both *Saguinus* and *Aotus* (zones B, C, and D) versus the rest of Mesoamerica (bootstrap of 87).

Thus, even with the strong limitations on a Brooks Parsimony Analysis due to poor phylogenetic resolution, the results suggest a model of at least four separate introductions to the isthmus: (1) *Alouatta pigra* and *Saimiri oerstedii*; (2) *Alouatta geoffroyi*, *Alouatta palliata* and its offshoot *A. coibensis*, and *Cebus capucinus*; (3) *Aotus zonalis* and *Saguinus geoffroyi*; and (4) *Ateles fusciceps* a last and very recent entrant on the isthmus, based on its highly restricted range near the southern entrance to the isthmus. The lack of *A. pigra* and *S. oerstedii* in other areas along the isthmus is almost certainly due to their extinction in intervening areas (see below). In addition, the BPA strongly suggests that certain zones used here are not separate biogeographic units but largely integrated and inter-connected regions for the later immigrants (B–C–D, F–H, and G–I–J–L–M).

A MODEL FOR THE BIOGEOGRAPHIC HISTORY OF MESOAMERICAN PRIMATES

A dominating aspect of the invasion of Mesoamerica by South American taxa is the continental effects of the Andean orogeny. This uplift long predates the establishment of contact with Mesoamerica and occurred over a 27+ my period in the last half of the Cenozoic. By 8–10 mya, the Cordillera Oriental in Colombia and Venezuela effectively isolated many taxa to either side of the northern Andes (see above). Subsequent to that time, there has been only limited movement of eastern Neotropical taxa (particularly Amazonian) around this barrier into the northwestern regions of Colombia and Ecuador that border the Mesoamerican isthmus.

Therefore, once a land connection was formed around 3.5 mya, the only lowland taxa available for migration were those already present in the northwestern area, occupying particularly the Chocó and also the Cauca and Magdalena river valleys and northern coast of Colombia. For primates, this limited source area had dramatic effects on the populating of Mesoamerica. The Andean barrier has kept many genera of primates from the northwestern source area, including all pitheciines, titi monkeys (*Callicebus*), and Goeldi's monkeys (*Callimico*). The Amazon and other southern barriers have further restricted most marmosets (*Callithrix*, *Mico*, and *Callibella*), golden lion tamarins (*Leontopithecus*), and muriquis (*Brachyteles*). While woolly monkeys (*Lagothrix*) are found in the headwaters region of the Cauca and Magdalena rivers, they appear to be recent migrants to this area from over Andean passes and do not range far enough north to disperse into the isthmus (Ford, in prep.). Pygmy marmosets (*Cebuella*) were collected in southern valleys in the Cordillera Central of Colombia, but there are no clear records that they have ranged into the northwestern basins. Certainly, there are no indications that *Cebuella* ever invaded the isthmus.

As a result, the only primates known to have been geographically available to disperse into the opening Mesoamerican region were howlers (*Alouatta*), spider monkeys (*Ateles*), owl monkeys (*Aotus*), capuchins (*Cebus*), and tamarins (*Saguinus*). All of these did indeed disperse northward—using the emergent isthmus as an open highway from northwestern Colombia. However, there are substantial differences in the degree of genetic isolation of the Mesoamerican populations from those found south of the Darién in Colombia and from one another ranging up the isthmus (see Groves, 2001; Rylands *et al.*, this volume). Howlers and spider monkeys range the farthest, reaching to Mexico, with a unique species of howler in the Yucatan region (*A. pigra*) and another on Azuero Peninsula and Isla de Coiba (*A. coibensis*). Genetic evidence suggests that *A. pigra* has been distinct from *A. palliata* and *A. coibensis* for some time (Cortés-Ortiz *et al.*, 2003; see also Froehlich *et al.*, 1991). Genetic relationships among other Mesoamerican primates are still uncertain.

Given recent evidence for at least two, and possibly more, separate waves of introductions of fauna to the isthmus since the connection was first made 3.5 mya, the potential is there for multiple independent invasions by monkeys, and Brooks Parsimony Analysis supports this model.

Far less resolved are relationships between neighboring Mesoamerican zones, particularly in Costa Rica and Nicaragua. The possibility for east–west migrations in the past through the southern Nicaraguan lowlands, currently largely blocked by Lake Nicaragua, and through valleys in the highlands of northern Nicaragua, in particular, may have allowed complex mixing and separations of populations through this region. Current taxonomy and exact ranges of subspecies in this area remain uncertain (see Rylands *et al.*, this volume; Groves, 2001). Nonetheless, a broad outline of movements into and up the isthmus emerges.

Wave One

Initial invaders, with the earliest development of an emergent pathway at 3.5–3.0 mya, were the precursors of *Alouatta pigra* and *Saimiri oerstedii.* Source populations of howlers were and are in northwestern Colombia (Zones A and OUT). However, no squirrel monkeys are currently present. After ruling out human transport (in agreement with Cropp and Boinski, 2000; Rylands *et al.*, this volume), the only possibility is that squirrel monkeys were present in the late Miocene or Pliocene in northwestern Colombia, isolated from Amazonian populations by the rise of the northern Andes around 8 mya along with other primates. Certainly, ancestral squirrel monkeys were in an area bordering this while the proto-Andes were still quite low, at La Venta in the late Miocene—currently in the Colombian Andes (Kay *et al.*, 1997). In the intervening time, squirrel monkeys in northwestern Colombia have become extinct. Once on the isthmus, squirrel monkeys may have migrated up the Pacific coast of eastern Panama into their current home in Pacific Costa Rica/Panama (Zone I). There is little obvious barrier to their expansion north up to the area where drier shrublands develop, and collecting records indicate they did fill this region at least in the beginning of the 20th century. Large collections made in the mid-20th century may have contributed to their diminished range. Squirrel monkeys are currently the most endangered Mesoamerican primate (Cropp and Boinski, 2000; Reid, 1997), limited to very low elevations and edge and disturbed forests.

Howlers, on the other hand, may have migrated up the Atlantic coast once past the central Gatún area, traveling eventually all the way to the Yucatan (Zone Q). Perhaps, as a result of competition with later invading monkeys (see also Cortés-Ortiz *et al.*, 2003) or other fauna, both howlers of *A. pigra* type and squirrel monkeys were extirpated from areas outside their current range, leaving relict populations in two far-flung pockets. While Cortés-Ortiz *et al.* suggest that *A. pigra* may have been pushed up the isthmus by the later invading *A. palliata*, the remarkable dispersal abilities of howlers (evidenced in fact by *A. palliata* itself) suggest that *A. pigra* may have already spread far north before the advent of *A. palliata*. Its current distribution represents a last stand against competition from *A. palliata*. With its back to the sea, *A. pigra* has nowhere to go should *A. palliata* continue its advance into the peninsula. Reid (1997) indicates far narrower adaptive choices for *A. pigra*, with no populations recorded above 500 m, while *A. palliata* has been found as high as 2500 m.

The differentiation between *S. oerstedii oerstedii* and *S. oerstedii citrinellus* is almost certainly the result of isolation during high water periods. *Saimiri* is restricted to lowland settings (below 500 m, see Reid, 1997), and a finger of the Costa Rican central range extends nearly to the Pacific between the two. Nores (1999) suggested a sea-level rise of approximately 100 m in the Pleistocene. The effects of such rise can be seen in Figures 7 and 9b—the distribution of *S. oerstedii* would be cut into two, precisely at the boundary of the current subspecies. On the other hand, testament to the ability of *Saimiri* to take advantage of low water stands is its presence (at least in 1902) on Sevilla Island and Almijas Island (= Isla Sabaneta) off the Pacific coast of western Panama.

The current limitation of *A. pigra* and *S. oerstedii* to isolated, far-flung areas of Mesoamerica with their presumed extinction elsewhere remains difficult to explain beyond competition with later primate immigrants to the isthmus. However, it is worth noting again that these two monkeys are the most restricted in terms of elevational range to lowland areas below 500 m (Reid, 1997). Pavelka and Chapman (this volume) describe the striking effect of a hurricane on a population of *A. pigra*, resulting in a dramatic decline in population, continuing over more than 2 years after the hurricane. They believe that this population decline may be due to a combination of effects from the hurricane, including loss of food trees, increased parasite loads, and social disruption. Black howlers and squirrel monkeys, due to their restriction to low lying, mostly coastal (in the narrow Mesoamerican isthmus) regions would have been most vulnerable over time to the ravages of storms that are common occurrences in the Mesoamerican region. The long-term effects of this type of random, brief, but dramatic event may be impossible to test for over the history of primates in Mesoamerica, but continued work on the short-term impact will help us understand the potential role of storms and catastrophic occurrences on population size, structure, and survival of Mesoamerican primates.

Wave Two

A second wave of introductions would have occurred with the re-emergence of a terrestrial connection around 2.0 mya. This wave included the ancestors of *Alouatta palliata* (spun from the same source population as the earlier *A. pigra*), *Ateles geoffroyi*, and *Cebus capucinus*. All spread broadly up both coasts of the isthmus, at least through Costa Rica (Zones B–I), and all successfully moved across the filter barrier into the Azuero Peninsula, differentiating in the process. *Alouatta* appears to have differentiated more completely (particularly *A. coibensis*, isolated during the Pleistocene high water levels predicted by Nores, 1999, and perhaps earlier, as seen in Figure 9), but in any event, the biogeographic implications are the same—offshoots of *A. palliata*, *A. geoffroyi*, and *C. capucinus* in the central (Zone D) and/or Pacific coastal (Zone H) area ferreted their way onto the peninsula, becoming isolated for some time.

The near absence of *A. geoffroyi* from Zone B, in the northeastern and central Darién of Panama, is almost certainly quite recent and due perhaps to competitive exclusion from the invading *Ateles fusciceps* (see below). Some interbreeding may be occurring in area C in the central valley (Rossan and Baerg, 1977), suggesting that genetic isolation of these two species is not complete despite perhaps 2 million years of separation. *A. geoffroyi* continues to range widely, up both coasts, to the northernmost extent of primates in the southern states of Mexico. Its northern boundaries appear to include the Sierra Madre mountains and Atlantic coastal grasslands in Mexico. However, it is so successful that it is the only primate to range currently on the west side of the continental divide in El Salvador and Pacific coastal Mexico.

A. palliata appears to have been only slightly less successful. As howlers ranged northward along the Pacific coast, the mountains of northwestern Nicaragua and El Salvador were effective barriers to their continued dispersal up the Pacific coast. Once into northern Nicaragua and eastern Honduras, however, *A. palliata* has successfully moved northward, skirting the range of *A. pigra*, nearly as far north as spider monkeys.

The difference in degree of adaptability of spider and howler monkeys from other areas of their sympatry, most notably western Venezuela, is notable. In Venezuela, howler monkeys are far better able to move into somewhat inhospitable habitats, following gallery forest into the Llanos grasslands. In contrast, spider monkeys range around the highlands of western Guatemala and Honduras to disperse along the forests of the Pacific coast, where howlers are absent. The effectiveness of the high mountains in northwestern Nicaragua and southwestern El Salvador as a barrier to *Alouatta* and *Cebus* suggests that they were also effective against *Ateles. Ateles* is the only monkey in Pacific coastal Mexico, and it likely migrated south from this region into El Salvador. Only substantial genetic information on the affinities of these populations will provide an adequate test of these hypotheses.

The range of *C. capucinus* is nearly as broad, but with less apparent differentiation between populations (the degree of differentiation is controversial; see Rylands, this volume) and they never make it beyond Honduras. This could have two possible explanations. The first is that *Cebus* arrived later, with *Saguinus* and *Aotus*, but was able to disperse farther. While this is possible, and its broader elevational range (see Table 1) might support this scenario, at present the Brooks Parsimony Analysis would support the second alternative: *Cebus* arrived in this earlier cycle (Wave Two), and its restriction to areas south of Mexico and Belize are due to some barrier that *A. geoffroyi* and *A. palliata* were able to cross. The form of such barrier is unclear, and unsubstantiated reports of the occurrence of *Cebus* into Belize exist (see Rylands *et al.*, this volume; Reid, 1997). However, it is notable that comparing the range of *Cebus* (Figure 5) with a world flooded by 100 m (Figure 9b) shows a perfect match with a low region on the Honduran/Guatemalan border that would have flooded back into the high mountains of the interior. However, this did not form a barrier for *Alouatta* and *Ateles.*

One other difference is their differential presence on islands, likely related to the greater home range needs of spider monkeys versus howlers (Bernstein *et al.*, 1976; Chapman, 1988; Crockett and Eisenberg, 1987; Kinzey, 1997a,b; Palacios and Rodriguez, 2001; Wallace *et al.*, 1998; Yoneda, 1990). *Ateles* is not reported from any offshore islands along the isthmus. *Alouatta*, on the other hand, has been collected on many islands, both large and small, all likely connected to the mainland during low water cycles in the Pleistocene. These include not only Isla de Coiba, but also Isla Colón on the Atlantic side of Panama, and other small islands dotting the coasts, particularly of Panama. *Cebus* has also been collected on Isla Colón and Isla Bastimentos, as well as the Pacific coastal islands of Panama of C'baco, Coiba, Insoleta, Brava, and Sevilla. Whether or not *Ateles* ever migrated to these areas during periods of connection, the small size of the islands apparently cannot support their ranging needs today.

Several studies of other Mesoamerican immigrants from the south document explosive radiations, with likely rapid spread up the isthmus into Mexico followed by later divergence into separate taxa. These include work on short-tailed bats (Hoffman and Baker, 2003), parrots (Eberhard and Bermingham, 2004), and freshwater fish (Bermingham and Martin, 1998; Perdices *et al.*, 2002), as well as a recent study on howler monkeys (Cortés-Ortiz *et al.*, 2003). In all of these cases, mtDNA analyses fail to clearly indicate branchings between various Mesoamerican populations, supporting models of rapid expansion across the region.

Wave Three

Without well-dated fossil localities, it is conjecture whether the remaining established Mesoamerican primates , *Saguinus geoffroyi* and *Aotus zonalis,* entered the isthmus with Wave Two or as part of a postulated independent, younger invasion, associated with a possible influx of freshwater fish around 1.0 mya (Martin and Bermingham, 2000). Both *Aotus* and *Saguinus* exhibit only limited dispersal northward. *Saguinus* only reaches Zone D (the lowland Canal Zone area of Panama). *Aotus* extends beyond this, both on the Atlantic side of the Panamanian Central Range and into Azuero Peninsula. It does reach, with certainty, nearly to the Costa Rican border. There is little apparent geographic barrier to a spread into Atlantic coastal Costa Rica, and Timm (1994; but see Rylands *et al.*, this volume) has argued for its presence in southeastern Costa Rica. In either event, there is no evidence for its ever having extended farther up the isthmus on either coast. This abbreviated presence coupled with their lack of divergence strongly suggests a late entry to the isthmus, particularly in light of the widespread successful dispersal of both these genera throughout much of tropical South America.

Aotus (collected on Isla Colón and Isla Bastimentos on the Atlantic coast of Panama) has also dispersed to island areas, like *Alouatta*, *Cebus*, and *Saimiri*. These distributions suggest that *Aotus* was present in the region during the low water cycles of the later Pleistocene or that the emergent low water pathways were available in the very recent past.

Wave Four

A last wave would be recent, filtered invasions by *Ateles fusciceps*, particularly into the northeastern (Atlantic) region of Panama. This is almost certainly very recent, given the highly limited presence of *A. fusciceps* in Mesoamerica. The Mesoamerican *A. palliata*, *C. capucinus*, *A. zonalis*, and *S. geoffroyi* all share extremely similar southern range extensions into northwestern Colombia and Pacific coastal Ecuador. These may be remnants of the original source populations for these Mesoamerican monkeys, or they may be the result of recent back migrations into South America through the same filter route being used by *A. fusciceps* to extend north into the isthmus.

Last, in South American we find *Alouatta seniculus*, *Cebus albifrons*, and — farther east—*Cebus apella* making inroads across northern Colombia, although none currently occur on the isthmus. All three are widespread in northern South America east of the Andean range. While they could represent source populations for the isthmian taxa, it is most likely that they are very recent immigrants who have managed to skirt the Andean range. The evidence of the absence in northwestern Colombia of other monkeys found east of the Andean ranges, such as pitheciines, *Saimiri*, *Callicebus*, and *Cebuella*, as well as the genetic and morphologic distinctions between all other trans-Andean versus cis-Andean primates suggest that the cross-Andean distributions of these three are highly unusual. All three are very adaptable primates, found in wide varieties of habitats and elevations, and their absence from the isthmus or the Chocó reinforces the hypothesis that they are recent immigrants to northern Colombia. As these successful monkeys continue to move westward, they may enter the isthmus via the same filter through the Darién Range that has been exploited by *A. fusciceps*, putting further pressure on the native monkeys of Mesoamerica.

SUMMARY

Mesoamerican primates derive from distinct source populations that were likely isolated in northwestern Colombia approximately 8 mya with the rise of the northern Andes. This community of monkeys must have included squirrel monkeys in addition to relatives of the other Mesoamerican taxa, although squirrel monkeys are now extinct/absent in the region. All primates known to be distinct parts of the trans-Andean Colombian fauna migrated into the isthmus.

With the complete emergence and establishment of a land connection across the Darién region around 3.5 mya, primates quickly moved widely into Mesoamerica. Evidence from a variety of sources suggests that the connection subsided again periodically over the last 3 my, resulting in at least a second major cycle of emergence/dispersal around 2 mya. Some evidence suggests a third subsidence/emergence cycle around 1 mya, with a filter present today. Filtered exchange of land fauna may have also occurred pre-emergence, around 6–8 mya. Although primates would have been present in the source Chocó region, there is no current evidence that they utilized any tenuous early connection that may have existed.

Modern distributions suggest that primates entered Mesoamerica in at least three and likely four waves. The first wave included ancestors of *Alouatta pigra* and *Saimiri oerstedii*, with initial major emergence of the isthmus. These now exist only in relict areas where they are endangered, with their ancestors elsewhere on the isthmus, and in the case of squirrel monkeys in northern Colombia, now extinct. The second wave was likely an explosive entry and rapid dispersal up the isthmus of ancestral *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus.* As gene flow between populations was interrupted by highlands, grasslands, and periodic rises in sea level, groups differentiated, including the distinctive howlers of Azuero Peninsula and Isla de Coiba. The third and fairly recent wave brought tamarins (*Saguinus geoffroyi*) and owl monkeys *(Aotus zonalis*). The final invader has been *Ateles fusciceps*, through a filter that may also have allowed back migrations of tamarins, capuchins, howlers, and owl monkeys into northwestern Colombia, although these may be part of the ancestral population pool that remained in this region. Three recent immigrants into northwestern Colombia (*Alouatta seniculus, Cebus albifrons,* and *Cebus apella*) may eventually invade the isthmus, placing pressure on the unique primate fauna of the Mesoamerican region.

Relationships between the areas inhabited by the various named subspecies of *A. geoffroyi*, *A. palliata*, and *C. capucinus* in Mesoamerica remain obscure.

Current models, derived from mtDNA analyses of howlers and other fauna, suggest explosive dispersal throughout the region followed by differentiation. A test of this model is needed; mtDNA data from populations of howlers, spider monkeys, and capuchins should show equidistant relationships between monkeys in each of the biogeographic zones identified here if this model is correct.

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