THE GREATER ANTILLEAN PLATYRRHINES: BIOGEOGRAPHY AND PALEOBIOLOGY

by

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ABSTRACT

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The Greater Antilles were once home to an endemic radiation of platyrrhine primates including five species, *Xenothrix mcgregori* from Jamaica, *Paralouatta varonai* and *P. marianae* from Cuba, the Hispaniolan species *Antillothrix bernensis*, and *Insulacebus toussaintiana* from Haiti. This dissertation seeks to expand our knowledge of this group through the analysis of biogeographical patterns, paleobiology with a particular focus on paleodietary reconstruction, and through the description of new fossil material.

To date, much of the scholarship on the Antillean fauna has focused on phylogeny and biogeography. Of particular concern is how and when the Antillean primates entered the Caribbean and to which mainland taxa they might be related. The evidence presented here suggests a Miocene entry by members of at least two platyrrhine clades, though an earlier colonization via the GAARlandia landspan and Caribbean monophyly cannot be excluded.

In the 1980s, a nearly complete primate dentition in association with gnathic fragments was recovered from the Tiburon Peninsula of western Haiti. This material represents a new species, *Insulacebus toussaintiana*, a likely relative of the Jamaican primate, *Xenothrix mcgregori*. *Insulacebus* has several unusual anatomical features including small maxillary lateral incisors, a P^2 that is small and simplified compared to P^4, lower canines that are triangular at the base, mandibular premolars and molars with closely approximated cusps, and polycuspate M_3s. The latter two features it shares with *Xenothrix*.

Paleodietary reconstruction for *Insulacebus* and the other Caribbean forms was best accomplished through the use of landmark-based three-dimensional measures of molar form. The sample included 208 extant platyrrhines from 9 genera and 22 individual extinct platyrrhines representing 15 species from Argentina, Colombia, Brazil, and the Greater Antilles. Principal component and discriminate function analyses of the landmark data found that the morphological variation across the sample corresponded largely to the dietary profiles documented in field studies, and not to the phylogenetic relationships of the taxa. While the landmark-based data could be used to successfully differentiate primates by dietary guild, measures of crown relief based on surface area ratios were much less successful in differentiating primates by diet. In all, the Caribbean forms represent an island radiation showing evidence for dietary flexibility particularly within the general category of frugivory in the species *Paralouatta varonai*, *Antillothrix bernensis*, and *Insulacebus toussaintiana*. The enigmatic *Xenothrix mcgregori* may have occupied an ecological niche with no modern platyrrhine analogue. As additional fossil evidence accumulates, we will be better able to evaluate their adaptations to the unique Caribbean environment.

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This dissertation is dedicated to my family.

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CHAPTER 1

BIOGEOGRAPHY OF THE GREATER ANTILLEAN PRIMATES AND OTHER MAMMALS

INTRODUCTION

The first hint that there might have been an endemic primate fauna in the Greater Antilles came with the description of *Montaneia anthropomorphus* by Florentino Ameghino (1910), a prolific Argentine paleontologist. The remains – a collection of isolated teeth, belonging to a single individual, had actually been found some twenty-two years earlier by Luis Montané in a cave in Sancti Spiritus, Cuba (MacPhee and Horovitz, 2002), but remained neglected in a pattern of discovery and delayed description that would frequently be repeated in the years to come. Only a few years after this discovery, however, doubt was cast on the status of this specimen as a new species. Miller (1916) suggested that the teeth belonged to a modern member of the genus *Ateles*, but he failed to identify the species. Later, Williams and Koopman (1952) suggested it was *Ateles fuscipes* [sic], found in Panama and Ecuador. Finally, eighty-six years after its description the status of the specimen as a modern *Ateles* was confirmed by radiocarbon dating (MacPhee and Rivero de Calle, 1996). By this point in time, the extent of the primate and mammalian fauna of the region had begun to take shape, and the loss of *M. anthropomorphus* as a unique species did not mean the end to Caribbean endemic primates. By the late 1990s, when *M. anthropomorphus* was definitively included in the genus *Ateles*, there were three known endemic platyrrhines in the Greater Antilles, *Xenothrix mcgregori* from Jamaica, *Antillothrix bernensis* found on Hispaniola, and *Paralouatta varonai* from Cuba. Since that time, two more species have been added to the mix, *Paralouatta marianae*, represented by a single astragalus from the Miocene of Cuba (MacPhee *et al.*, 2003) and *Insulacebus toussaintiana*, a monkey found on the Tiburon Peninsula in western-most Haiti (Cooke *et al.*, 2011). A complete list of the published specimens of primates is given in Table 1.01.

Table 1.01. Endemic Greater Antillean platyrrhine specimens

Taxon	Locality	Element	Museum and Number
Paralouatta varonai	Cueva Alta and Cueva del Mono Fosil, Cuba	M^1 or M^2	MNHNH V104
		I^2	MNHNH V105
		P^4	MNHNH V106
		P^2	MNHNH V115
		P^4	MNHNH V116
		P_2	MNHNH V117
		P_3	MNHNH V118
		P_4	MNHNH V119
		M^1 or M^2	MNHNH V120
		M^1 or M^2	MNHNH V121
		M^3	MNHNH V122
		M_1 or M_2	MNHNH V123
		M_3	MNHNH V124
		I_1	MNHNH V126
		Mandibular C	MNHNH V127
		P_2	MNHNH V128
		P_3	MNHNH V129
		P_3	MNHNH V130
		P_3	MNHNH V131
		P_3	MNHNH V132
		M_3	MNHNH V134
		M_3	MNHNH V135
		M_1 or M_2	MNHNH V136
		M_1 or M_2	MNHNH V138
		M_1 or M_2	MNHNH V139
		M_1 or M_2	MNHNH V140
		M_1 or M_2	MNHNH V141
		M_1 or M_2	MNHNH V142
		M_1 or M_2	MNHNH V144
		M_1 or M_2	MNHNH V145
		P_4	MNHNH V146
		P_4	MNHNH V147
		P_4	MNHNH V148
		I^2	MNHNH V149
		I^1	MNHNH V150
		I^2	MNHNH V151
		I^1	MNHNH V152
		I^1	MNHNH V153
		I^1	MNHNH V154
		I^2	MNHNH V155
		I^1	MNHNH V156
		I^1	MNHNH V157
		I^1	MNHNH V158

Table 1.01. continued

Taxon	Locality	Element	Museum and Number
Paralouatta varonai	Cueva Alta and Cueva del Mono Fosil, Cuba	P^2	MNHNH V160
		P^2	MNHNH V161
		P^2	MNHNH V162
		P^3	MNHNH V163
		P^2	MNHNH V164
		P^2	MNHNH V165
		dP^4	MNHNH V166
		P^4	MNHNH V167
		P^4	MNHNH V168
		P^3	MNHNH V169
		P^4	MNHNH V170
		P^4	MNHNH V171
		P^4	MNHNH V172
		P^4	MNHNH V173
		P^3	MNHNH V174
		P^3	MNHNH V175
		P^3	MNHNH V176
		P^3	MNHNH V177
		P^3	MNHNH V178
		M^1 or M^2	MNHNH V179
		M^1 or M^2	MNHNH V180
		M^1 or M^2	MNHNH V181
		M^1 or M^2	MNHNH V182
		M^1 or M^2	MNHNH V183
		M^1 or M^2	MNHNH V184
		M^3	MNHNH V185
		M^1 or M^2	MNHNH V186
		M^1 or M^2	MNHNH V187
		M^1 or M^2	MNHNH V188
		M^1 or M^2	MNHNH V189
		M^1 or M^2	MNHNH V190
		M^3	MNHNH V191
		M^3	MNHNH V192
		M^3	MNHNH V193
		Cranium - missing premaxilla	MNHNH V194
		Mandible	MNHNH V195
		P^3	MNHNH V578
		M_1 or M_2	MNHNH V579
		R. humerus	MNHN Cu 76.1010
		L. humerus - diaphysis	MNHN Cu 76.1011
		R. humerus - head	MNHN Cu 76.1012
		R. humerus - distal articular end	MNHN Cu 76.1013
		R. ulna - triceps process	MNHN Cu 76.1014

Table 1.01. continued

Taxon	**Locality**	**Element**	**Museum and Number**
Paralouatta varonai	Cueva Alta and Cueva del Mono Fosil, Cuba	L. radius - proximal end	MNHN Cu 76.1015
		L. ulna - proximal end	MNHN Cu 76.1016
		L. ulna - proximal end	MNHN Cu 76.1017
		L. femur - proximal end	MNHN Cu 76.1018
		L. femur - distal epiphysis	MNHN Cu 76.1019
		L. calcaneus - talar facet	MNHN Cu 76.1020
		R. middle cuneiform	MNHN Cu 76.1021
		R. metacarpal 1	MNHN Cu 76.1022
		R. metacarpal 2	MNHN Cu 76.1023
		L. humerus - distal articular end	MNHN Cu 76.1024
		L. metatarsal 1	MNHN Cu 76.1025
		R. metatarsal 1 - proximal end	MNHN Cu 76.1026
		L. metatarsal 3	MNHN Cu 76.1027
		R. metatarsal 3	MNHN Cu 76.1028
		R. proximal phalanx	MNHN Cu 76.1029
		3 phalanges	MNHN Cu 76.1030a-c
		12 middle phalanges	MNHN Cu 76.1031a-l
		4 distal phalanges	MNHN Cu 76.1032a-d
		1 distal phalanx	MNHN Cu 76.1033
		R. tibia - shaft and distal end	MNHN Cu 76.1034
		L. humerus - shaft and distal end	MNHN Cu 76.1035
		R. os coxa -partial	MNHN Cu 76.1036
		R. astragalus - body	MNHN Cu 76.1037
Paralouatta marianae	Domo de Zaza, Cuba	R. astragalus	MNHN Cu-P 3059
Xenothrix mcgregori	Long Mile Cave, Jamaica	L. mandible - ramus and M1-2	AMNH 148198
Xenothrix mcgregori	Long Mile Cave, Jamaica	R. femur - missing head	AMNH 259900
	Long Mile Cave, Jamaica	R. humerus - proximal end	AMNH 259901
	Long Mile Cave, Jamaica	R. tibia - proximal end	AMNH 259902
	Long Mile Cave, Jamaica	L. tibia - proximal end	AMNH 259903
	Long Mile Cave, Jamaica	L. os coxa - partial	AMNH 259904
	Long Mile Cave, Jamaica	R. humerus - shaft	AMNH 259905
	Long Mile Cave, Jamaica	L. humerus - distal end and shaft	AMNH 259906
	Long Mile Cave, Jamaica	R. ulna - proximal end	AMNH 259907
	Long Mile Cave, Jamaica	Sacrum - partial	AMNH 259908
	Skeleton Cave, Jamaica	L. mandible - ramus and P3 - M2	AMNH 268001
	Drum Cave, Jamaica	R. humerus - proximal end	AMNH 268002
	Somerville Cave, Jamaica	R. femur - distal end	AMNH 268003
	Skeleton Cave, Jamaica	L. mandible M1-2	AMNH 268004

Table 1.01. continued

Taxon	Locality	Element	Museum and Number
	New (?) (See MacPhee and Meldrum, 2006)	L. humerus - proximal end	AMNH 268005
	Lloyd's Cave, Jamaica	Skull -maxilla, nasal area, lower orbits, P4-M2	AMNH 268006
	Lloyd's Cave, Jamaica	L. maxillary fragment P3-M2	AMNH 268007
	Drum Cave, Jamaica	R. humerus - missing head	AMNH 268008
	Skeleton Cave, Jamaica	R. os coxae - partial	AMNH 268009
	Somerville Cave, Jamaica	R. ulna - proximal end	AMNH 268010
primate	Coco Ree Cave, Jamaica	R. femur - proximal end	UF 40097
?primate	Sheep Pen Rock Shelter, Jamaica	R. femur - proximal end and shaft	UF 58350
Antillothrix bernensis	Cueva de Berna, Dominican Republic	R. maxilla	CENDIA 1 (MHD)
	Bahia de Semana, Dominican Republic	R. tibia - distal end	USNM 254682
	La Jeringa, Parque del Este, Dominican Republic	Partial skeleton	MHD 01
Antillothrix bernensis	Padre Nuestro, Parque del Este, Dominican Republic	Cranium and postcranial elements	PNE-PNP-PN-09-01 (cranium) (*Museo del Hombre Dominicano* and Indiana University, Bloomington)
Insulacebus toussaintiana	Trouing Jeremie 5, Haiti	Associated nearly complete dentition, mandibular and maxillary fragments	UF 114714
primate	Trouing Marassa, Haiti	I1	UF 114715 (lost)
	Trouing Marassa, Haiti	M1	UF 114716 (lost)
	Trou Jean Paul, Haiti	L. femur	UF 114717
	Trouing Carfineyis, Haiti	R. humerus – distal end and shaft	UF 114718
	Trou Woch Sa Wo, Haiti	L. mandible - fragment M1	UF 28038 (lost)

In addition to the primates, the Greater Antilles once harbored a much larger endemic mammalian fauna that included rodents, bats, sloths, and the euliptophylans *Solenodon, Apotogale,* and *Nesophontes* (Dávalos, 2004). Today, however, over eighty percent of the endemic non-volant mammals, and twenty-four percent of endemic bats in the West Indies have become extinct (Morgan and Woods, 1986), leaving the evaluation and interpretation of much of this biological diversity squarely within the realm of paleontological inquiry. In this chapter, I will review the history of discovery, biogeography, and evolutionary relationships of this fauna with a particular emphasis on the primates. While the treatment will not be exhaustive (the rodents alone warrant a sizeable monograph), it will cover the major problems in the study of the Greater Antillean mammals.

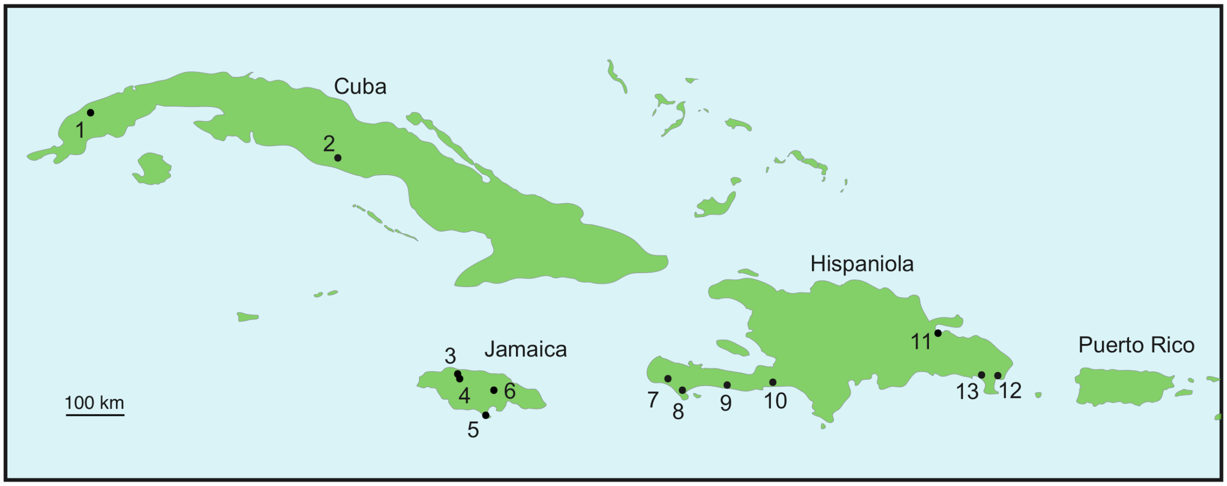

Figure 1.01. Schematic map of Greater Antillean primate localities. 1) *Paralouatta varonai*, Cueva de Mono Fósil, Cueva Alta. 2) *P. marianae*, Domo de Zaza, 14.68 MA ^{87}Sr/^{86}Sr analysis, 16.3-18.8 MA stratigraphic analysis (MacPhee *et al.*, 2003) 3) Possible primate femur, Sheep Pen Cave. 4) *Xenothrix mcgregori*, Long Mile Cave, 2145 ± 220 BP ^{14}C (MacPhee, 1984) 5) *X. mcgregori*, Jackson's Bay Caves, 6410 ± 110 BP 14C (McFarland et al., 2002) 6) Possible primate femur, Coco Ree Cave, 35,000 - 38,000 BP ^{14}C (Ford and Woods, 1986) 7) *Insulacebus toussaintiana*, Trouing Jérémie #5 8) Primate mandible, Trou Woch Sa Wo, 9550 ± 150 BP ^{14}C (MacPhee and Woods, 1982) 9) Primate humerus, Trou Carfinéyis 10) Primate femur, Trou Jean Paul 11) Primate tibia, Samaná Bay 12) *Antillothrix bernensis*, Cueva de Berna, Boca de Yuma, 3850 ± 135 BP ^{14}C (Rímoli, 1977) 13) *A. bernensis*, La Jeringa Cave and Padre Nuetro Cave, Parque Nacional del Este, Dominican Republic.

A BRIEF HISTORY OF THE GREATER ANTILLEAN PRIMATES

Xenothrix mcgregori

At the time that the status of *Montaneia anthropomorphus* as a true endemic Caribbean primate was under scrutiny, several paleontological expeditions were about to begin or were already underway. Throughout the 1920s, expeditions to the Caribbean region were sponsored by the Smithsonian Institution and the American Museum of Natural History. Both museums received large collections from these efforts. Garrett Miller primarily worked in the Dominican Republic and Haiti and was sponsored by the Smithsonian Institution, and Harold Anthony was responsible for recovering several late Pleistocene subfossil primates from Jamaica. Anthony's specimens included an associated mandibular fragment (AMNH 148198) and femur (AMNH 259900) from Long Mile Cave (Fig. 1.01). No new species were named until 1952, however, when Williams and Koopman (1952) described the species *Xenothrix mcgregori* from the Long Mile Cave partial mandible. They remained circumspect in placing it taxonomically and stated that it bore little resemblance to any living form, with its dental formula of callitrichines, a molar crown pattern resembling *Cebus*, and an expanded mandibular angle reminiscent of *Callicebus*. The primate femur described in Harold Anthony's records was not included in the hypodigm of the new species, but Williams and Koopman (1952) did note that the poorly preserved postcrania in the collection of Jamaican material at the American Museum of Natural History might be primate.

Over the next twenty years, several scholars addressed the problem of *Xenothrix*. Hershkovitz (1970) placed the specimen in its own family, Xenothricidae, (later changed to Xenotrichidae in Hershkovitz, 1977) a move that was accepted by Simons (1972) and Hoffstetter (1974). Rosenberger (1977) discussed its relationship with the living platyrrhines and suggested the absence of the third molar was not homologous with this character state in callitrichines. He based his assessment on the length of the molars relative to the molar row, and the inferred retention of hypocones on M_{1-2}, which have been greatly reduced in the marmosets and tamarins. He further postulated that *Xenothrix* should be allied with *Callicebus* or *Aotus*, based on the deep mandibular corpus and the placement of the entoconid away from other talonid cusps. His conclusions were tentative due to the fragmentary nature of the material. In later work, Rosenberger supported the hypothesis that *Xenothrix* was the sister taxon to *Callicebus* (Rosenberger, 1981), but amended this placement with the discovery of additional cranial material (Rosenberger, 2002).

The postcranial subfossils discovered by Harold Anthony in the 1920s were eventually described by MacPhee and Fleagle (1991) who attributed the femur, os coxae, and tibia to the order Primates, and identified non-capromyid humeri, as well as an ulna and a sacrum, which they left unallocated. MacPhee and Fleagle stated that the primate postcrania bore little resemblance to modern forms, but they interpreted the femur as being indicative of slow climbing. Interestingly, the femur also shared some similarities with *Potos flavus*, the kinkajou. They provisionally accepted Hershkovitz's family Xenotrichidae until further analysis could fully elucidate the relationships of *Xenothrix*.

In the 1990s, several expeditions to Jamaican cave sites resulted in the recovery of additional cranial and postcranial material attributed to *Xenothrix*, including a partial lower face containing the palate with left and right P^4-M^2, most of the maxilla and parts of the sphenoid. This discovery confirmed that the dental formula of this taxon is 2.1.3.2/2.1.3.2. With the new partial face, Horovitz and MacPhee (1999) were able to further develop the hypothesis, first proposed by MacPhee *et al.* (1995), that all the Antillean monkeys belonged to a monophyletic group linked most closely with modern *Callicebus*.

Rosenberger (2002) has objected to this hypothesis and has suggested that *Xenothrix* was a Jamaican owl monkey, thus modifying his earlier view. He based his conclusions on the fairly large orbit size as inferred from the preserved orbital rim, large inferior orbital fissure, and the large I^1

alveolus as compared to the I^2 alveolus. These characters are shared with *Aotus*. MacPhee and Horovitz (2004) tested this alternative phylogeny with extensive anatomical comparisons and by extending their parsimony analysis using PAUP* (Swofford, 2002). They maintained that the monophyly of the Antillean monkeys was still supported in the most parsimonious trees, but in slightly less parsimonious trees, *Aotus* did appear to be linked with *Xenothrix*. MacPhee and Horovitz (2004) assigned the Antillean monkeys to the tribe Xenotrichini, which included *Antillothrix* and *Paralouatta* in addition to *Xenothrix*. Xenotrichini is considered the sister to Callicebini.

Antillothrix bernensis

Antillothrix was, until recently, the least known of the Caribbean platyrrhines. In 1928, Miller discovered a distal tibia near Samaná Bay in the Dominican Republic (Miller, 1929) that would later be included in the *Antillothrix* hypodigm. The recent discovery of an additional primate species of similar body size on Hispaniola may complicate the inclusion of this specimen within *Antillothrix*, however. Miller was unable to find a platyrrhine or cercopithecoid with similar morphology, and he catalogued the tibia as "*Cercopithecus*? sp.?" based on the robusticity of the shaft, suggesting that it might represent an imported animal. Ford (1980a, b, 1986, 1990a, b) questioned this interpretation and proposed that the tibia might have been part of a callitrichine lineage that entered the Greater Antilles and underwent island gigantism. She based her conclusions on four derived characters that the Samaná tibia shared with callitrichines. Additionally, Ford held that the dental formula of *Xenothrix* might provide additional evidence for a Greater Antillean callitrichine. Based largely on size, MacPhee and Woods (1982) felt that the species represented by the tibia might be conspecific with craniodental remains that had been recovered by Rímoli (1977) in the Dominican Republic.

Rímoli's (1977) discovery had included a maxillary fragment with $P^4 – M^2$. He named this specimen *Saimiri bernensis* and thought that it shared a close relationship with mainland *Saimiri*, though it was considerably larger. Rosenberger (1978) suggested that it might represent a new genus. Several years later, another specimen was discovered in Haiti. The small mandibular fragment contained one fairly worn M_1 and the alveolae of $P_{3\text{-}4}$ and the roots of P_2. In their description of this material, MacPhee and Woods (1982) postulated that *Saimiri bernensis* was more closely related to *Cebus* monkeys based on its overall reduced crown relief, and its reduced M_1 prehypocristid. Unfortunately, this material has been lost (although casts remain) and thus cannot be compared directly to other Haitian primate material.

With the discovery of the Cuban primate, *Paralouatta varonai* (Rivero and Arredondo, 1991), and with the increasing number of late Quaternary subfossil specimens, MacPhee *et al.* (1995) proposed a new genus for *Saimiri bernensis*, *Antillothrix*. By this time, it had become clear that the *bernensis* material was quite different from modern squirrel monkeys and ought to be so classified. In their discussion of *Antillothrix bernensis*, MacPhee *et al.* (1995) proposed that it was closely related to the newly described Cuban primate, *Paralouatta varonai*. The discovery of *P. varonai* and of an Early Miocene (16.3-18.8 Ma) primate, *P. marianae*, from Domo de Zaza, Cuba indicated that the colonization of the Greater Antilles by primates occurred quite early. Indeed, the fossil remains from Domo de Zaza are approximately from the same time period as the Patagonian Santa Cruz and Pinturas formations. Previously, all of the Caribbean primate material was sub-recent in age. While researchers had certainly noted the morphological differences between the Caribbean forms and the mainland species (see Rosenberger, 1978), the question of the timing of colonization remained obscure in the absence of earlier fossil remains. With this early colonization in mind, MacPhee *et al.* (1995) proposed that *Antillothrix bernensis* and *Paralouatta varonai* were sister-taxa based on several derived characters.

Within the last year, several new specimens of *Antillothrix bernensis* have been recovered including two crania and many postcranial elements (Rosenberger *et al.*, 2011; Kay *et al.*, 2011). Both specimens were found within several kilometers of the site of the *Antillothrix* type specimen, *Cueva de Berna*, in the southeastern Dominican Republic. The first specimen published (MHD-01) was discovered in an underwater cave, *La Jeringa, in Parque Nacional del Este* during the summer of 2009 and was then recovered from the site by cave divers, Walter Pickel and Curt Bown, during a *Museo del Hombre Dominicano*-sponsored expedition in October 2009. It included a cranium, femur, ulna, vertebra, and ribs, and rib fragment. It is a young adult with an erupted M_3, but epiphyses that were not yet completely fused at the time of death. Rosenberger *et al.* (2011) described the specimen as difficult to place cladistically but settled on a cebid affiliation because of a close correspondence of the teeth with Patagonian cebids, however, a subsequent discovery of a mandible and additional postcranial material in July of 2010 have altered that assessment.

The second collection of recently discovered primate material came from *Padre Nuestro* Cave and is part of a large collection of fossil mammal material now housed at Indiana University, Bloomington. To date, only the primate cranium (PNE-PNP-PN-09-01) has been published in a brief report (Kay *et al.*, 2011), but an edentulous mandible and primate postcranial material exists from this site (Kay, per. comm.). Kay *et al.* (2011) hold that this specimen shows no clear resemblance to the modern radiation of platyrrhine primates, and the authors hypothesize that it is part of an early radiation unrelated to the modern groups. Kay (1990, Kay *et al.*, 2008; Kay and Fleagle, 2010) proposed a significant radiation of platyrrhines existed in Patagonia during the early Miocene, which predated the modern platyrrhine clades. Any shared characters with the modern platyrrhine lineages are interpreted as parallelism. This assessment of the Caribbean primate material is not out of keeping with his interpretations of platyrrhine phylogeny and evolution more generally.

Paralouatta varonai and P. marianae

During the late 1980s and early 1990s, a number of fossils representing a new Cuban monkey were discovered. This taxon, *Paralouatta varonai*, would greatly add to our knowledge of Greater Antillean primates. The first specimens discovered of *Paralouatta* included a fairly complete cranium and a distal humerus from a poorly dated cave site. The cranium bore a striking resemblance to modern *Alouatta* in the hafting of the face and the long, low cranial vault (Rivero and Arredondo, 1991); thus it was considered a primitive alouattin by its discoverers.

Over the course of the next several years, continued work resulted in the discovery of a mandible, numerous isolated teeth, and many postcranial bones. At the time that the type specimen was described, few unworn teeth were known for the taxon. The additional isolated teeth show morphology that is distinct from both modern *Alouatta* and the Middle Miocene alouattin, *Stirtonia*. With the discovery and description of this new material, MacPhee and colleagues proposed that *Paralouatta* was not a close relative of *Alouatta*, but was rather a member of a monophyletic Antillean clade (MacPhee *et al.,* 1995; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004).

More recently, a primate astragalus discovered in the Laguntas Formation (16.3-18.8 Ma) at Domo de Zaza was named as the type specimen for *Paralouatta marianae* (MacPhee *et al.,* 2003). This astragalus differed from one attributed to *P. varonai* in being smaller, with a lower trochlea and a deeper astragalar sinus (Iturralde-Vinent and MacPhee, 1995; MacPhee *et al.,* 2003). It is the oldest securely dated Antillean primate, thus marking the latest possible date of a colonization event in the Greater Antilles by the platyrrhine primates. *P. varonai*, however, has never been securely dated and Horovitz and MacPhee (1999) have suggested that it may be much older than the Quaternary remains found at many cave sites elsewhere in the Caribbean.

Postcranially, *Paralouatta* is unique among platyrrhines in that it appears to resemble some semi-terrestrial Old World Monkeys (MacPhee and Meldrum, 2006). MacPhee and Meldrum (2006) suggest that its humerus presents a suite of semi-terrestrial traits such as a narrow trochlea and deep olecranon fossa, and that the metapodials support short robustly built phalanges. Additionally, the talus is large and robust and the tibio-talar joint was likely quite stable. The species did have an "inset" radial facet, a feature seen in tree-dwelling primates, perhaps indicating an at least partially arboreal milieu. MacPhee and Meldrum were hesitant in firmly committing to this hypothesis, because of the large number of autapomorphic characters in the postcranial anatomy.

Insulacebus toussaintiana

The fossil material described as *Insulacebus toussaintiana* (see Chapter 2) was recovered from Haiti in the mid-1980s by Dan Cordier as part of an extensive collection effort sponsored by Charles Woods and the University of Florida, Gainesville. Much of their collection efforts focused on the Plain de Formon region of southwestern Haiti, though other areas of Hispaniola were sampled as well. The hypodigm of *Insulacebus* includes a nearly complete dentition, mandibular fragment, and maxillary fragment (Chapter 2, Fig. 2.03-2.04). The primate subfossils remained undescribed until recently and are hypothesized to be phylogenetically linked with *Xenothrix* (Cooke *et al.*, 2011). Postcranial remains are also known from two different sites in the region and include a primate humerus (UF 114718) from Trou Carfinéyis and a femur (UF 114719) from Trou Jean Paul. The postcrania were not included in the hypodigm of *Insulacebus* because they were not found in association with the cranio-dental material, and because there is no reliable way of differentiating the postcrania of *Antillothrix* and *Insulacebus* with the current fossil evidence. All postcrania of *Antillothrix* have been recovered in association with cranial remains. Definitive *Antillothrix* material has come from the Dominican Republic on the eastern portion of Hispaniola, but overlapping ranges of these two species cannot be excluded as a possibility at this time.

SETTLING THE GREATER ANTILLES: BIOGEOGRAPHICAL SCENARIOS OF COLONIZATION

Non-primate Caribbean biogeography

The biogeography of the Caribbean region is central to the question of Caribbean platyrrhine evolution, adaptation, and phylogeny. Wallace noted the region was unique in flora and fauna and discussed its biodiversity extensively (1876, 1881). Interest in the region continued into the 20th century. For much of the early 20th century, the major debate between biogeographers concerned whether land bridges (Barbour, 1914, 1916) or over-water dispersal (Matthew, 1915, 1918; Darlington, 1938, 1957; Simpson, 1940, 1952, 1958, 1965) had been the primary mechanism for faunal dispersal. Simpson's classic 1940 paper laid out a convincing case for overwater dispersal based on the depauperate nature of the Antillean fauna, and Darlington (1938) concentrated on mathematical modeling of hypothetical overwater dispersal events. These debates occurred before the modern theories of sea floor spreading and plate tectonics were accepted by the majority of geologists. During the 1960s and 1970s, as the evidence mounted for the movement of the earth's continents, explanations for the biogeographic patterns observed in the Caribbean began to change.

Many of the geological aspects of the following discussion are based on the work of Iturralde-Vinent and MacPhee (1999) and Iturralde-Vinent (2006). Extensive debate about the origins and evolution of the Caribbean plate is on-going (see *Geologica Acta*, 2006, vol. 4, issue 1-2 for a collection of papers on the subject), but here, the discussion will be limited to geological developments directly relevant to the biogeographical questions of mammalian dispersal in the region.

The precursor of the Caribbean region first began to form as Pangea broke up during the late Triassic leaving a space for the Caribbean plate to form between Laurasia and Gondwana. The Caribbean did not reach a form that was recognizably similar to the modern geography until the late Cretaceous when the maximum separation between the Maya Block and South America had been reached (Lawver *et al.*, 1999; Pindell *et al.*, 2006). Evidence suggests that the large igneous province (LIP) that makes up much of the Caribbean plate might have formed over the course of the Cretaceous (Hoernle *et al.*, 2004). A large volcanic archipelago that would later become the basement of the Greater Antilles, Lesser Antilles, and Aves Ridge was present between the North and South American plates. As the Caribbean plate migrated eastward a chain of volcanic islands formed along its boundary, in the approximate position of Central America: the proto-Antilles.

Rosen's (1975) vicariance model of mammalian dispersal was based on the transitory presence of the proto-Antilles between North and South America. It was widely influential and one of the first works to take continental movements into account in the explanation of Greater Antillean biogeography, though for completeness, it should be mentioned that del Corral (1940) discussed the Cuban mammalian fauna in the context of continental drift. Rosen (1975, 1985) proposed that during the Cretaceous and after, the islands received fauna from North and South America. As the proto-Antilles migrated eastward along the edge of the Caribbean plate, they carried the fauna as well. Rosen (1975) suggested that his model needed independent testing and a number of scholars have since offered criticism. First, researchers suggested that it was not strictly a vicariance model, as Rosen posited, since some over water dispersal would be required to colonize the proto-Antillean islands (Williams, 1989; Iturralde-Vinent and MacPhee, 1999; Hedges, 2001). Depending on the size of the water gaps between the islands of the proto-Antilles, there may have been a filter effect, which would limit the continental fauna that was able to move into these islands. But more importantly, it is unlikely that these landmasses remained subaerial continuously from the Cretaceous to the present, a clear problem for an argument of faunal continuity. It is probable that the proto-Antilles were periodically inundated as geological changes occurred and sea levels rose and fell (Iturralde-Vinent, 1982, 2006; Iturralde-Vinent and MacPhee, 1999).

Divergence dates for two extant mammalian species do provide limited evidence for Rosen's

(1975) model, however, *Solenodon paradoxus* and *Atopogale cubanus* (formerly *Solenodon cubanus,* see Roca *et al.*, 2004). According to a recent genetic analysis, this lineage diverged from eulipotyphlan insectivores around 76 Ma, a date that is compatible with Rosen's vicariance model, but does not exclude the possibility of a later colonization from a North American ancestor (Roca *et al.*, 2004). Asher *et al.* (2005) suggested *Solenodon* is the basal member of a Holarctic clade of insectivorans including erinaceids, soricids, talpids and the extinct genus *Centetodon*, a Tertiary North American insectivoran. In addition to the mammalian fauna, a widespread extant genus of frog, *Eleutherodactylus,* and a lizard genus, *Cricosaura,* are also indicative of a very early divergence from mainland taxa (Poinar and Cannetella, 1987; Hass and Hedges, 1991; Hedges *et al.*, 1991; Hedges, 1996; Heinicke *et al.* 2007) as are some fresh water fish (Doadrio *et al.*, 2009), though the authors of these studies do not necessarily support Rosen's hypothesis as originally proposed. These taxa do provide an interesting datum in considering the timing of colonization, but most other Antillean vertebrates do not show evidence of such an early divergence from mainland relatives.

While it remains unclear if these forms colonized the islands prior to the Tertiary, at 65 Ma the region was certainly transformed by the impact of the extraterrestrial biolide at Chicxulub (Hildebrand and Boynton, 1990; Crother and Guyer, 1996). The impact triggered earthquakes in the western Caribbean, which caused significant collapse of carbonate platforms throughout the Caribbean (Tada *et al.*, 2003). The collapse of this material delivered large quantities of sediment into the sea causing tsunamis perhaps a kilometer in height (Maurrasse, 1991). All low-laying land may have been inundated. It has also been suggested that very large hurricanes would have been triggered in the region (Emanuel *et al.*, 1994), which also would have had a devastating effect on the local fauna. The combination of these local events with the addition of climate change globally would have resulted in massive Caribbean extinction. The degree that highlands were affected by these events is unclear, but currently there is little evidence that the subaerial land present at the end of the

Cretaceous remained so throughout the Tertiary. It has been postulated that portions of Puerto Rico and other Antillean islands may have been emergent continuously (Donnelly, 1992; Hedges, 2001), but the presence of marine sediment from later time periods up to and including the Eocene above earlier terrestrial sediments indicate that the islands were periodically submerged throughout the Cretaceous and Paleogene (Iturralde-Vinent and MacPhee, 1999).

From the Paleocene through the Middle Eocene two volcanic arc systems were present at the edges of the Caribbean basin: a Central American volcanic arc system referenced by Rosen (1975) and one along the leading edge of the Caribbean plate (Bartolini *et al.*, 2003; Iturralde-Vinent and Lidiak, 2006). Portions of present-day Jamaica were in contact with the Chortis Block-Nicaragua Rise, and these sediments may have been in contact with the continent. There is fossil evidence for an earlier Eocene fauna from North America present in the sediments that would later separate from the continent and become the western part of Jamaica. These terrestrial sediments are found below later marine sedimentary deposits (Domning *et al.*, 1997). In contrast to the later Neotropical Antillean fauna, the terrestrial material recovered from the Eocene Jamaican deposits is Holarctic in origin (Domning *et al.*, 1997, Portell *et al.*, 2001). The fossils include a rhinocerotoid, *Hyrachus* sp. and a mammalian petrosal (MacPhee *et al.*, 1999). Sea cows are also present. This is a prime example of the "Viking Funeral Ship" model of McKenna (1973; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006), where the sediments containing the remains of an extinct fauna migrated as the Caribbean plate moved eastward.

In the Middle to Late Eocene, a period of general uplift occurred (Mattson, 1984; Iturralde-Vinent and MacPhee 1999), which culminated in a possible mainland connection – the GAARlandia (Greater Antilles – Aves Ridge) landspan between South America, and the Greater Antilles during the Eocene-Oligocene transition at 35-33 Ma (Fig. 1.02) (Iturralde-Vinent and MacPhee, 1999). It is during this period that the greatest amount of land would have been subaerial in the Caribbean.

Cuba, Hispaniola, Puerto Rico, and the Virgin Islands may have been separated by short water gaps or may have been part of one large island. By the Late Oligocene, the landspan had broken up into an archipelago making up the Aves Rise in the south and portions of the Greater Antilles in the north. While Iturralde-Vinent and MacPhee (1999) support a continuous connection between these islands and the continent, the possibility that the Aves Rise was a chain of closely spaced islands cannot be eliminated (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent 2006) - an interpretation that has been supported by Hedges (2001) and some biogeographical data. The idea that there was once substantial land exposure along the Aves Ridges had been proposed before, but most previous analyses have suggested closely spaced islands without a direct a mainland connection (see Holcombe and Moore, 1977; Pindell and Barrett, 1988; Pindell, 1994).

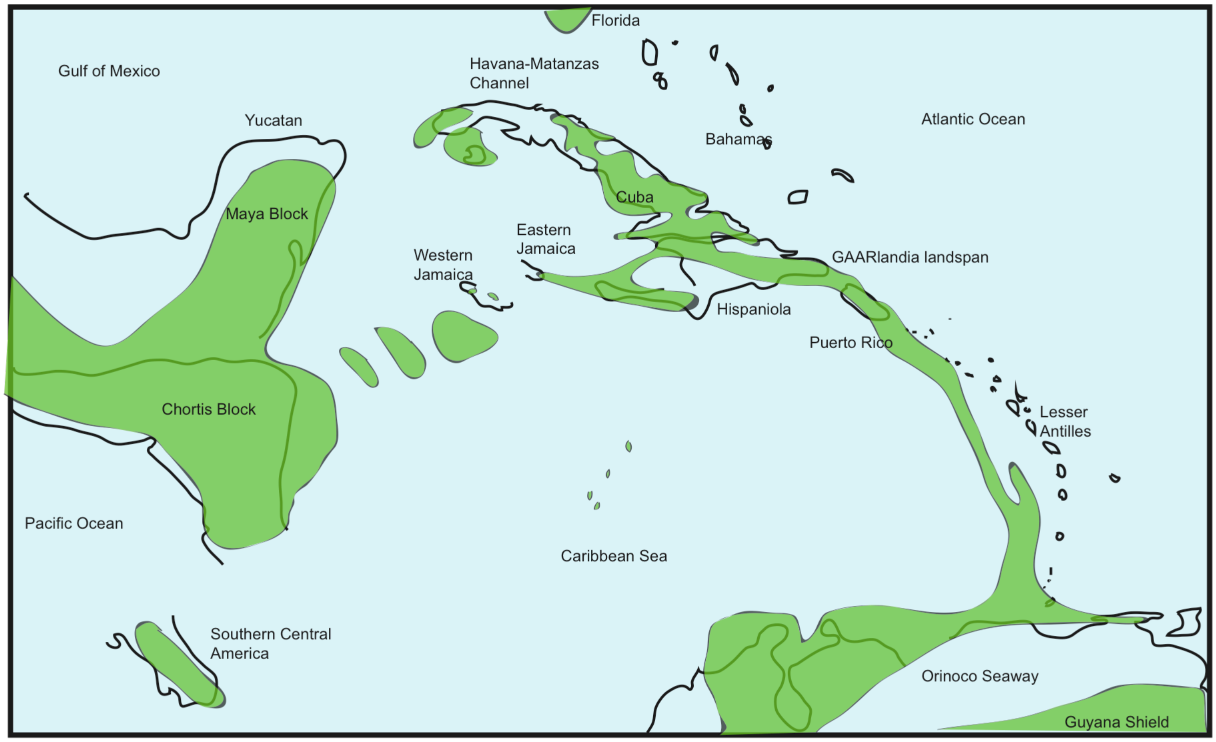

Figure 1.02. Schematic map of the Caribbean basin showing the GAARlandia landspan, 35-33 Ma. Subaerial land is shown in green, black outlines show the modern continental margins, islands or geological blocks. Based on maps from Iturralde-Vinent and MacPhee (1999).

The presence of the landspan informs the biogeographical interpretations of MacPhee and colleagues (MacPhee and Iturralde-Vinent, 1994, 1995; MacPhee *et al.*, 1995; Iturralde-Vinent and MacPhee, 1999; Horovitz and MacPhee, 1999 *et seq.*). During the brief period that GAARlandia may have been in place, they hypothesized that fauna dispersed into the Greater Antilles and became isolated when the landspan was once again submerged. Subsequent vicariance events occurred when deep-water channels formed to separate the Greater Antillean islands. The authors hold that the depauperate nature of the mammalian fauna observed today could be the result of numerous extinctions that have occurred on the Antillean islands since the submergence of GAARlandia. If there was a mainland connection, an originally diverse fauna should be observed in the fossil record. The incompleteness of the fossil record, particularly for the Eocene-Oligocene transition, makes paleontological testing of this model difficult, however.

Since the initial publication of the GAARlandia hypothesis, numerous studies on living non-mammalian taxa have been conducted in an effort to examine the degree of support for it based on possible dates of colonization. For the most part, these studies have focused on divergence dates between Antillean forms and hypothesized mainland relatives. The results have been mixed. Some support for colonization of the Antilles through the GAARlandia landspan has been found in the divergence dates of *Selenops* spiders (Crews and Gillespie, 2010) and some groups of poeciliid fresh water fish (Hrbek *et al.*, 2007), though additional analyses (Doadrio *et al.*, 2009) showed some poeciliid groups do not adhere to the divergence patterns identified by Hrbek *et al.* (2007). Studies on *Platynus* beetles (Liebherr and Godwin, 2004) and anoles (Polcyn *et al.*, 2002) and some bird species (Vázquez-Miranda *et al.*, 2006) were equivocal, and neither the possibility of entrance through GAARlandia nor via overwater dispersal could be eliminated. In the case of the birds, Vázquez-Miranda *et al.* (2006) hold that both avenues of colonization were likely used, though clearly birds are far better dispersers than the other taxa considered.

The vast majority of studies on the herpetofauna of the Caribbean have been conducted by S. Blair Hedges and colleagues. It is from this group that the most strident objections to the GAARlandia model come (Hedges, 1996, 2001; Hass *et al.*, 2001 *et seq.*). They strongly support an over water dispersal model, primarily based on molecular divergence dates, which suggest that the fauna entered the islands over many millions of years (Hedges, 1996; Hass *et al.*, 2001; Hedges, 2001; Hedges *et al.*, 2009). The molecular clock studies of Hedges and colleagues have not escaped criticism. Iturralde-Vinent and MacPhee (1999) took issue with much of the data and suggested that Hedges (1996) may have incorrectly interpreted the immunological distance data used in his molecular clock analyses. Iturralde-Vinent and MacPhee (1999) suggest that differing rates of evolution in the disparate lineages of herpetofauna may significantly affect hypothesized divergence dates. Additionally, there is the possibility that Hedges (1996) did not compare the Caribbean taxa to the most recent sister groups on the mainland. Finally, there is some question as to the direction of the water currents during much of the Cenozoic. While Hedges (1996, 2001) maintained that the water currents flowed from the South American coast to the Caribbean islands, Iturralde-Vinent and MacPhee (1999) hold that water current patterns prior to the last four million years would not favor dispersal from South America to the Caribbean islands.

Very few endemic extant mammals remain in the Caribbean so detailed genetics-based divergence date studies remain difficult. Limited paleontological evidence does show early colonization by rodents, sloths, primates, and insectivores, and the oldest primate is Early Miocene (MacPhee and Iturralde-Vinent, 1995; MacPhee *et al.*, 2003). From the same geological formation, the earliest capromyid rodent, *Zazamys veronicae*, is also known, as is the first true megalonychid sloth, *Imagocnus zazae,* though sloth material has also been recovered from the Early Oligocene of Puerto Rico (MacPhee and Iturralde-Vinent, 1995; White and MacPhee, 2001). Earlier evidence for insectivores is found in Dominican amber dating to Late Oligocene or Early Miocene (MacPhee and

Grimaldi, 1996). Besides these deposits, there is little fossil evidence of the endemic mammals of the Caribbean until the Late Pleistocene and Holocene subfossil cave deposits. To date, there is no fossil evidence for bats prior to the sub-recent Quaternary cave deposits.

In addition to the paleontologically derived first appearance data, some molecular clock-based divergence dates have been produced for bats, rodents, and the Caribbean insectivorans. Galewski *et al.* (2005) conducted an extensive analysis of the echimyid rodents and included the capromyid *Capromys pilorides* from Cuba in their study. They found it to be sister to the echimyids, though, some analyses returned trees with *C. pilorides* nested within the echimyids, perhaps indicating that the capromyids should be included within this group. The species had a divergence date from the echimyids of 18.2 Ma – the Early Miocene. Dávalos (2004) combined molecular and morphological data in phylogeny reconstructions. These cladograms were mapped onto possible land connections in the Caribbean from the Early Oligocene to the present. In only one case, the megalocnine sloths, were the molecular divergence dates entirely consistent with the timing of the GAARlandia landspan. Dávalos could not eliminate the possibility of an entry into the Greater Antilles through GAARlandia for hystricognath rodents, two lineages of bats (Stenodermatina and the *Brachyphylla-Phyllonycteris-Erophylla* group), nor for primates, though her primate phylogeny was based on the work of Horovitz and MacPhee (1999). Hypothesized divergence dates for other taxa, the choloepodine sloths, natalid and mormoopid bats, cricetid rodents, and the insectivores, did not easily fit the GAARlandia hypothesis. Additional molecular studies on the bats led to the conclusion that the lineages sampled diverged from the mainland taxa sometime during the Miocene (Dávalos, 2009). The divergence dates coincided with periods of low sea level and significant land exposure. Dávalos (2009) does suggest, however, that back-colonization to the mainland from the Antilles for certain bat lineages might have occurred. This could alter divergence date estimates between mainland groups and the island bats, if a form that had diverged recently within the Antilles that then re-entered the continent was sampled rather than a true mainland form.

Platyrrhine Biogeography

The first fossil evidence for the platyrrhine primates in South America comes from the Oligocene of Bolivia (26 Ma) (Hoffstetter, 1969; Rosenberger *et al.*, 1991a) almost a full 7-9 million years after the submergence of the GAARlandia landspan. While it is generally agreed that the Bolivian platyrrhine fossils do not represent the first platyrrhines (Hershkovitz, 1977, Szalay and Delson, 1979; Rosenberger *et al.*, 1990, 1991a; but for an alternate view see Takai *et al.*, 2000), the timing of platyrrhine entry into the Antilles via the GAARlandia landspan is still difficult if one is to take into account only the fossil evidence. The molecular clock based divergence dates estimate a platyrrhine–catarrhine divergence in the neighborhood of 40 Ma (Goodman *et al.*, 1998; Steiper and Young, 2006; Poux *et al.*, 2006; Hodgson *et al.*, 2009; Perelman *et al.*, 2011), a date that is compatible with the entrance of the rodents into South America as well (Poux *et al.*, 2006). But the phylogenetic hypothesis of Antillean platyrrhine monophyly with *Callicebus* is not compatible with entrance through GAARlandia. If the Antillean platyrrhines were isolated from the mainland forms at this early period in platyrrhine evolution, it would necessitate an early divergence of Pitheciidae from the other platyrrhine families. Most molecular divergence studies do support the Pitheciidae as the first branch, but all studies set the divergence date at approximately 20 Ma (Steiper and Young, 2006; Hodgson *et al.*, 2009; Perelman *et al.*, 2011). If *Callicebus* is indeed the sister taxon to all of the Caribbean platyrrhines as MacPhee and colleagues maintain (MacPhee *et al.*, 1995; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004 *et seq.*), or if it is sister to some of the endemic platyrrhines (Rosenberger, 1977; Rosenberger *et al.*, 2011; Cooke *et al.*, 2011), at the earliest, the ancestor of the endemic Antillean platyrrhines could only have entered the Antilles during the Early Miocene.

Any Early Miocene entrance date via overwater dispersal for the platyrrhine primates seems to be supported by most of the evidence available thus far, and is in concordance with an hypothesized period of low sea level (Haq *et al.*, 1993), which may have exposed more land in the Caribbean than at other points after the period of maximum exposure during the Eocene–Oligocene transition. Haq *et al.* (1993) studied global sea levels, however, and Iturralde-Vinent and MacPhee (1999) have cautioned that these global changes might not mean significant local changes in sea level. The morphological signature of the Antillean platyrrhines is decidedly Miocene (see Chapters 2 and 3 for additional discussion). They bear morphological resemblance to the Early Miocene forms of Patagonia (Rosenberger *et al.*, 2011; Cooke *et al.*, 2011; Chapter 3), though not particularly to the later Laventan community of the northern Neotropics, suggesting that entrance into the region pre-dated the Laventa horizon. Additionally, if support continues for a special relationship between several of the Caribbean endemic platyrrhines and the pitheciids, an Early Miocene entry would not be incompatible with the molecular divergence dates for the pitheciids.

An alternate scenario exists, however. An early platyrrhine pre-dating the divergence of the modern platyrrhine families could have entered the Antilles through GAARlandia. MacPhee (2005) has noted that the Greater Antilles does have earlier first appearance dates for some mammals than exist on the mainland, though he cautions that this may be due to the vagaries of the fossil record rather than a being a real phenomenon. Most recently, Kay *et al.* (2011) have supported this scenario, though they remained silent on the role the GAARlandia landspan might have played in this phylogenetic interpretation. Kay and colleagues have advocated the existence of a separate radiation of platyrrhine primates not monophyletically related to any of the modern platyrrhine families and represented at the terminal end by the Miocene Patagonian forms (Fleagle *et al.*, 1997; Kay *et al.*, 2008; Kay and Fleagle, 2010). If this phylogenetic position continues to receive support with increased fossil evidence and additional analysis, it would indicate that the pitheciid-like morphology observed in many of the early platyrrhines, including the Caribbean forms, was either primitive for the platyrrhines generally or the result of parallel evolution between the early stem platyrrhines and later pitheciid family.

INTER-ISLAND PATTERNS OF BIOGEOGRAPHY

The endemic non-primate mammals

While the relative importance of dispersal or vicariance events for the initial colonization of the Greater Antilles by mammals remain a matter of debate, it is clear that once the fauna entered the Greater Antilles, either all at once, by a series of dispersal events, an array of inter-island dispersal and vicariance events occurred, eventually resulting in a complex pattern of biogeographical relationships between islands.

Order	**Family**	**Island**	**Number of Species**	**Endemic Species**	**Percentage of Endemic Species**
Xenarthra	Megalonychidae	CHP	17	17	100
Rodentia	Cricetidae (Muridae)	J	1	1	100
	Echimyidae	CHP	7	7	100
	Capromyidae	CHJP	41	41	100
	Heptaxodontidae	HJP	4	4	100
Lipotyphla (Insectivora)	Nesophontidae	CHP	11	11	100
	Solenodontidae	CH	4	4	100
Chiroptera	Noctilionidae	CHJP	1	0	0
	Mormoopidae	CHJP	7	3	43
	Phyllostomidae	CHJP	26	20	77
	Molossidae	CHJP	8	0	0
	Natalidae	CHJ	6	5	83
	Vespertilionidae	CHJP	11	7	64
Primates	Atelidae	C	2	2	100
	Pitheciidae	HJ	3	3	100

Table 1.02. Synopsis and endemism of the Greater Antillean mammals relative to the mainland. C Cuba, H Hispaniola, J Jamaica, P Puerto Rico. Data sources: Williams (1989); Woods *et al.* (2001); Rodriguez-Duren and Kunz (2001); White and MacPhee (2001); Rega *et al.* (2002); Dávalos (2004).

Jamaica is by far the most distinctive of the Greater Antillean islands in terms of its mammalian fauna (Dávalos, 2004). It lacks sloths, eulipotyphlan insectivores, as well as echimyid rodents, and is the only Greater Antillean island with a cricetid rodent, though cricetids are known from the Lesser Antilles (Table 1.02). Additionally, Jamaica was home to the arguably most derived of the Antillean primates: *Xenothrix mcgregori*. The geological history of the island is complex. The western portion of what would become Jamaica was in close approximation to present-day Central America and part of the Nicaraguan Rise during the Eocene (Pindell, 1994; Domning *et al.*, 1997; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006), and as a whole it was never part of the GAARlandia landspan (Fig. 1.02). The separate eastern Blue Mountains block may have been continuous with southwestern Hispaniola and consequently may have shared a land connection with GAARlandia, however. During much of the Oligocene and Miocene, western Jamaica was inundated and little if any land was subaerial. By the Middle Miocene (Fig. 1.03) the western portion of Jamaica had collided with the Blue Mountains Block. During the rest of the Miocene and Pliocene the Caribbean plate continued its eastward movement. At the interface of contact between the North American and Caribbean plates, deep marine straits formed completing the breakup and isolation of the Greater Antilles. Although there were ephemeral connections between small islands during this period, the Greater Antilles remained separate from each other and from the continent.

The geological history of Jamaica necessitates at least some overwater dispersal to account for the patterns of biogeography. Buskirk's (1985) review, though now dated, provides an excellent analysis of the Jamaican non-mammalian fauna. Her work suggests this fauna shows Central American origins to a greater extent than the fauna observed on other Greater Antillean islands. The mammals also appear to be Central American in origin, as first noted by Simpson (1956). Jamaica has many fewer mammal species than the other, larger Antillean islands.

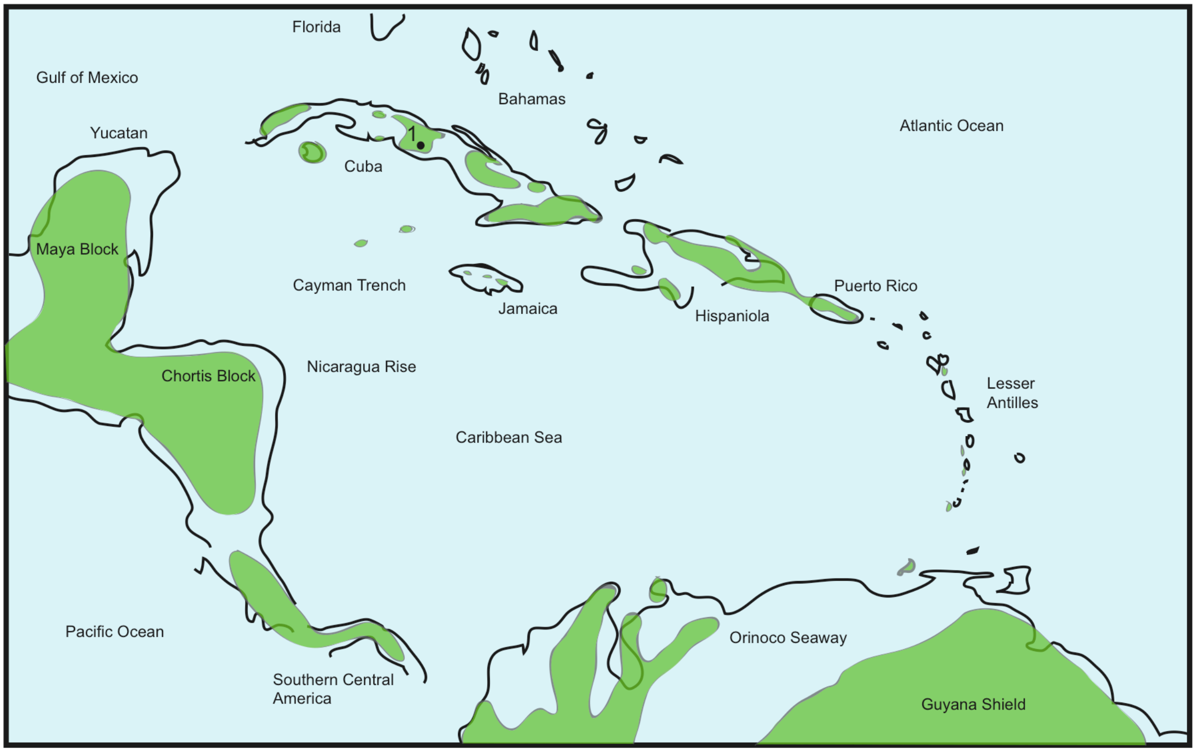

Figure 1.03. Schematic map of the Caribbean basin during the Middle Miocene, 14-16 Ma. Subaerial land is shown in green, black outlines show the modern islands and continental margins. 1 represents the site of Domo de Zaza, Cuba, the type site for *Paralouatta marianae*. Based on maps from Iturralde-Vinent and MacPhee (1999).

The rodents mostly appear to be migrants from Hispaniola and Cuba, though *Oryzomys antillarum* may have originated from Central America (Honacki *et al.*, 1982; MacPhee, 1984; Woods, 1989; Woods *et al.*, 2001). The latter might have arrived fairly recently, by geological standards at least, and has been considered to be conspecific with *O. couesi* (MacPhee, 1996; Musser and Carleton, 2005), though now most consider it to be a separate species (Morgan, 1993; MacPhee, 1996; Woods, 1989; Woods *et al.*, 2001; Weksler *et al.*, 2006). Currently, a large taxonomic revision of the oryzomyine rodents is underway by Weksler and colleagues (see Weksler, 2003, 2006; Weksler *et al.*, 2006; Voss and Weksler, 2009; Turvey *et al.,* 2010), which will involve additional analyses on the phylogenetic affinities of *O. antillarum*. To account for the phylogenetic relationships and ranges of these different groups of rodents, several inter-island overwater dispersal events were necessary (MacPhee, 1984; Woods, 1989; Woods *et al.*, 2001). Of the twenty-two species of bats known from Jamaica six are endemic, which makes Jamaica second only to Cuba in Greater Antillean chiropteran endemism. This may be indicative of a eastward migration of bat species as Hispaniola and Puerto Rico seem to have fewer species than should be expected for their landmasses (Griffiths and Kingener, 1988), though Dávalos' (2009) analyses do not necessarily suggest this.

In contrast to Jamaica, the least diverse of the primate-inhabited Greater Antilles, as far as we now know, Cuba and Hispaniola have much more mammalian diversity, though they are still depauperate by continental standards. Cuba has twenty-five species of capromyine, one isolobodontine, and two echimyid rodents, approximately eight sloth species, fifty-five bats, seven eulipotyphlans, and two primates. Hispaniola harbored fourteen rodent species in four different subfamilies, seven sloth species, two species of *Solenodon*, three species of *Nesophontes*, and twenty bat species in addition to the two primates. Both Cuba and Hispaniola have a substantial degree of endemism in the herpetofauna, avifauna, insects, and flora (*e.g.,* Olson, 1978; Hedges 1996; Glor *et al.*, 2004; Ricketts *et al.*, 2005; Townsend *et al.*, 2007; Vásquez-Miranda *et al.*, 2007; Cariaga *et al.*, 2008; Ricklefs and Bermingham, 2008; Sanborn, 2009; Hernández *et al.*, 2010). Because of the intermittent land connections between these two islands, their geological history will be discussed together.

During the Eocene-Oligocene transition, southeastern Cuba would likely have been in contact with northern Hispaniola (Fig. 1.02). The southern portion of Hispaniola, the present-day Tiburon Peninsula, may also have been part of this landmass, but the degree of connection between this region and the main body of GAARlandia is unclear (Iturralde-Vinent and MacPhee, 1999). During this period, western Cuba was isolated from GAARlandia by the Havana-Matanzas Channel. The Cayman Trench had not yet formed. Through the Oligocene, rising sea levels (Haq *et al.*, 1993;

Berggren *et al.*, 1995) and subsidence separated Hispaniola from parts of Cuba, though there may have been a connection between the southernmost portion of Cuba and northern Hispaniola. The main body of Cuba was broken up in an archipelago and remained so until the closing of the Havana-Matanzas channel in the Late Miocene (Iturralde-Vinent, 2003, 2006).

Into the Miocene, Hispaniola may have had a land connection with Puerto Rico, though initial formation of the Mona Passage likely began in the Oligocene and was subsequently periodically inundated (MacPhee *et al.*, 2003; Iturralde-Vinent, 2006). Today, Hispaniola is made up of two former paleoislands to the north and south, which may have remained separated into the Late Quaternary (Maurrasse *et al.*, 1982; Mann *et al.*, 1991; Iturralde-Vinent and MacPhee, 1999). The southern paleoisland, which included the current Tiburon Peninsula, was further subdivided into two major physiographic provinces, the Massif de la Hotte in the west and the Massif de la Selle and Sierra de Baoruco in the east, which were also periodically separated by a sea channel during some or all of the Plio-Pleistocene (Maurrasse *et al.*, 1982). During the Plio-Pleistocene, Cuba was similarly subject to periodic inundation and may have been separated into three or more separate islands divided by shallow marine straits until the very late Pleistocene (Iturralde-Vinent, 2006).

The vertebrate fauna of Cuba shows local endemism that reflects these historical divergences. The *Anolis* lizard distribution closely matches the geology of the sub-recent paleoislands (Glor *et al.*, 2004), as does the distribution of *Eleutherodactylus* frogs (Rodriguez *et al.,* 2010) and some species of fresh water fish (Doadrio *et al.*, 2007). But intra-island studies of vertebrate biogeography are only beginning to be undertaken in Cuba (Ricklefs and Bermingham, 2007). Hispaniola, by virtue of its high level of ecological variability, has extremely complex patterns of biodiversity as well. Perhaps one of the most diverse places on the island is the former paleoisland region of the Tiburon Peninsula where the Pic Macaya National Park is located. This is one of the few places left on Hispaniola where there is still original forest cover, and there are extremely high levels of endemism among the herpetofauna (Thomas, 2000) and avifauna (Rimmer *et al.*, 2006; Townsend *et al.*, 2007; Rimmer *et al.*, 2010). The eastern drier regions of the island also have unique species that conform to distributions predicted by paleoislands. Gifford *et al.* (2004) found a complex distribution in the teiid lizards, which they proposed speciated during periods of inundation and uplift.

Studies on mammalian inter-island biogeography in Cuba and Hispaniola are largely confined to paleontological work. Because the Greater Antillean radiation was so extensive, rodents may provide the best group for assessing historical biogeography in a geological context. Woods (1989a) and Woods *et al.* (2001) have assessed the rodent fauna of the Antilles and found evidence in accordance with geological reconstructions of Hispaniola and Cuba. Cuba may have had more rodent species than did Hispaniola, but fewer lineages were represented – most belonging to Capromyinae. However, Morgan and Woods (1986) cautioned that the true number of species might have been overestimated on Cuba. Woods (1989a) suggested that the Cuban rodent radiation was fairly recent because morphological diversity within the capromyines was limited (Kratochvil, 1978). Further, diversity in this group might have been the result of speciation associated with the most recent Pleistocene marine incursions into Cuban rather than deeper divergences during the Miocene or earlier.

Hispaniola presents a more diverse rodent fauna, with five subfamilies, including two endemics (Woods, 1989a; Woods *et al.*, 2001). The subfamilial ranges and distributions on Hispaniola seem consistent with paleogeographical reconstructions. Woods (1989a) suggested that the separate paleoislands of Hispaniola acted as centers of diversification among the capromyid subfamilies Hexolobodontinae and Isolobodontinae, which originated in the northern aspect of the island, and Plagiodontinae, which originated in the southern paleoisland. Hexolobodontines and plagiodontines remained isolated on Hispaniola, but one species of isolobodontine did manage to disperse into Cuba. The fossil evidence, scant though it may be, also seems to indicate that at least one plagiodontine species, *Rhizoplagiodontia lemkei*, remained confined to the Tiburon Peninsula (Woods, 1989b). The echimyid rodents seem to group into northern and southern species (Woods, 1989a). Woods (1989a) hypothesized that the Antillean rodents entered from South America sometime during the Late Oligocene or Early Miocene and diversified in Hispaniola and Puerto Rico before moving off into Cuba, though Buskirk (1985) proposed a later invasion and diversification.

Within Cuba and Hispaniola there is a certain degree of chiropteran endemism, but many species are distributed across a number of islands and in some cases the mainland (Rodriguez-Duren and Kunz, 2001; Morgan, 2001; Dávalos, 2004, 2009, Tejedor *et al.*, 2005). Molecular studies of the bats have been used to test various hypotheses of entrance into the Antilles (Dávalos, 2004, 2009), but because of their excellent dispersal abilities, bats are less ideal for evaluating inter- and intra-island patterns of biogeography. Additionally, McFarlane (1989, 1991) has proposed that many of the bat distribution patterns in the Greater Antilles might be better explained by competition for resources than by geological forces, though others have found this argument wanting and suggest that ecological explanations are only part of the picture (Rodriguez-Duran and Kunz, 2001). There are several biogeographical trends that can be identified. Jamaica has greater bat species richness than Cuba, and several taxa are endemic only to these two islands. Cuba and Hispaniola share no endemics, though Hispaniola and Puerto Rico have two shared species. These patterns are at odds with biogeographical patterns observed in non-volant mammalian fauna, but do share patterns with the avifauna (Fleming, 1982), suggesting that similar dispersal scenarios may pertain to these two groups.

Recent phylogenetic analyses of the sloth fauna indicate that the Antillean megalonychids had a diphyletic origin implying two separate colonization events (White 1993a, b; White and MacPhee, 2001). Fossil evidence indicates that they had entered the Antilles by the Oligocene (MacPhee and Iturralde-Vinent, 1995; White and MacPhee, 2001; MacPhee *et al.*, 2003) and were distributed across the islands such that island-to-island vicariance is likely the best explanation for the biogeographical patterns observed (White and MacPhee, 2001). However, Rega *et al.* (2002) hypothesize an overwater dispersal event between Hispaniola and Puerto Rico, rather than vicariance between the two islands during the Miocene. With the exception of the Miocene form, *Imagocnus zazae*, all of the known genera are dispersed across Cuba and Hispaniola. Little work has been completed on within-island distributional patterns.

The two surviving species of insectivores, *Solenodon paradoxus* and *Atopoglae cubanus*, are located in Hispaniola and Cuba respectively. Recent molecular studies have shown a very deep split in this lineage with a divergence occurring 25 million years ago (16-38 Ma), resulting in the suggestion that these two species belong to different genera, *Solenodon paradoxus* and *Atopogale cubanus* (Roca *et al.*, 2004, Asher, 2005). This estimate does correspond with biogeographical scenarios of the separation of Cuba from Hispaniola. Within each island, two species are known. Hispaniola has *S. paradoxus* and *S. marcanoi* and on Cuba, *A. cubanus* and *S. arredondoi*. The Hispaniolan *S. paradoxus* has two distinct populations on the northern and southern parts of the island, respectively, but both Hispaniolan species are absent from northern Haiti (Ottenwalder, 2001). It is unclear if this is a result of an incomplete fossil record or is a true biogeographical phenomenon. In Cuba, *A. cubanus* historically was found throughout the island, with the exception of the lowlands in the central region, which might have been periodically inundated submerged during the Pleistocene (Iturralde-Vinent and MacPhee, 1999). Today its range is restricted to the southeast. *S. arredonoi* has been found in cave deposits only in the north of Cuba (Ottenwalder, 2001). The relationships between the extant insectivores and the smaller-bodied extinct *Nesophontes* remains unclear (Asher, 1999; Widden and Asher, 2001; Asher, 2005), though historically they have been considered sister-taxa (*e.g.*, McDowell, 1958). No work on their intra- and inter- island biogeographical patterns has been completed that references modern biogeographical scenarios (see MacFadden, 1980, MacPhee *et al.*, 1999 for very brief discussion).

The endemic primates

With current fossil evidence, only a few statements can be made about the intra-island patterns of diversity. To date, only one species has been described from Jamaica, *Xenothrix mcgregori* (Williams and Koopman, 1952), which is represented by both craniodental and postcranial specimens (*e.g.*, Williams and Koopman, 1952; MacPhee and Fleagle, 1991; Horovitz and MacPhee, 2004; MacPhee and Meldrum, 2006) from Long Mile Cave and the Jackson's Bay cave complex. Two additional purportedly primate femora have been recovered, UF 40097 from Coco Ree Cave (Ford and Morgan, 1986; Ford, 1990a, b) and UF 58350 from Sheep Pen Cave (Ford and Morgan, 1988; Ford, 1990a, b). The authors (Ford 1990a, b; Ford and Morgan, 1986, 1988) have suggested that these femora are distinct from each other and that both are different from the Long Mile Cave femur (AMNHM 259900), which was recovered along with craniodental material (MacPhee and Fleagle, 1991) resulting in the hypothesis that Jamaica may have once harbored at least three primate species (Ford, 1990b). MacPhee and Meldrum (2006) also found these femora to be distinct from the more recently recovered Somerville Cave femur (AMNHM 268003), but remained silent on the possibility of additional primate species inhabiting the island.

Both the Sheep Pen and Coco Ree femora are less robust than the other *Xenothrix* femora, but the Sheep Pen femur is most distinctly different from the range of morphological variation present in platyrrhine primates in general. It has a wide femoral neck, very proximally placed lesser trochanter, (Ford and Morgan, 1988; Ford, 1990a), and a deep and mediolateraly elongate trochanteric fossa. The possibility that this specimen belongs to a hitherto unknown rodent has not been seriously considered, but work is currently underway to evaluate this hypothesis (Cooke and Tallman, in prep.). The Coco Ree femur shows a more primate-like placement of the lesser trochanter and bears some resemblance to the as of yet undescribed Haitian femur (UF 114717) (Ford, 1990b). While the Coco Ree femur is too fragmentary to draw strong conclusions about inter-relationships, this point of congruence is interesting given the proposed phylogenetic relationship between *Insulacebus* and *Xenothrix*, and the early land connection between the Blue Mountain Block and the southern portion of Hispaniola (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006). If this connection did exist, it was present very early in the history of the Caribbean, and if primates were to have dispersed across it, the ancestral species would have to have been in place during the Late Eocene or Early Oligocene. While small parts of Jamaica may have remained subaerial continuously, most reconstructions suggest that the vast majority of the island was submerged until the Miocene. By this point in time, Jamaica was separated from Hispaniola by the southern extension of the Windward Passage and separated from Cuba by the deep water Cayman Trench (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006).

Between Cuba and Hispaniola there are four described species of primate. While *Paralouatta varonai* is one of the better-represented endemic platyrrhines in the fossil record, little is known of its distribution in Cuba. All of the *P. varonai* fossils come from two adjacent caves in the northwestern portion of the island, each one poorly dated (Fig. 1.01, Table 1.01). While most of the fossils from the Caribbean are sub-recent, it remains possible that all of the Cuban material is much older (Horovitz and MacPhee, 1999), as Cuba does harbor the oldest of the Antillean platyrrhines, the congeneric *P. marianae* (MacPhee *et al.*, 2003). Biogeographically, the two *Paralouatta* species were found on two different portions of Cuba that were separated from each other by shallow marine waters for much of the history of the island. In the absence of a firm date for *P. varonai*, no biogeographical conclusions can be draw about this separation.

Hispaniola currently shows an incredible amount of ecological diversity with ecotones ranging from dry scrub to tropical rainforest, mountain forest and cactus forest as well as grassland.

Many of these regions show local endemism in flora and fauna (Woods, 1989b; Rimmer *et al.*, 2006; 2010; Santiago-Valentin, 2004; Huber *et al.*, 2010). The degree to which this ecological diversity existed in the past is unknown, but given that the mountains in the Caribbean began to take on their modern appearance during the Pliocene (Iturralde-Vinent, 2006), it is likely that a diversity of ecotones, or at least ecological partitioning by altitude, began to appear during this period.

The two known primate species from the island are similar in body size and morphology, though important dental differences do exist (Cooke *et al.*, 2011; Chapter 2, 3). *Insulacebus* is known only from the Tiburon Peninsula of Haiti and was described based on dental and mandibular evidence. Definitive specimens of *Antillothrix* are from a relatively small region of the eastern Dominican Republic and now include cranio-dental and postcranial specimens. An additional specimen was found in the same region as the *Insulacebus* material (MacPhee and Woods, 1982), but because of the abraded nature of the fossil and the similarity between *Insulacebus* and *Antillothrix*, it is not clear to which species the material belongs. Regardless, today the two species are found in ecologically very different regions of the island. The locality of *Insulacebus* along the foothills of Pic Macaya is approximately 800m in elevation and is moist forest. *Antillothrix* is found in a low-lying area marked by greater aridity, though these differences may be quite recent.

SUMMARY AND CONCLUSIONS

The Greater Antilles presents a complex array of biogeographical and geological problems that have kept paleontologists, biologists, and geologists busy for the better part of a hundred and fifty years. In the absence of a significantly larger sample of platyrrhine primate fossil material from the region, firm conclusions about the timing of Greater Antillean colonization as well as the inter- and intra-island biogeographical relationships must remain tentative. However, some patterns pertinent to the mammalian fauna remain clear.

1. The euliptophylan insectivores show deep divergences from mainland taxa and are the only mammalian forms that support Rosen's (1975) vicariance hypothesis to explain the distribution of vertebrates (and more specifically fish) in the Greater Antilles.
2. There was an Oligocene or earlier entrance into the island by at least two lineages of sloth, perhaps via the GAARlandia landspan or a series of closely spaced islands. Subsequent vicariance events between islands can account for sloth distributions within Hispaniola and Cuba.
3. Some of the rodent fauna, which is likely a composite of several dispersal events, may have entered the Antilles over the GAARlandia landspan. The radiation of Greater Antillean rodents seems to have initially taken place in Hispaniola with a more recent radiation occurring in Cuba among the capromyine rodents. Dispersal to Jamaica over water from the other Greater Antillean islands as well as from Central America is hypothesized for several species. Intra-island biogeography also reflects historical marine inundations, which would have separated the different subfamilies of the Capromyidae through vicariance.
4. A Miocene entrance into the Greater Antilles is hypothesized for many of the chiropterans. The bat fauna shows species distributions that do not reflect paleoisland separations and are better accounted for by a series of Miocene dispersal events (Dávalos, 2004, 2009) or by competition (McFarlane, 1989, 1991). Bat distribution partially mirrors that of the birds (Fleming, 1982).
5. The original notion of an entrance over GAARlandia by a primate population that was *also* derived from a common ancestor of *Callicebus* is very unlikely based on the molecular studies of divergence dates, which posit the origins of the *Callicebus* lineage at a much younger age.
6. The primates did enter the Greater Antilles by the Early Miocene, however, as evidenced by *Paralouatta marianae* from Domo de Zaza, Cuba. If they were present on the islands for a

substantial period of time prior to this date is unclear.

7. Jamaica harbored one identified platyrrhine species, *Xenothrix mcgregori*, which may share a phylogenetic relationship with *Insulacebus* on Hispaniola. There is a historical geological connection between the Blue Mountain Block, which makes up eastern Jamaica and the Tiburon Peninsula of Haiti, though this connection occurred quite early in the evolution of the Greater Antilles.
8. Hispaniola has two primate species found at opposite ends of the island, *Insulacebus toussaintiana* found in western Haiti and *Antillothrix bernensis* from the eastern Dominican Republic. No primate remains have been located in the central region, but this may be a result of poor sampling rather than a real biogeographic phenomenon. If the Hispaniolan pattern is accurate, it does reflect historical separation of the eastern and western portions of the island.

CHAPTER 2

INSULACEBUS TOUSSAINTIANA: AN EXTINCT MONKEY FROM HAITI[1]

INTRODUCTION

The history of Caribbean New World monkeys is one of the lesser-known chapters in primate evolution. The existence of an endemic, extinct splinter radiation of platyrrhines in the Greater Antilles (Fig. 1.01) was first demonstrated definitively with the description of *Xenothrix mcgregori* (Fig. 2.01) from Jamaica in 1952 (Williams and Koopman, 1952). Two other genera, each one confined to a different island, have since been reported: in Hispaniola, *Antillothrix bernensis* (Fig. 2.02) (Rímoli, 1977; MacPhee *et al.*, 1995; Rosenberger *et al.*, 2011; Kay *et al.*, 2011), and in Cuba, *Paralouatta varonai* (Fig. 3.07) and *P. marianae* (Rivero and Arredondo, 1991; MacPhee *et al.*, 2003). The ages of all are inexactly known. Although most fossil material from the Caribbean is of Late Quaternary age, the oldest primate, *P. marianae,* may be approximately 16.5-18.8 million years old, and the *P. varonai* fossils are poorly dated (MacPhee *et al.*, 2003). The youngest associated dates are late Holocene, with *Xenothrix* dated to 2145 ± 220 ^{14}C years before present (MacPhee, 1984), and this species may have persisted into the European-era historical period (MacPhee and Fleagle, 1991; MacPhee and Flemming, 1999). Two ^{14}C dates pertaining to material from Hispaniola are 3850 ± 135 (Rímoli, 1977) and 9550 ± 150 (MacPhee and Woods, 1982). *Insulacebus toussaintiana* represents the newest addition to this enigmatic fauna. While the specimens have not been dated thus far, the condition of the material would suggest a recent age in line with the other Holocene remains known from the area.

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[1] This Chapter is based on a previously published article (Cooke *et al.*, 2011) and includes an expanded and updated description of the fossil material.

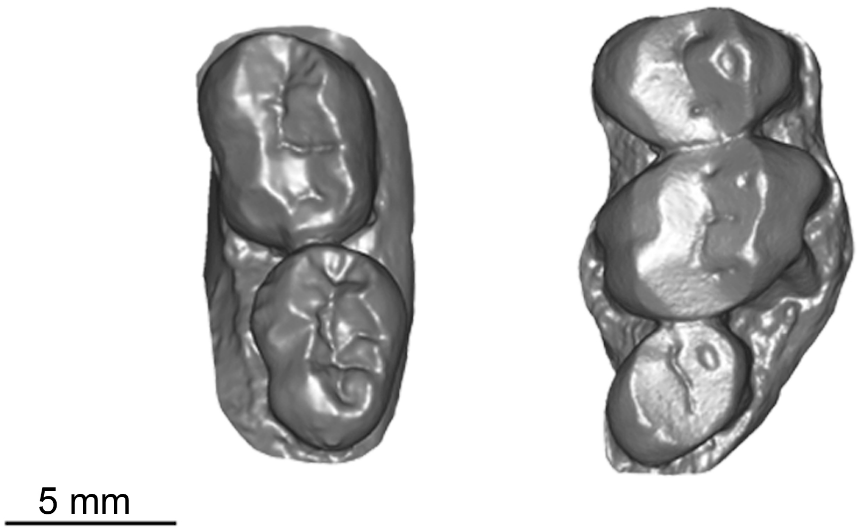

Figure 2.01. Laser scan-generated images of the maxillary and mandibular dentition of *Xenothrix mcgregori*. Left to right: right M_{1-2} (AMNHM 148198), left P^4-M^2 (AMNHM 268006). Mesial is to the top of page. Dentition illustrated here and throughout the chapter were scanned at 25 micron inter-point distances using an LDI RPS 120 laser scanner. The images were edited and rendered in Geomagic Studio 11.

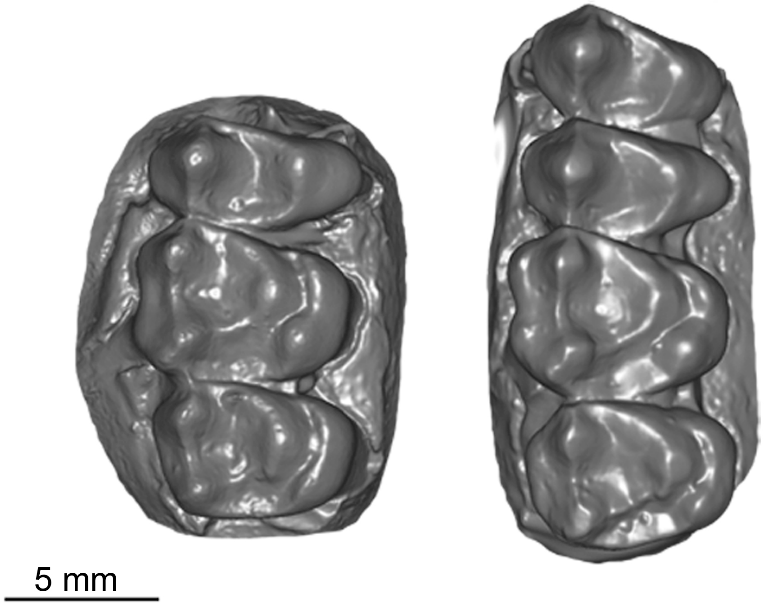

Figure 2.02. Laser scan-generated images of the maxillary dentition of *Antillothrix bernensis*. Left to right: right P^4-M^2 (CENDIA 1), right P^3-M^2 (MHD 01). Mesial is to top of page.

SYSTEMATIC PALEONTOLOGY

Order Primates Linnaeus, 1758

Suborder Anthropoidea Mivart, 1864

Parvorder Platyrrhini Geoffroy, 1812

Superfamily Ateloidea Gray, 1825

Family *incertae sedis*

Tribe Aotini Poche, 1904[2]

Insulacebus toussaintiana gen. et sp. nov.

HOLOTYPE

UF 114714 (Florida Museum of Natural History), a nearly complete dentition including a dP_4, examples of all adult tooth crowns except I_2, and an associated maxillary and mandibular fragment (Fig. 2.03, 2.04, Table 2.01), the latter preserving alveoli from left P_4 to the right canine.

ETYMOLOGY

Insula (L.), island, and *cebus* (Gr.), monkey; *toussaintiana* in honor of Toussainte Louverture (1743-1803), a Haitian hero and a founding father of the nation.

TYPE LOCALITY AND SITE DESCRIPTION

The material was recovered in June 1984 from Late Quaternary deposits in Trouing Jérémie #5 (18° 20'N, 74°03'W), a sinkhole site located on the Plain of Formon, Department du Sud, 17 km west of Camp Perrin in southwestern Haiti (Fig. 1.01). This excavation was one of a series

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[2] There are two contrasting views on the taxonomic placement of *Aotus* with the molecular studies indicating an affinity with the Cebinae (Baena *et al.*, 2007; Opazo *et al.*, 2006) and morphological evidence suggesting a relationship with Pitheciinae (Rosenberger and Tejedor, in press)

conducted from February through August in 1984 by the University of Florida, Gainesville under the direction of Charles Woods (Woods, 1989b). Trouing Jérémie #5 is also the type locality for the extinct rodent *Rhizoplagiodontia lemkei* and the extinct sloth *Neocnus toupiti* (Woods, 1989b; MacPhee *et al.*, 2000).

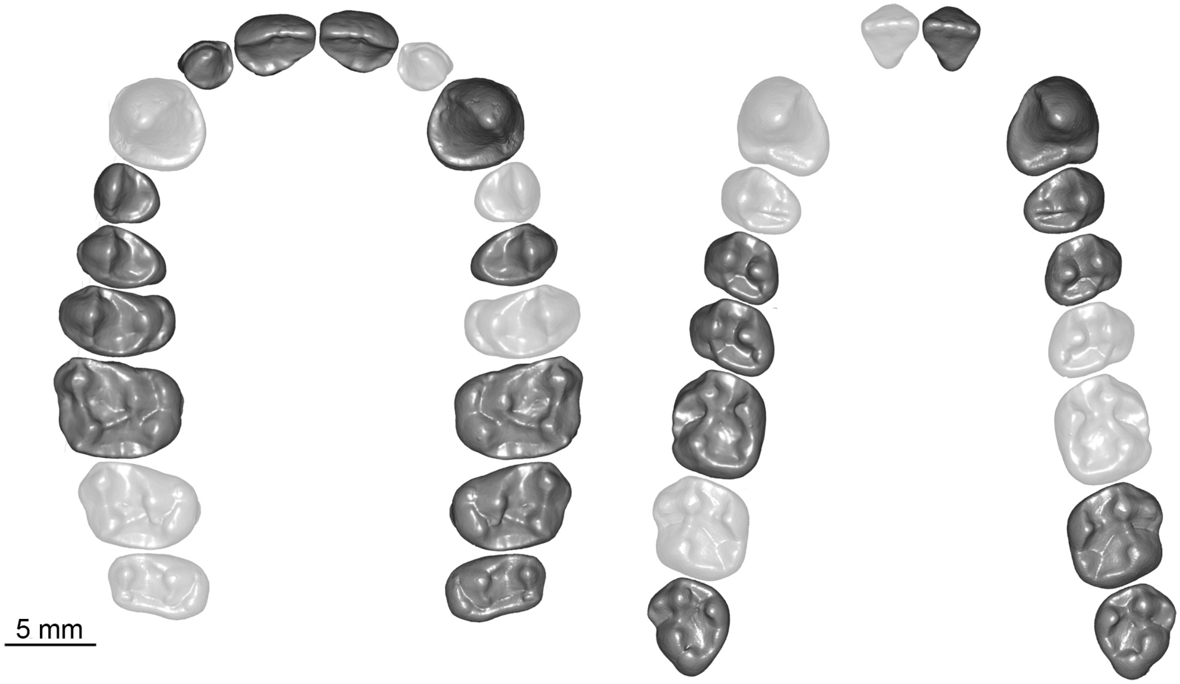


Figure 2.03. Laser scan-generated images of the *Insulacebus toussaintiana* dentition. Dark gray teeth are part of the original UF 114714 assemblage, while light gray teeth are mirror images used to reconstruct a complete dental arcade. The exact shape of the palate is unknown so *Xenothrix mcgregori* was used as a guide in creating this image.

DIAGNOSIS OF GENUS AND SPECIES

Insulacebus toussaintiana, a large platyrrhine comparable in body size to a large Tufted Capuchin, *Cebus apella,* 4.6-4.7 kg (Tables 2.02, 2.03), is distinguished from all other platyrrhine primates by the following combination of traits: large spatulate central upper incisors in tandem with smaller conical lateral upper incisors; maxillary and mandibular canines are low-crowned and stout; maxillary premolars are heteromorphic, increasing in crown size and complexity posteriorly, with $P^{2\text{-}3}$ small, single-rooted and lacking lingual cingula while P^4 is much larger, double-rooted, buccolingually wide and with a well-developed lingual cingulum; maxillary molars decrease in size posteriorly with M^2 generally resembling M^1 except for its smaller size, reduced talon, hypocone and lingual cingulum; $P_{3\text{-}4}$ possess a protoconid and metaconid of equal height, closely spaced together but lacking a clear protocristid; $M_{1\text{-}2}$ with restricted trigonid and talonid basins due to narrowly spaced protoconid-metaconid and hypoconid-entoconid, and a basally wide trigonid owing to prominent bulge of enamel below protoconid cusps; M_3 is smaller and irregularly shaped, with a marked trigonid buccal flare and two prominent talonid cusps.

DESCRIPTION

Insulacebus toussaintiana is described from the nearly complete dentition (Fig. 2.03, Table 2.01), maxillary fragment, and partial mandible of a subadult. At the time of preservation, only the incisors had fully formed roots, with root formation of the cheek teeth grading from nearly complete in the premolars and first molar to nearly absent in the third molar. The third molar shows no wear, so it is unlikely that it had come into complete occlusion. The canine was unerupted (Fig. 2.04). All enamel caps of the teeth were fully formed. Partially because of the young age of the individual, this specimen is one of the most complete, pristine dentitions of any fossil or subfossil platyrrhine and has little wear. Only the teeth of *Lagonimico conculatus* from the middle Miocene of La Venta, Colombia (Kay, 1994) may be comparable in completeness and quality of preservation.

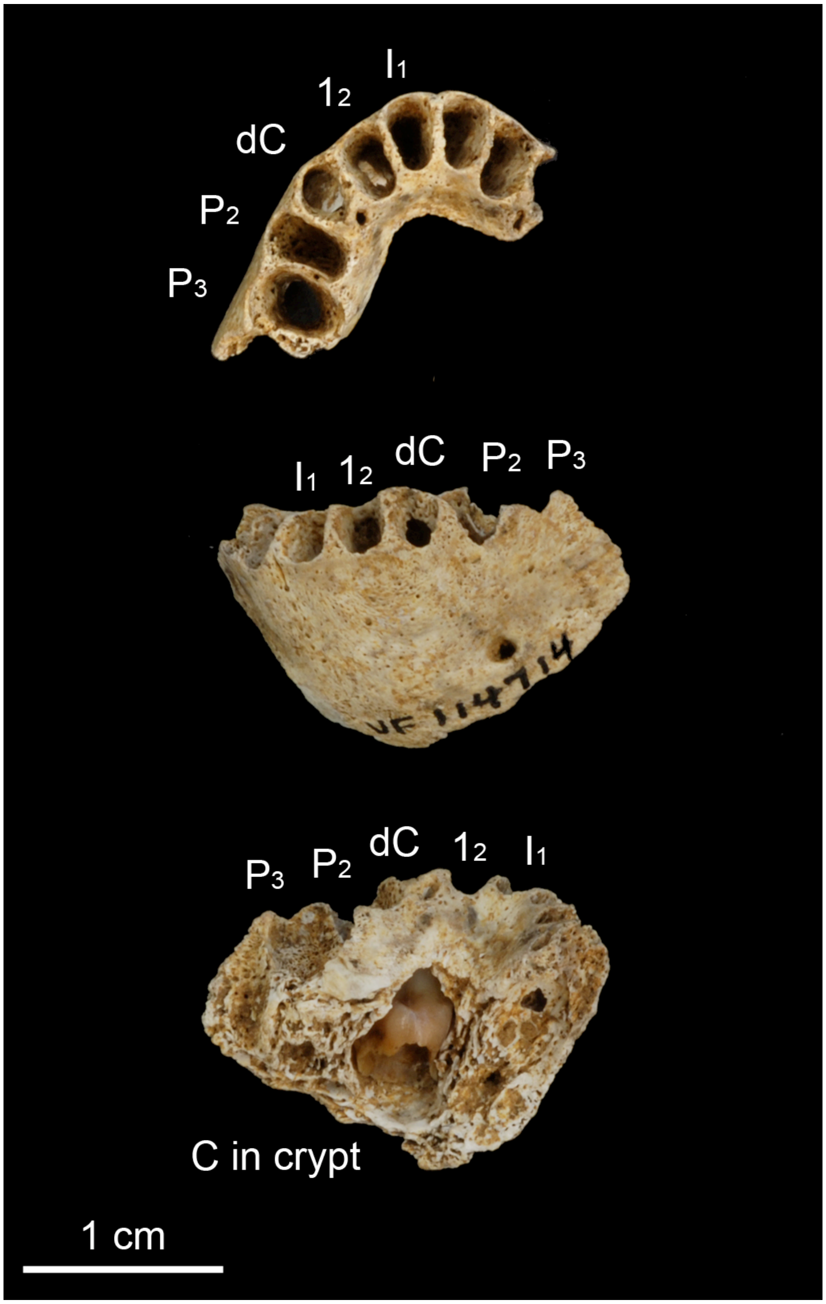


Figure 2.04. Mandible of *Insulacebus toussaintiana* with adult canine shown in the crypt. Top to bottom: superior, lateral, and medial views.

The upper central incisors are broad and spatulate with an inconspicuous lingual cingulum, while the lateral incisor, whose crown is slightly damaged, is conical in shape, almost peg-like, and small in comparison with I^1 (Fig. 2.05). Among extant platyrrhines, where incisor morphology is often clade specific (Rosenberger, 1992), comparable crown morphology, with markedly heterogeneous sizes and shapes, is found in *Aotus* and to a somewhat lesser degree in *Saimiri*. Among the extinct Caribbean forms, this combination has also been hypothesized for *Xenothrix* based on relative alveolus size (Rosenberger, 2002), although MacPhee and Horovitz (2004) found a great deal of variability in the relationship between alveolar size and incisor crown morphology and concluded that there was little evidence for *Aotus*-like incisors in *Xenothrix*. In the absence of *Xenothrix* specimens with intact incisors, their relative crown size remains unknown.

	Right		Left	
	Length (M-D)	Breadth (B-L)	Length (M-D)	Breadth (B-L)
I^1	4.28	3.32	4.43	3.29
I^2			2.69	2.66
C			5.31	5.5
P^2	3.08	3.57		
P^3	3.21	4.94	3.06	5.15
P^4	3.58	6.41		
M^1	5.13	6.63	5.15	6.81
M^2			4.52	6.58
M^3			3.35	5.26

	Right		Left	
	Length (M-D)	Breadth (B-L)	Length (M-D)	Breadth (B-L)
I_1	3.13	3.6		
I_2				
C			4.29	5.62
P_2	3.39	4.51		
P_3	3.39	4.39	3.26	4.28
P_4			3.65	4.89
M_1	5.5	(damaged)	5.5	5.06
M_2	5.02	5.24		
M_3	4.66	4.62	4.76	4.66

Table 2.01. Maximum mesiodistal lengths and buccolingual breadths of *Insulacebus toussaintiana* (UF 114714) in mm.

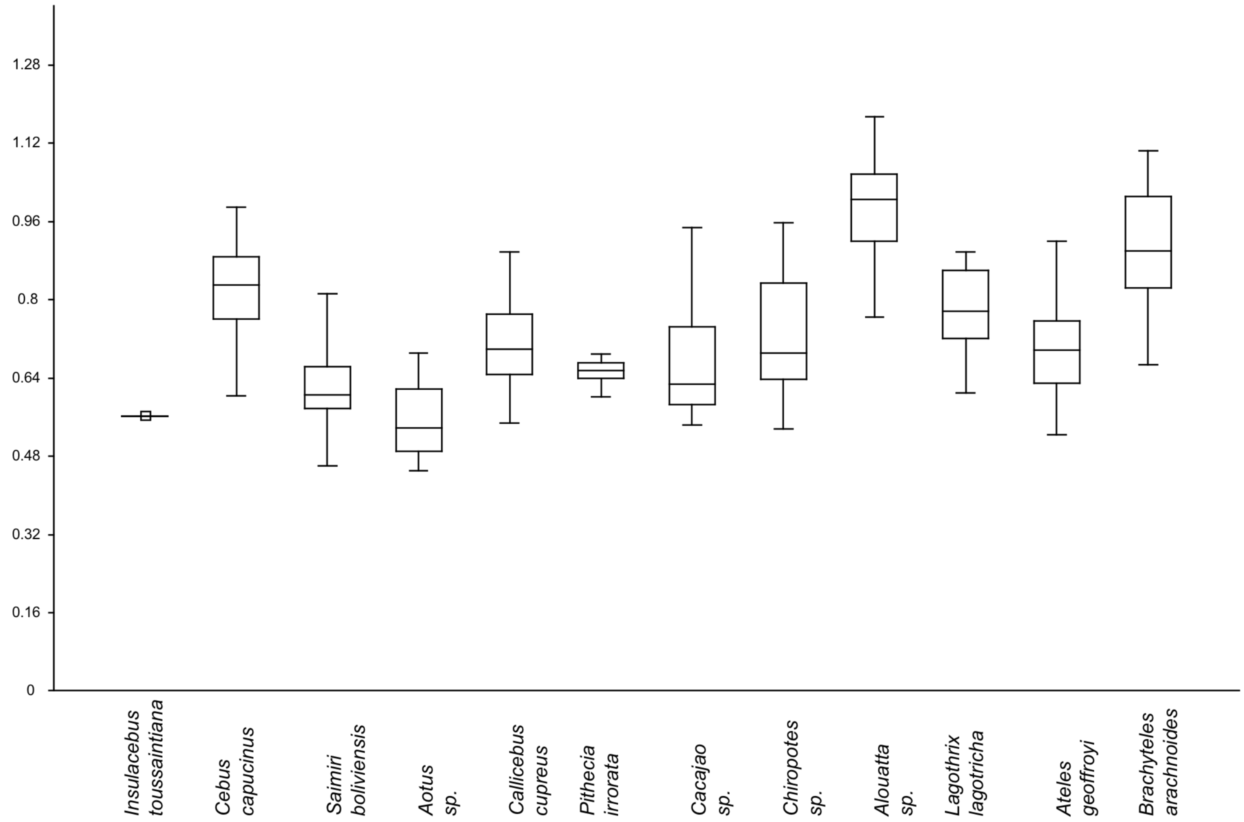


Figure 2.05. Ratio of I^2 to I^1 area in selected platyrrhine primates. Mesiodistal length was multiplied by buccolingual breadth to obtain a proxy for crown area. The ratio is the area of I^2 divided by the area of I^1. The mixed-sex extant sample includes *Cebus capucinus* (29), *Saimiri boliviensis* (31), *Aotus* sp. (17), *Callicebus cupreus* (28), *Pithecia irrorata* (7), *Cacajao* sp. (18), *Chiropotes* sp. (19), *Alouatta seniculus* (18), *Lagothrix lagotricha* (16), *Ateles geoffroyi* (25), *Brachyteles arachnoides* (18).

While *Insulacebus* is similar to *Aotus* and *Saimiri* in the ratio of I^1 to I^2 area, it differs markedly from living taxa in the relative area of the incisors as compared to molars. In all living taxa that have relatively broad spatulate incisors, there is a concomitant decrease in overall molar area, and the reverse also remains true, with the small-incisored *Brachyteles* and *Alouatta* showing a relatively large molar area. This has been documented previously and is generally explained in terms of dietary adaptation (Anapol and Lee, 1994). In *Insulacebus* a different pattern emerges: broad central incisors and small lateral incisors are maintained, but total incisor area accounts for 26% of the total molar area, in contrast to the much greater relative area of the incisors seen in *Aotus* (52%) and *Saimiri* (54%) (Fig. 2.06). In absence of non-dental data on body size, it is impossible to say whether this pattern reflects relatively large molars, small incisors, or a combination of both; however, it demonstrates a unique dental pattern unobserved in extant mainland platyrrhines.

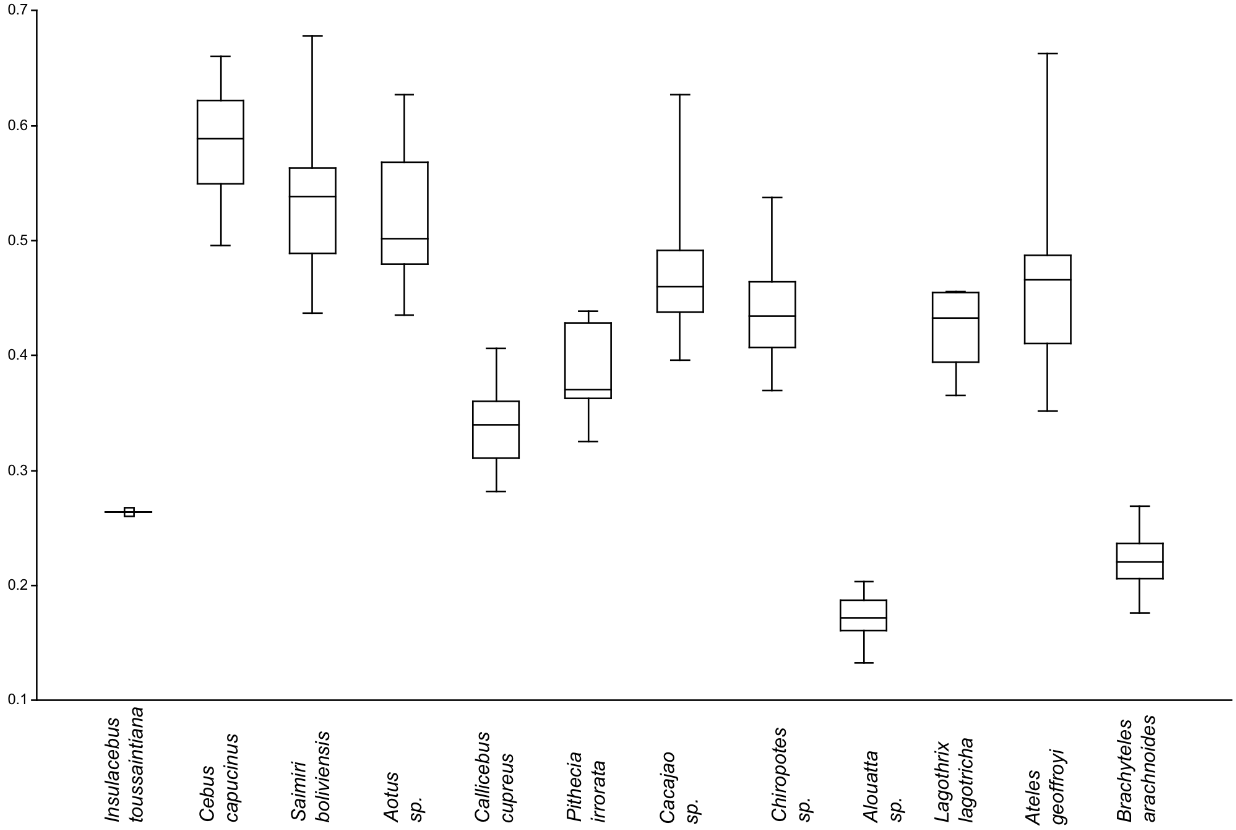


Figure 2.06. Ratio of the total incisor area to total molar area. Mesiodistal length was multiplied by buccolingual breadth to obtain a proxy for crown area. Total incisor area was calculated as the summed areas of I^1-I^2, and total molar area was calculated as the summed areas of M^1-M^3. The mixed-sex extant sample includes *Cebus capucinus* (15), *Saimiri boliviensis* (24), *Aotus* sp. (22), *Callicebus cupreus* (28), *Pithecia irrorata* (7), *Cacajao* sp. (18), *Chiropotes* sp. (19), *Alouatta seniculus* (16), *Lagothrix lagotricha* (11), *Ateles geoffroyi* (13), *Brachyteles arachnoides* (12).

The maxillary canine is a simple stout crown of low to moderate height, perhaps indicating by its robusticity that this individual was male, but monomorphically small, minimally projecting canines are also found in *Aotus, Callicebus*, and *Brachyteles* among the modern platyrrhines. In the Caribbean taxa, relatively small canines are present in *Paralouatta varonai* and thought to be present in *Xenothrix*. The mandibular canine of *Insulacebus* is distinctive, however, as a strongly developed, bluntly pointed tooth with several features variously resembling *Aotus* and select Miocene forms including *Soriacebus ameghinorum*, *Cebupithecia sarmientoi,* and *Nuciruptor rubricae* (Fig. 2.07, 2.08). It presents a somewhat triangular cross-section near the base largely due to mesiolingual and distal flattening of the tooth's surface. The basal cingulum curves around the distal aspect and forms a peak directly distal to the apex of the crown, a feature also observed in the relatively large lower canine of *Cebupithecia*. On the lingual surface, the crown is reinforced by a moderately well developed, rounded torus running from tip to cingulum. It offsets the distal surface and contributes to forming the triangular cross sectional shape. Also noteworthy is the location of the canine apex, which is found directly over the base when the canine is oriented such that the cingulum is parallel to the occlusal surface of the tooth row, a trait also shared with *Cebupithecia*. The most advanced condition of this canine morphology is found in the pitheciins where the lower canines are massive and everted. Functionally, the pitheciine canine is used to husk hard-shelled fruit, suggesting that the torus might serve to reinforce the tooth against bending stress and the position of the apex may minimize eccentric loading of the crown shaft via the tip. This contrasts with the condition observed in most other platyrrhine primates where the canine apex is positioned more laterally and distally, resulting in a more elliptical as opposed to triangular crown cross-section and a recurved rather than erect canine shaft. While the polarities of these features remain unclear, the position of the apex, the unusual peaked cingulum, and triangular form of the base are suggestive of a relationship with the pitheciine clade.

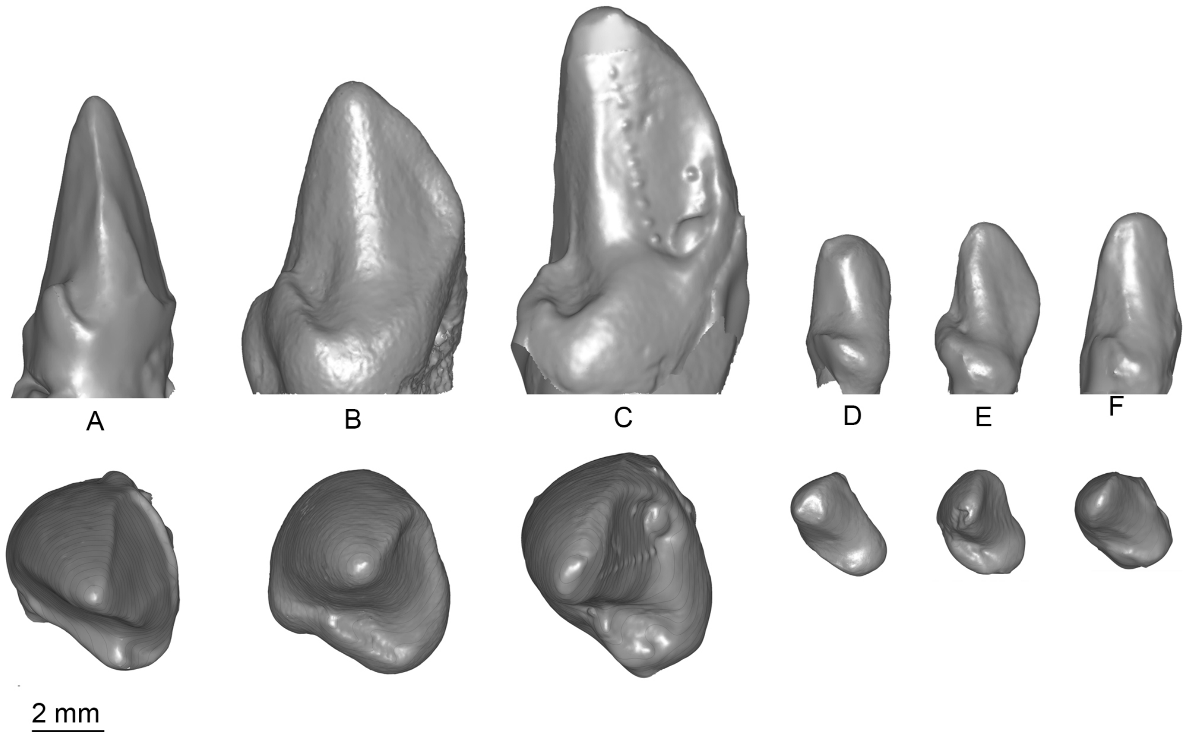


Figure 2.07. Mandibular canines of selected platyrrhine species in lingual (top) and apical (bottom) views. Left to right: A) *Cebupithecia sarmientoi*, B) *Insulacebus toussaintiana,* C) *Cebus capucinus*, D) *Saimiri boliviensis,* E) *Aotus vociferans,* F) *Callicebus cupreus.* The extant forms are female. The canines were laser scanned at 25 microns using an LDI RPS 120 laser scanner. The images were edited in Geomagic Studio 11 and contour lines (below; visible with higher magnification) were spaced at 0.25 mm. Note the centrally positioned canine apex of *Insulacebus* and the elevated distolingual cingulum that is prolonged bucally beyond the distal style.

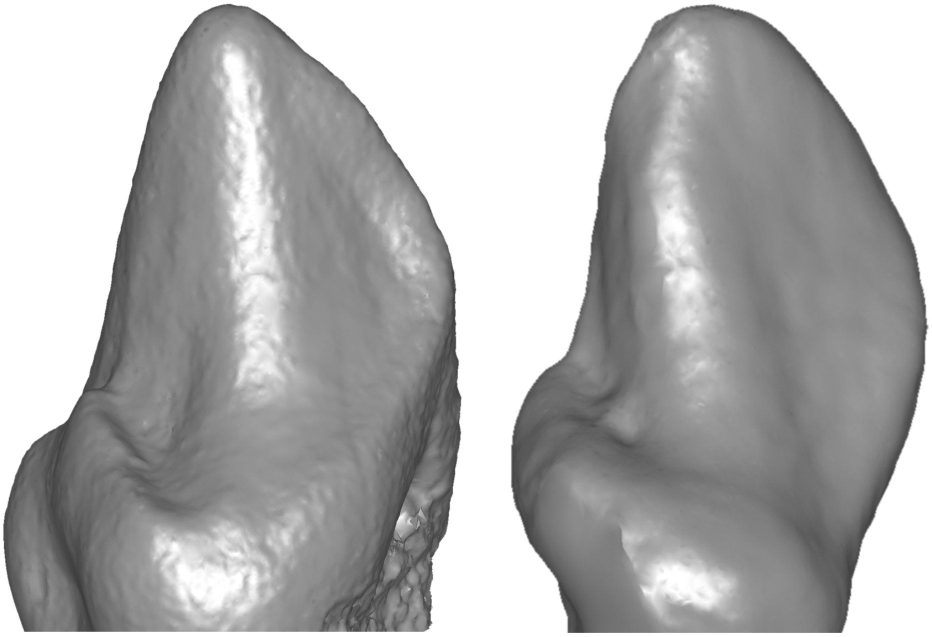


Figure 2.08. The mandibular canines of *Insulacebus toussaintiana* (left) and *Aotus vociferans* (right) scaled to the same size.

The maxillary premolars are distinctive in presenting a marked width increase from front to back, which corresponds with increasingly large occlusal basins and cusp development resulting in unique premolar proportions (Fig. 2.09). P^2 is a one-cusped and single-rooted tooth. There is a blunt paracone positioned mesially, giving the tooth crown a somewhat trapezoidal appearance when viewed from the buccal side. A small lingual cingulum is present that ends in a meisal style. P^3 is single rooted and has a prominent paracone and negligible protocone enclosing a small basin. P^3 is elongate buccolingually as a result of the gradual lingual slope of the protocone. The P^4 is double-rooted and wide in comparison to the mesial premolars. It has a prominent paracone, protocone, and distal fovea with a well-developed cingulum, with a protostyle and postprotostyle. Bucally, there is a small parastyle and a distostyle.

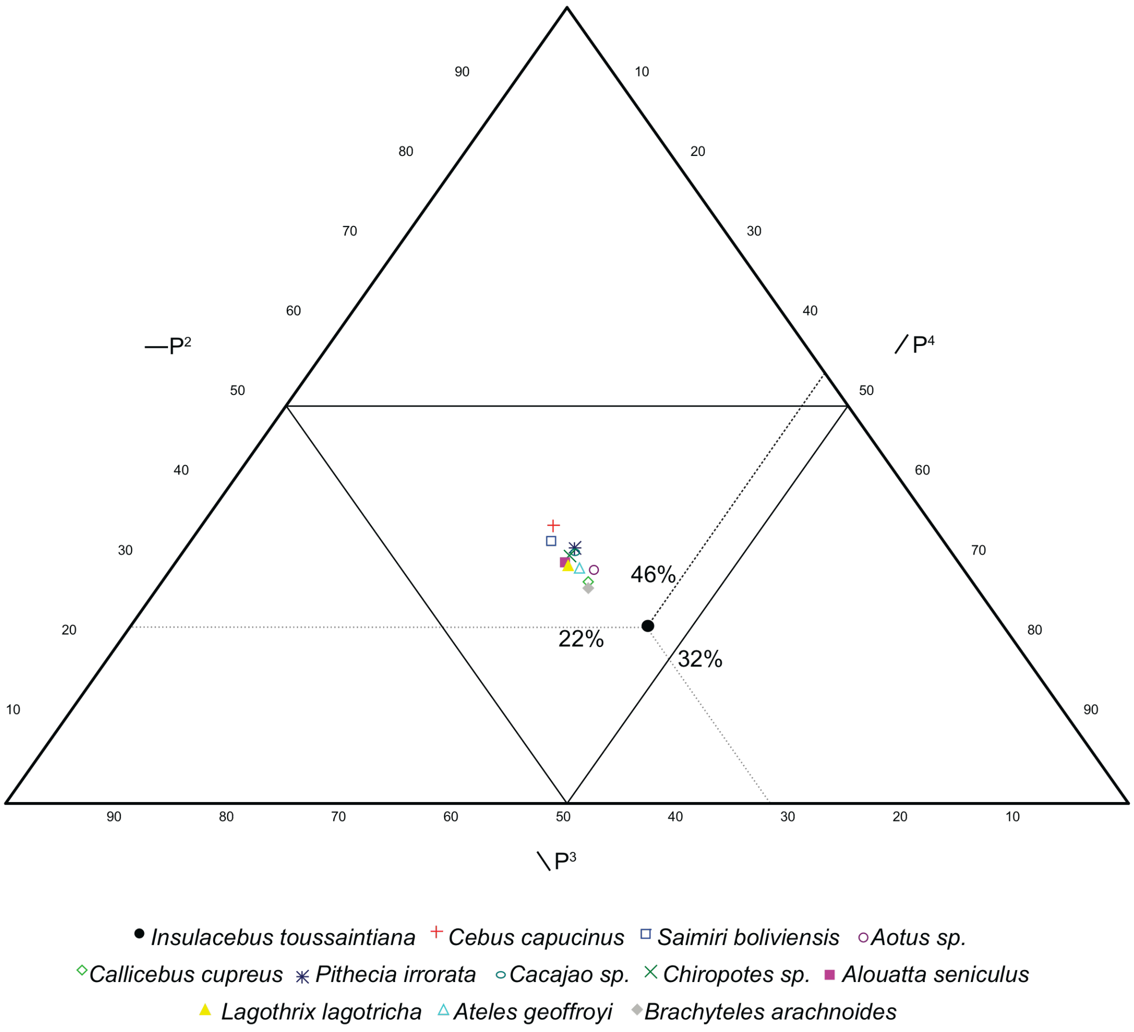


Figure 2.09. Proportional area of maxillary premolars as expressed as a percentage of total premolar area. The ternary plot shows the mean relative proportional area of each premolar in relation to the summed area of all three premolars. The mixed-sex extant sample includes *Cebus capucinus* (22), *Saimiri boliviensis* (32), *Aotus sp.* (30), *Callicebus cupreus* (30), *Pithecia irrorata* (10), *Cacajao* sp. (10), *Chiropotes* sp., (19), *Alouatta seniculus* (29), *Lagothrix lagotricha* (24), *Ateles geoffroyi* (24), *Brachyteles arachnoides* (19). In a principle components analysis of these data, *Insulacebus toussaintiana* falls outside of the 95% confidence intervals of all modern taxa sampled.

The P_2 is one-cusped and lingually expanded; a protocristid divides the crown into a meisal and distal fovea. A small distostylid is present. P_3 has a protoconid and metaconid equal in height and closely spaced. The cusps are separated by a deep groove, and there is no clear protocristid. The tooth is somewhat bulbous buccally. P_4 is morphologically similar to P_3, but larger in size with a more prominent distal fovea.

While the anterior premolars exhibit an *Aotus*-like pattern in simplicity and overall morphology, the P^4 is reminiscent of *Saimiri* in its width relative to M^1 and the well-developed cingulum. This morphology contrasts with *Antillothrix*, which has premolars of all approximately equal breadth that lack prominent cingula (Rosenberger *et al.*, 2011) (Fig. 2.02). Additionally, though the sample is limited, *Antillothrix* has a double rooted P^3 and a double or tripled rooted P^4, while *Insulacebus* has a single rooted P^3 and double rooted P^4. The mandibular premolars are also heteromorphic in size, shape and cusp and basin development. Compared with living platyrrhine primates, the morphology of the *Insulacebus* $P_{3\text{-}4}$ is unique in two ways; the cusps are close in approximation, and they lack the protocristid that normally links them. The former feature is mirrored in the mandibular molars.

The maxillary $M^{1\text{-}2}$ are buccolingually broad with trigon cusps connected by strong cristae. The metacone is somewhat lingually placed relative to the paracone and is separated from the hypocone by a large distal fovea. The protocone is located on the mesial third of the tooth. The hypocone arises out of the cingulum and is low in height relative to the trigon cusps. A large protostyle, only slightly smaller than the hypocone, is present on the mesial aspect of the cingulum in M^1, but is greatly reduced in M^2. A small distolingually directed crest, MacPhee *et al.*'s (1995) "distal crest," runs from the protocone toward the hypocone, but is separated from it by a small furrow. This feature is more obviously displayed in the right M^1 and left M^2 and may be variable across this species given its near absence on the left M^1. The "distal crest" is also present in *Antillothrix* and the Colombian Miocene alouattin, *Stirtonia victoriae.*

The maxillary molars of the fossil decrease in size toward the rear and grade morphologically in typical primate fashion, with the prominent M^1 hypocone, talon and cingulum becoming smaller on the morphologically similar M^2. In contrast to *Insulacebus,* the M^1 of *Antillothrix* has a smaller, less prominent lingual cingulum and a smaller hypocone, and the *Antillothrix* M^2 lacks a clear hypocone altogether, an unusual heteromorphy not seen among modern platyrrhines that retain a third molar. The upper M^1 of *Xenothrix* appears to lack the strong cristae present in *Antillothrix* and *Insulacebus.*

M^3 is essentially a bicuspid crown with a well-formed distolingual cingulum. There is a prominent paracone with a parastyle and protocone. The metacone is greatly reduced and there is a continuous distal shelf that runs from the metacone to the lingual cingulum, but there is no crista obliqua. The lingual cingulum is prominent, but there is no clear hypocone.

The lower molar pattern of *Insulacebus* is unusual in several ways and does not closely match other platyrrhines, except for particular features evident in *Xenothrix* and the other Caribbean platyrrhines and, to a lesser extent, *Soriacebus ameghinorum.* Like the posterior premolars, each molar's protoconid and metaconid are spaced closely together and are sharply divided by a sulcus (Fig. 2.10). The entoconid and hypoconid cusps are also closely approximated relative to the buccolingual breadth of the talonid. On M_2, the cristid obliqua runs nearly directly mesially from the hypoconid to the protoconid. Buccally, all three molars present a prominent bulge, a flaring of the enamel sidewall near the base of the protoconid, exaggerating the breadth of the trigonid moiety and effecting a deep crease at the ectoflexid notch.

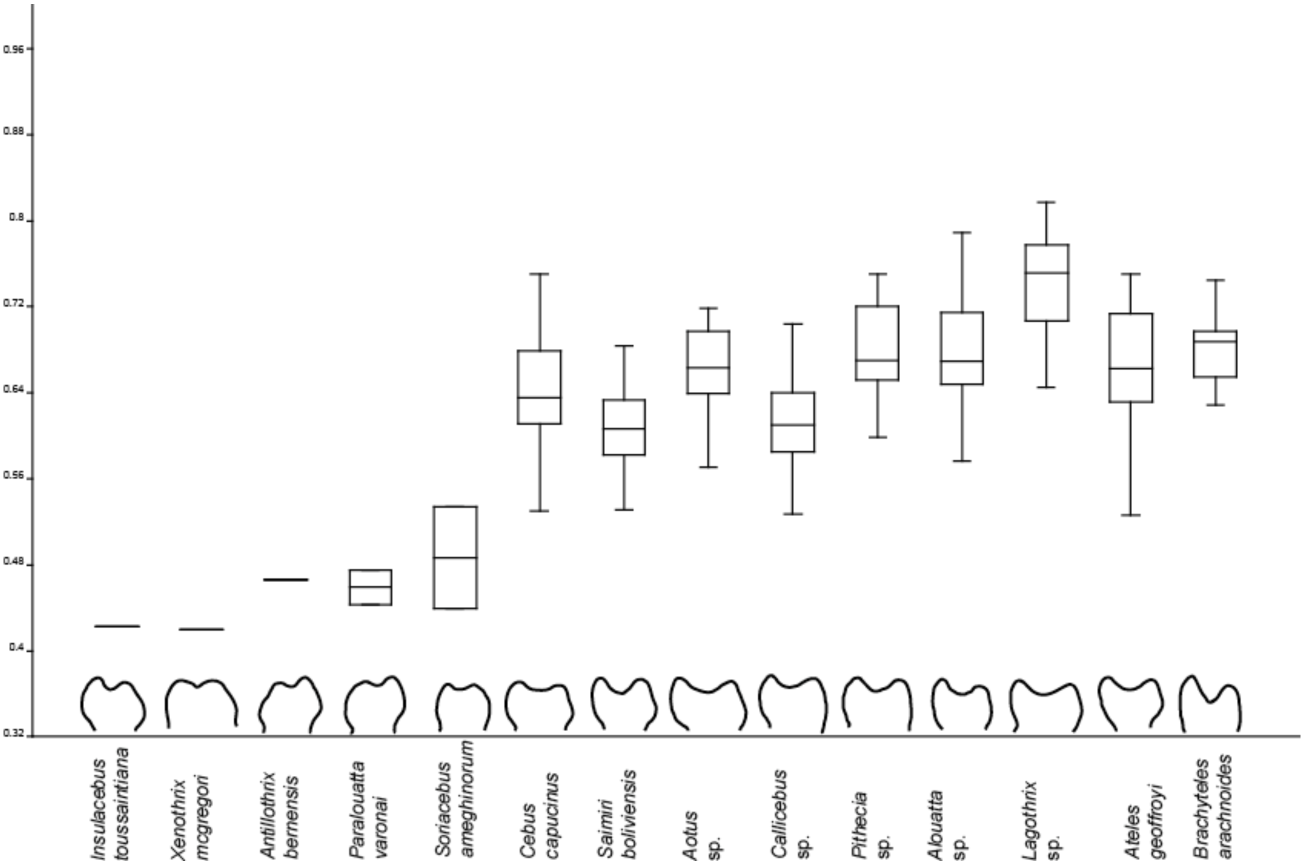


Figure 2.10. Cusp Approximation Ratio. The ratio is the linear distance between the protoconid and metaconid divided by the maximum buccolingual breadth of the trigonid. A cross section through the protoconid and metaconid of each right M_2 is shown below each box plot; these are schematic and not to the same scale. These data were collected and cross sections created from laser scan-generated models. The extinct sample includes *Insulacebus toussaintiana* (UF 114714), *Xenothrix mcgregori* (AMNHM 148198), *Antillothrix bernensis* (MHD 01), *Paralouatta varonai* (MNHNH-V123 and MNHNH Cueva Alta 1996) and *Soriacebus ameghinorum* (MACN SC-2, 33 and MACN SC-379). The mixed-sex extant sample includes *Cebus capucinus* (25), *Saimiri boliviensis* (30), *Aotus* sp. (29), *Callicebus* sp. (29), *Pithecia* sp. (19), *Alouatta seniculus* (28), *Lagothrix* sp. (23), *Ateles geoffroyi* (30), *Brachyteles arachnoides* (21).

The buccolingually constricted trigonid and talonid basins of M_{1-2} are noteworthy for the Cusp Approximation Ratio (CAR) value, distinctively low in *Insulacebus* and the other Greater Antillean primates. Of the extinct platyrrhines included in this study (Table 3.03), only *Soriacebus ameghinorum* falls within the range of the Caribbean forms, which fall outside the ranges of the three-molared living platyrrhines sampled from the major clades. The cross-sectional morphology of platyrrhine crowns suggests that the metric documenting this pattern reflects a complex effect, involving both a narrowing of intercuspal distances as well as augmentation of the mesial and distal crown breadths due to a flaring contour of the buccal sidewall. In surface area measures of the trigonid and talonid basins, the Caribbean platyrrhines stand out as well. They have relatively much smaller basins as compared to the total surface area of the tooth crown. This pattern is not present in *Soriacebus*, however (Fig. 2.11). A small basin with compressed cusps has been recognized as one of the distinctive features of *Xenothrix* (Rosenberger, 1977), and now is evidently present in the other Caribbean taxa.

The third molar of *Insulacebus* is unusual among three-molared platyrrhines in being relatively smaller than M_{1-2} yet morphologically well formed and complex. The trigonid has a strongly flaring protoconid sidewall and the talonid is well-developed, with a prominent hypoconid, and a large distal midline cusp in the hypoconulid position, not seen elsewhere among living platyrrhines. Of particular note is the resemblance to *Aotus dindensis* (IGM-KU 98001; Takai *et al.*, 2009), which also shares the unusual midline placement of the M_3 hypoconulid-like cusp.

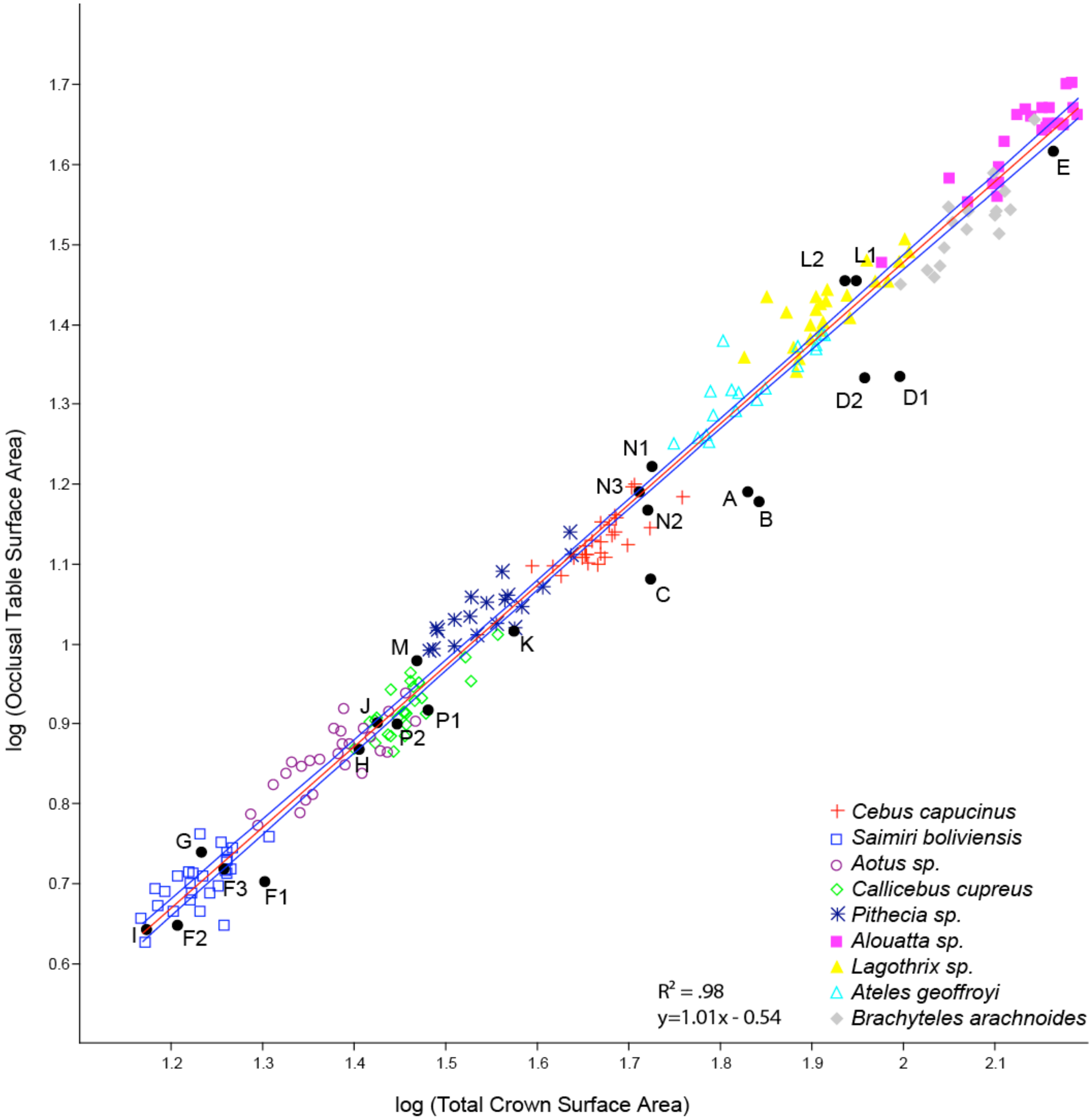


Figure 2.11. Plot of the linear regression of the occlusal table surface area (OTSA) against the total crown surface area (TSA). OTSA is the three-dimensional surface area of the occlusal basin of the tooth as bounded by the cusps and crests of the crown. TSA is the surface area of the enamel cap of a tooth from the cemento-enamel junction. See Appendix A for error studies on these measurements. The mixed-sex extant sample includes *Cebus capucinus* (25), *Saimiri boliviensis* (27), *Aotus* sp. (29), *Callicebus* sp. (27), *Pithecia* sp. (19), *Alouatta* sp. (22), *Lagothrix* sp. (23), *Ateles geoffroyi* (19), *Brachyteles arachnoides* (17). Extinct forms are shown as black dots and the key is below.

Figure 2.11 legend continued.

Species		Symbol
Antillothrix bernensis	MDH 01	A
Insulacebus toussaintiana	UF 11417	B
Xenothrix mcgregori	AMNHM 148198 (type)	C
Paralouatta varonai	MHNH Cueva Alta 1996	D1
P. varonai	MNNH V123	D2
Caipora bambuiorum	IGC-UFMG 05 (type)	E
Neosaimiri fieldsi	UCMP 39205 (type)	F1
N. fieldsi	IGM-KU 89002	F2
N. fieldsi	IGM-KU 89034	F3
Laventiana annectens	IGM-KU 8801a	G
Mohanimico hershkovitzi	IGM 181500	H
Patasola magdalenae	IGM 184332	I
Aotus dindensis	IGM-KU 8601 (type)	J
Cebupithecia sarmientoi	UCMP 38762	K
Stirtonia tatacoensis	IGM-KU 8102	L1
S. tatacoensis	IGM-KU 8215	L2
Dolichocebus gaimanesis	MPEF 5146	M
Carlocebus carmenensis	MACN-SC 43	N1
C. carmenensis	MACN-SC 250	N2
C. carmenensis	MACN-SC 63	N3
Soriacebus ameghinorum	MACN-SC 2 (type)	P1
S. ameghinorum	MACN-SC 379	P2

The preserved portion of the mandibular symphysis (Fig. 2.04) includes the alveoli of right and left adult incisors, the left deciduous canine alveolus, adult canine crypt, and P_{2-3}. The symphysis is smoothly parabolic with the lateral incisors positioned slightly behind the central incisors. It compares favorably with adult examples of *Xenothrix mcgregori* (MacPhee and Horovitz, 2004). The mandible of the Cuban *Paralouatta varonai* differs from these species both in its larger size and its relatively deeper symphysial region. Finally, a small right maxillary fragment containing the crypt of the adult canine, the alveolus of the deciduous canine, and two small foramina is also known, but provides little additional evidence.

BODY MASS

The insular location of the new monkey and other primates in the Caribbean naturally raises questions about the possibility of island effects. Table 2.02 provides estimates of body weight for the fossils derived from predictive equations based on lower molar area and compares them to mainland taxa and other pertinent fossils. An impressively large number of the Caribbean platyrrhines – *Insulacebus toussaintiana*, *Xenothrix mcgregori*, *Paralouatta varonai,* and a jaw from the Haitian site Trou Woch Sa Wo, of poor condition and uncertain assignment – are large when compared with mainland forms, either falling outside or at the very top of the body weight range of living counterparts such as *Aotus* or *Callicebus* (Table 2.03). *Antillothrix bernensis*, with limbs as large as a *Cebus* and a skull larger than a *Saimiri*, appears to have been larger than all living pitheciids and cebids except *Cebus* (Rosenberger *et al.*, 2011), however weight estimates for this form must be approached with caution given its relatively large molars as compared to cranial size. The Caribbean primates are larger than all fossil primates from La Venta except for the alouattins *Stirtonia tatacoensis* and *S. victoriae*.

The possibility of island gigantism occurring among the Greater Antillean primates has been proposed before (Ford, 1990). While Ford (1990) remained equivocal regarding the exact phylogenetic affinities of the Antillean postcrania at her disposal, and nothing is known concerning how large any were when first entering the Caribbean, the current evidence does suggest that selection for increasing or maintaining comparatively larger body size amongst these island bound primates has been a real pattern and a departure from the mainland norm. As a group with a modal weight of roughly 4kg-5kg, there is nothing in the modern faunal assemblage that compares with this niche-defining parameter. There is a gap in the modern platyrrhine size distribution between approximately 3.5kg, the size of *Cebus* and the pitheciins, and 5kg, the size of the smallest *Alouatta*.

Species	N	M_1 BL	M_1 MD	Area	Ln Area	Monkey "grade" (17)	Anthropoid "grade" (17)	All primates (17)	Female platyrrhines (18)	Body Weight Range
Caribbean Primates										
Insulacebus toussaintiana	1	5.1	5.5	27.8	3.3	5443	5443	4788	4805	4159-5443
Xenothrix mcgregori (1†)	1	5.1	6.1	31.1	3.4	6477	6483	5840	5720	4881-6483
Trou Woch Sa Wo mandible (1†)	1	4.9	5.5	27.0	3.3	5177	5175	4521	4569	3971-5177
Paralouatta varonai (1*†)	5	5.7	7.0	39.9	3.7	9551	9582	9104	8444	6981-9582
La Venta, Colombia Primates										
Neosaimiri fieldsi (2)	12	2.7	3.3	8.8	2.2	894	885	608	786	608-894
Laventiana annectens (IGM-KU 8801a)	1	2.4	3.1	7.4	2.0	689	680	451	605	451-689
Aotus dindensis (IGM-KU 8601) (3*)	1	3.5	3.0	10.6	2.4	1199	1189	850	1054	850-1199
Mohanamico hershkovitzi (IGM 181500) (4*)	1	2.7	3.3	8.9	2.2	919	909	627	807	627-919
Micodon kiotensis (IGM-KU 8401) (5†)										“Saguinus or Callithrix sized”
Patasola magdalenae (IGM 184332) (6*)	1	2.3	2.7	6.4	1.9	547	540	347	480	347-547
Lagonimico conclucatus (IGM 184531) (6*)	1	2.5	2.9	7.3	2.0	677	669	443	595	650-1206
Miocallicebus villaviejai (IGM-KU 97001) (7†)										“Cebus sized"
Cebupithecia sarmientoi (UMCP 38762)	1	3.7	3.7	13.8	2.6	1821	1810	1370	1603	1370-1821
Nuciruptor rubricae (IGM 251074) (8*)	1	3.9	3.9	15.5	2.7	2180	2168	1682	1919	1682-2180
Stirtonia tatacoensis	2	5.2	5.9	30.4	3.4	6243	6247	5600	5513	5513-6247
Stirtonia victoriae (†9)										10000

Table 2.02. Body size in extant and extinct Caribbean and Laventan platyrrhine primates. The body weights of extinct forms were calculated using published regression equations (Conroy, 1987, Kay *et al.* 1998) based on m1 area.

* Molar measurements taken from a published source and body weight calculated here. † Published body weight estimate. 1) MacPhee and Meldrum, 2006; 2) Takai, 1994; 3) Setoguchi and Rosenberger, 1987; 4) Luchterhand, Kay, and Madden, 1986; 5) Setoguchi and Rosenberger, 1985; 6) Kay and Meldrum, 1997; 7) Takai *et al.*, 2001; 8) Meldrum and Kay, 1997; 9) Fleagle, 1999

While a tendency toward island gigantism has been found to be variable across different mammalian taxa (see Meiri *et al.*, 2004) the tendency of primates to increase in size on island habitats has been established (Bromham and Cardillo, 2007; Welch, 2009), and with additional fossil evidence and better resolution of the phylogenetic affinities of the Caribbean platyrrhines, it may become clear that an increase in body size occurred in this group.

Extant Primates	**N**	**M_1 BL**	**M_1 MD**	**Area**	**N (Body Weight)**	**Body Weight of Wild Sample**
Cebus capucinus	30	4.6	4.5	20.7	11	2610-3970
Saimiri sciureus	7	2.8	2.7	10.3	11	540-830
Aotus nancymai	1	3.34	3.29	14.3	248	808-980
Callicebus personatus	15	3.3	3.7	16.1	11	970-1650
Pithecia irrorata	10	3.5	3.6	16.2	3	1980-2920
Cacajao calvus	12	4.0	4.3	21.5	3	2880-3450
Chiropotes satanas	14	3.7	3.6	16.9	39	2660-2880
Aloutta seniculus	28	5.9	7.3	50.4	62	6020-7620
Lagothrix lagotricha	16	5.0	5.5	33.0	13	5540-6670
Ateles geoffroyi	26	4.8	5.0	29.0	56	7420-8000
Brachyteles arachnoides	24	5.5	7.2	46.8	8	6900-10200
Callithrix argentata	2	1.9	2.1	6.1	18	330-360
Callimico goeldii	4	2.6	2.7	9.7	2	278-500
Leontopithecus chrysomelas	22	2.8	3.2	12.0	15	480-700
Saguinus geoffroyi	10	2.2	2.7	8.5	95	432-558

Table 2.03. Body weights and M_1 dental measurement of selected extant platyrrhines. Body weight data were compiled by Ford and Davis (1992) from wild-caught individuals in sex-pooled samples. BL, buccolingual; MD, mesiodistal

EVOLUTIONARY RELATIONSHIPS OF *INSULACEBUS* AND THE GREATER ANTILLEAN PRIMATES

Because of the underlying primitiveness of the dental morphology of the Caribbean primates (Rosenberger *et al.*, 2011), and the unique post-cranial adaptations unknown elsewhere in the platyrrhine radiation (MacPhee and Fleagle, 1991; MacPhee and Meldrum, 2006), phylogenetic reconstruction has been difficult for this group. Currently, two main hypotheses purport to explain their relationships. Proponents of a multi-lineage hypothesis argue several clades are present, each aligned with different mainland lineages (Rímoli, 1977; Rosenberger, 1977, 2002; Ford, 1986; Rivero and Arredondo, 1991; Rosenberger *et al.*, 2009, 2011; Cooke *et al.*, 2011). This could mean either colonization by a community derived from mainland South America or by episodic dispersal, possibly over an extended period of time. Alternately, a single-lineage model suggests the Caribbean platyrrhines form a monophyletic group most closely allied with modern *Callicebus*, stemming from a single ancestral population that differentiated after leaving the mainland (MacPhee *et al.*, 1995, Horovitz and MacPhee, 1999; Iturralde-Vinent and MacPhee, 1999; MacPhee and Horovitz, 2004).

The multiple-lineage model has grown out of the work of a number of researchers. In their initial description of the *Xenothrix* mandible, Williams and Koopman (1952) came to no strong phylogenetic conclusions, and it was Rosenberger (1977) who first allied this taxon with the either *Callicebus* or *Aotus*, later supporting a closer affinity to *Callicebus* (Rosenberger *et al.*, 1990). Upon the discovery of additional cranial specimens, he re-evaluated this idea and suggested that the Jamaican primate should be grouped with *Aotus*, which he considered a pitheciid as well (Rosenberger, 2002). The *Aotus*-*Xenothrix* connection was largely based on the large orbit size as inferred from the preserved orbital rim, large inferior orbital fissure, and the large I^1 alveolus as compared to the I^2 alveolus. This position was not supported by MacPhee and Horovitz (2004) who showed that *Aotus* and *Xenothrix* have distinct differences in the relative size and position of the zygomatic and maxillary components of the inferior orbital fissure that correlate with differences in orbit size. They were also unable to consistently correlate incisor alveolus size with crown size. While *Xenothrix* shows some very derived morphology such as a reduced number of molars, there are several features that appear to unite it with the pitheciids including low molar relief, a deep madibular corpus, and placement of the entoconid away from other molar cusps (Rosenberger, 1977).

The Hispaniolan *Antillothrix*, initially considered a member of the genus *Saimiri* (Rímoli, 1977), was later grouped with the Cebidae more generally (MacPhee and Woods, 1982; Ford, 1990;

Rosenberger *et al.*, 2011). Until recently, all that was known of this taxon was the type specimen consisting of a maxillary fragment containing P^4-M^2 and the aveolae for P^{2-3}, a distal tibia, and a mandibular fragment containing a very worn M_1, though the taxonomic identity of the last specimen remains unclear, and the tibial fragment was attributed to the taxon by default. Most of the phylogenetic work concentrated on the dentition of the maxillary fragment whose molars are similar in appearance not only to *Saimiri*, but also to several of the Miocene Patagonian primates with a clearly delineated trigon and prominent cingulum. These features are likely primitive for the platyrrhines as a clade (Kinzey, 1973; Rosenberger, 1977; Kay 1980; Rosenberger, 1992), making clear statements about inter-relationships based solely on upper molar morphology difficult at best. Most recently, new cranial and post-cranial material of this species has caused a re-assessment of its phylogenetic affinities – perhaps indicating that it is not, in fact, a cebid as previously held.

Paralouatta varonai bore a striking resemblance to modern *Alouatta* when the lone cranium was first discovered, which caused Rivero and Arredondo (1991) to suggest a phylogenetic connection between the two forms, a position supported by Rosenberger and colleagues (2002; Rosenberger *et al.*, 2009). But with the discovery of additional dental material in an unworn state, it became clear that the phylogenetic picture for *Paralouatta* might be more complex. This taxon lacked the heavily crested molars of modern *Alouatta* or even *Stirtonia* and instead showed molar morphology far more primitive without any clear adaptations to leafy diet of the more modern alouattins (Horovitz and MacPhee, 1999; also see Chapters 3 and 4). Among those supporting a multi-lineage model of Antillean platyrrhine evolution, this is evidence for an earlier stage in alouattin evolution prior to development of a commitment to a partially leafy diet (Rosenberger *et al.*, in press). In the large sub-fossil alouattin *Protopithecus brasiliensis* there is further evidence for this earlier branch of the alouattin group (Cook *et al.*, 2007; Rosenberger *et al.* in press).

While proponents of the multi-lineage model interpret these morphologies as indicative of disparate lineages, the parsimony algorithm–based studies of MacPhee and colleagues (MacPhee *et al.*, 1995, Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004) have supported a monophyletic Caribbean radiation with *Antillothrix* and *Paralouatta* as sister taxa and *Xenothrix* as basal to the group. There are several characters that the Antillean platyrrhines share to the exclusion of other groups. These include a nasal fossa that was wider than the palate at the level of M_1, a mandibular canine alveolus that was buccolingually smaller than the alveolus of P_4, and a mandibular M_1 protoconid with a bulging buccal surface (Horovitz and MacPhee, 1999). Additionally, five unambiguous characters support *Callicebus* as the sister to the Caribbean forms. Since the publication of these analyses, additional *Antillothrix* material as well as this description of *Insulacebus* may alter parts of this proposed phylogeny.

In the present analysis, the possibility of Caribbean monophyly cannot be excluded, though I currently remain dubious about the position of *Paralouatta varonai* within this framework. *Insulacebus* may share a phylogenetic relationship with *Xenothrix*, providing support for MacPhee and colleague's inter-Antillean platyrrhine clade. Both *Insulacebus* and *Xenothrix* share an unusual occlusal pattern on the low-relief $M_{1\text{-}2}$ in which trigonid and talonid cusp are closely approximated and both have remarkably small basins. Both also have unusual, extensively flared buccal crown sidewalls, especially exaggerated in the trigonid moiety. These patterns are also shared with the other Caribbean forms, but no modern platyrrhine exhibits this morphology. Only the Early Miocene fossil *Soriacebus ameghinorum* from Patagonia (Fleagle *et al.*, 1987; Fleagle 1990; Rosenberger *et al.*, 1990; Fleagle and Tejedor, 2002) resembles the Caribbean forms in having such closely approximated cusps, but it also exhibits different, unusually narrow crown morphology. Another phenetic resemblance of *Insulacebus* and *Xenothrix* that bears mentioning for completeness, though still of uncertain cladistic significance, is the tendency toward polycuspate final lower molar crowns, M_3 or M_2 as the case may be. A third molar is unknown for *Antillothrix*, but *Paralouatta* does not seem to show this morphology. Finally, *Xenothrix* and *Insulacebus* share a smoothly parabolic mandibular symphysis.

The relationship between *Antillothrix* and *Insulacebus* is currently under study in light of the discovery of new material from the eastern Dominican Republic (Rosenberger *et al.*, 2011; Kay *et al.*, 2011). There are clear differences between the two taxa in terms of maxillary dental morphology including differences in premolar size and shape, differences in M^2 cusp patterns, and overall lesser degree of bunodonty in *Antillothrix* than in *Insulacebus*. Some similarities remain, however, and only additional analyses will indicate if this is a result of primitive retention or recent shared ancestry.

Insulacebus and *Xenothrix* may share a relationship with the modern genus *Aotus* although this phylogenetic connection is far from secure. The unusual incisor proportions and morphology exhibited by *Insulacebus*, their simplified anterior premolars, and the multi-cusped M_3 of *Insulacebus* are suggestive of an *Insulacebus*-*Aotus* connection. Characters that unite *Xenothrix* with *Aotus* include the possibility of an enlarged orbital region, small canines, and a deep mandibular corpus with an anteroposteriorly short ramus. However, to date, the fossil evidence is insufficient to exclude MacPhee and colleague's *Callicebus*-Caribbean connection, and there is some evidence to suggest that at least the Jamaican and Hispaniolan species should be allied with *Callicebus* and the other pitheciids (see Horovitz and MacPhee, 1999). Additionally, that all of the Caribbean forms do show similarities in molar morphologies is suggestive of a close relationship, though it is difficult to say if these characters are primitive retentions or synapomorphies.

ORIGINS, DIFFERENTIATION, AND BIOGEOGRAPHY

While the exact date of primate entry into South American is unknown, the first fossil evidence, from Salla, Bolivia, is dated to the late Oligocene (Takai, 2000; Fleagle and Tejedor, 2002), and by the early middle Miocene, at least ten species of New World monkeys were present in

Patagonia. In general, the Patagonian primates, for whom dental remains exist, were primitive, with molar teeth resembling morphotype reconstructions for Platyrrhini (Rosenberger, 1977; Kay, 1980; Rosenberger, 1992). Regardless of their hypothesized phylogenetic affinities, some of these primates had maxillary molars with a distinct trigon and well-delineated cingulum bearing a hypocone. The mandibular molars had a slightly elevated trigonid and a marked ectoflexid. In other aspects, more derived patterns exist among the Patagonian forms. For example, aotin-like cranial morphology is present in *Tremacebus harringtoni* (Rosenberger, 1979; Szalay and Delson, 1979). While the phylogenetic affinities of this fossil have been debated (Kay *et al.*, 2010; Rosenberger, 2010; Hodgson *et al.*, 2009), the species, known only by a skull, does appear to show at least some orbit enlargement (Fleagle and Rosenberger, 1983; Kay *et al.*, 2004), a derived hallmark of the nocturnal and crepuscular habits of the Owl Monkey lineage. Cebines may be represented by *Killikaike blakei* (Tejedor *et al.*, 2006) and the *Saimiri*-like *Dolichocebus gaimanensis*, which possess derived cranial characteristics of the subfamily including a narrow interorbital region and a domed frontal (see Kay *et al.*, 2007 for an alternate view). The thin procumbent lower incisors of *Soriacebus ameghinorum* in combination with a somewhat laterally projecting canine are suggestive of pitheciine affinities (Fleagle *et al.*, 1987; Fleagle, 1990). By 15.71 ± 0.07 Ma, the first definitive pitheciine, *Proteropithecia neuquenensis,* was present (Kay *et al.*, 1998). These fossils demonstrate that crown platyrrhine lineages, albeit still primitive in form, may have already differentiated by the early Middle Miocene.

While it is tempting to compare the Caribbean primates with the less temporally remote Laventan primates from the late Middle Miocene of Colombia, it is clear from the presence of the alouattins *Stirtonia tatcoensis* and *S. victoriae*, the *Saimiri*-like *Neosamiri fieldsi*, the pitheciine *Cebupithecia sarmientoi,* and the earliest known member of an extant genus, *Aotus dindensis*, that elements approaching the modern radiation had appeared in South America by this juncture. This implies the dentally somewhat more primitive *Insulacebus toussaintiana* was likely derived from a fauna that was evolving on the mainland well before the La Venta horizon, and that it stemmed from a pre-Middle Miocene colonization from the mainland (Rosenberger, 1979; MacPhee *et al.*, 1995; Horovitz and MacPhee, 1999).

There is undoubtedly a complex geographic history behind the arrival or arrivals of primates in the Caribbean and their differentiation within the Greater Antilles, perhaps involving both island to island and continent to island vicariance and dispersal. Faunal continuity at the generic level between Cuba, Hispaniola, and Puerto Rico is well established and has often been interpreted as the result of intra-Antillean vicariance rather than multiple overwater dispersal events (MacPhee *et al.*, 2000; Roca *et al.*, 2004). Throughout much of their history these islands experienced progressive disruption and fragmentation (MacPhee and Iturralde-Vinent, 1995; Iturralde-Vinent and MacPhee, 1999). Jamaica, however, remained largely distinct and partially submerged during much of this period and lacks such characteristic Greater Antillean mammal groups as the megalonychid sloths, insectivores, and echmiyid rodents. There was, however, a possible land connection between the Jamaican Blue Mountains Block and the southern peninsula of Hispaniola (Iturralde-Vinent and MacPhee, 1999), which may have served as a route of faunal exchange between these two landmasses. The possible phylogenetic connection between *Insulacebus* and *Xenothrix* was anticipated by Ford (1990b), who suggested that an as of yet undescribed primate femur from western Haiti (UF 114717) was nearly indistinguishable from the likely primate femur from Coco Ree Cave in Jamaica (UF 40097) (see Chapter 1 for additional discussion).

Within Hispaniola, *Insulacebus toussaintiana* has only been found on the Tiburon Peninsula, while convincing specimens of *Antillothrix bernensis* are confined to the eastern portion of the island. If this east-west dichotomy holds true, it is consistent with the geotectonic history of the island and with current knowledge of Hispaniolan mammalian biogeography. All three of these regions are biogeographically distinct and are characterized by substantial levels of endemism in birds, reptiles, amphibians, invertebrates, and plants (Mertens, 1939; Williams, 1961; Schwartz, 1980; Dod, 1984; Ricketts *et al.*, 2005; Townsend *et al.*, 2007). Among the mammals, Woods (1989b) described a genus and species of extinct capromyid rodent, *Rhizoplagiodontia lemkei*, which was apparently restricted to the Massif de la Hotte, and Ottenwalder (2001) classified Hispaniolan solenodons (*Solenodon paradoxus*) from the north and south palaeo-islands as distinct subspecies.

The unique geological and biogeographical conditions within Hispaniola likely have contributed to its being an important location of mammalian diversity within the Caribbean. While the much larger Cuba outnumbers Hispaniola in terms of the quantity of species present, Hispaniola has much more phylogenetic diversity: of the eight subfamilies of rodents present in the Greater Antilles, three are endemic only to Hispaniola, and five are present there. In contrast, Cuba and Puerto Rico each have two non-endemic subfamilies. The phylogenetic relationships of the Jamaican rodents remain obscure, but there may be one endemic subfamily. Hispaniola also once had nearly equal diversity with Cuba in insectivore and sloth species. The discovery of *Insulacebus toussaintiana* now brings Hispaniola's endemic land mammal fauna to 25 species, of which only two still survive today, the insectivore *Solenodon paradoxus* and the rodent *Plagiodontia aedium* (MacPhee and Flemming, 1999; Turvey, 2009). While further study is needed to clarify these patterns of evolution and diversity, the description of a new primate species and its potential affinity with the Jamaican *Xenothrix mcgregori* provides a new line of evidence in understanding the evolution of the primitive Caribbean primates and the mammalian fauna more generally.

CHAPTER 3

PALEODIET OF EXTINCT PLATYRRHINES WITH EMPHASIS ON THE CARIBBEAN FORMS: THREE-DIMENSIONAL GEOMETRIC MORPHOMETRICS OF MANDIBULAR SECOND MOLARS

INTRODUCTION

The extant platyrrhines show a great deal of dietary diversity with most species exploiting a variety of food sources seasonally to meet their nutritional needs (Table 3.01). This makes the strict classification of diet and the concomitant identification of clear morphological correlates problematic. This is particularly vexing when attempting to classify the dietary profiles of extinct species, but a number of techniques for dietary profiling have been developed and applied to the reconstruction of paleodiets. At their core, all dietary profiling methodologies attempt to identify the morphological elements essential for processing different types of foods, as different food types require different "tools" to break them down. In recent years, a large body of research on the dental morphology of the living platyrrhines in combination with work on the material properties of leaves, fruits, seeds, and insects has greatly advanced our understanding of the functional capacities of primate dentition. Through analogy with these living forms, paleodietary patterns can be inferred for extinct primates.

Beginning in the 1970s, several workers identified and quantified aspects of molar tooth morphology thought to be adaptations to different diets. Initially, there were several lines of thought on how diet might influence morphology. Kay (1975) suggested that a food type would only exert selective pressure on molar shape if that food were consumed habitually, though he noted that some less frequently consumed, yet important foods might have a "special selective influence." Rosenberger and Kinzey (1976) introduced the idea of "critical function" whereby the major selective pressures on molar morphology would largely be determined by the mechanical properties of foods that were both essential for adequate nutrition and required specialized adaptations to process. For example, *Alouatta* consumes significant quantities of easily processed soft ripe fruit in addition to leaves. While soft ripe fruit can be broken down without difficulty, leaves must be finely sheared to gain maximal nutritional value. The primary molar adaptation or "critical function" is to the leaves – not to the easily processed fruit.

The idea of critical function was echoed in subsequent studies. Anapol and Lee (1994) found a significant correlation between the type of protein consumed and the morphology of the dentition, such that two primates that consumed approximately equal quantities of fruit, but relied on very different protein sources, had very different dental morphology. Additionally, fallback foods (foods that are readily available when preferred foods are scarce; see Marshall and Wrangham, 2007) also play a significant role in the evolution of dental morphology (Rosenberger and Kinzey, 1976; Kinzey, 1978; Altman, 1998; Marshall and Wrangham, 2007; Lucas *et al.*, 2009). For many primate species, fallback foods require morphological specializations to process, *i.e.*, they may be tough or hard. Fallback foods may make up a relatively small percentage of the annual diet, but during periods of preferred food scarcity, fallback foods are relied upon for a major portion of the diet making them important for survival (Marshall and Wrangham, 2007).

A variety of methodologies have been developed to identify the morphological correlates to these dietary patterns. Perhaps the most influential has been Kay's shearing quotient (SQ) (Kay, 1978, 1984), a measure of the relative length of a tooth's shearing crests. SQ is calculated by first regressing the total length of shearing crests on a molar against a proxy for body size – usually molar length – in a sample of frugivores. The SQ is then calculated from the residuals between the expected length of shearing crests on a tooth if a primate were a frugivore and the actual shear length. Kay found primates that are heavily reliant on leaves or insects have relatively longer shearing crests than do more frugivorous species; frugivores can be further broken down by SQ into ripe fruit specialists and those specializing in hard objects. Hard object specialists are distinguishable from ripe fruit specialists by their extremely low degree of molar shear. However, SQ alone was not successful in distinguishing between the molars of folivorous and insectivorous primates in the absence of information on body size. In addition to work on living forms, SQ has been employed in the reconstruction of paleodiet in many different taxa including platyrrhines (*e.g.,* Meldrum and Kay, 1997), early anthropoids (*e.g.,* Kay and Simons, 1980), cercopithecoids (*e.g.,* Benefit, 2000), and Miocene apes (*e.g.,* Ungar and Kay, 1995).

Attempts to quantify morphological adaptation to diet have now extended beyond SQ to include a number of three-dimensional measures relevant to molar crown function including characterizations of dental topography (*e.g.*, Reed, 1997; Zuccotti *et al.*, 1998; Dennis *et al.*, 2004), measures of relief (*e.g.*, M'Kirera and Ungar, 2003; Boyer, 2008), and analyses of geometric complexity using orientation patch count (OPC) (Evans *et al.*, 2007). These methodologies have been argued to have some advantages over SQ, but may not necessarily provide additional data and do not seem to be independent of phylogenetic effects as initially claimed. They are discussed in detail in chapter 4.

This chapter further contributes to this line of inquiry through the use of three-dimensional geometric morphometric techniques (3DGM) in the analysis of platyrrhine molars. While 3DGM has been extensively and successfully used in the analysis of cranial, and to a lesser extent, postcranial morphology (*e.g.*, Frost *et al.*, 2003; Wiley *et al.*, 2005; Harvati *et al.*, 2004; Nicholson and Harvati, 2006; Baab, 2008; Tallman, 2010), few studies have utilized landmark-based 3DGM as a tool for exploring primate molar shape and functional anatomy. This is partially because until recently few data collection techniques were available to handle dentition. Most 3DGM data are collected using a microscribe digitizer or similar measurement tool. These types of tools cannot accurately measure very small dentitions, and researchers interested in applying 3DGM techniques to the study of dental morphology mainly employed a stereophotogrametric system to collect *x,y,z* coordinate landmarks on dentition (*e.g.,* Savara, 1965; Teaford, 1982; Hartman, 1989). The combination of the use of laser scan or CT scan generated models of teeth with data collection programs such as Landmark Editor (Wiley *et al.*, 2005) have, for the first time, made collecting detailed 3DGM data possible on small specimens with relative ease. However, because of the newness of the techniques only a few authors have begun to publish these types of dental analyses.

In a series of papers, Skinner *et al.* (2008, 2009a, 2009b) collected three-dimensional data on CT scans to examine shape differences in the enamel-dentin junction (EDJ) among different species and subspecies of *Pan* and between *Australopithecus africanus* and *Paranthropus robustus*. The authors were able to distinguish different species and different tooth positions. Their work has particular use in paleontological contexts where dental wear may completely obliterate crown surface morphology.

Additional research on tooth crowns using three-dimensional point data was conduced by Singleton *et al.* (2011). The authors quantified the metameric shape variation in the mandibular molars of *Pan* and found that different *Pan* species share patterns of allometry and metameric variation. They were also able to detect differences between M_1 and M_2 morphology that allowed them to sort molars by tooth position, which would certainly be valuable in a paleontological context.

To date, no research has examined functional correlates of platyrrhine molar shape in the context of a landmark based three-dimensional analysis. Here, *x,y,z* coordinate landmarks are used to quantify shape in extinct and extant platyrrhine molars. Three main research questions are addressed:

1. Can coordinate-based landmark data be used to accurately classify living forms by diet?
2. What does shape variation in platyrrhine mandibular M_2s tell us about diet?
3. What are the hypothetical diets of the fossil platyrrhines included in this study?

	Species	Dietary Classification	Fruit	Flowers	Leaves	Seeds	Insects/ Arthropods	Other	Reference
Cebidae	*Cebus capucinus*	Frugivore/ Omnivore	65		15		20		Freese and Oppenheimer, 1981
			81.2	0.2	1.3		16.9		Chapman, 1988
	C. apella		24[1]				76[2]		Terborgh, 1983
			53.9	11.1	6.3	16		15.4	Galetti and Padroni, 1994
	C. albifrons		36[1]				64[2]		Terborgh, 1983
	Saimiri boliviensis	Frugivore/ Insectivore	93					7	Soini, 1986
	S. sciureus		55.1				44.9		Lima and Ferrari, 2003
			18[1]				82[2]		Terborgh, 1983
	Aotus nigriceps	Frugivore	65-80	0-30	3-5		10-20		Wright, 1989
Pithecidae	*Callicebus brunneus*	Frugivore	55-65	0-3	25-40		10-25		Wright, 1989
	C. personatus		55-57	2-22	18-26			5-15	Price and Piedade, 2001
			81		18			1	Kinzey and Becker, 1983
	Pithecia albicans	Frugivore/seed predator	33.8	6.5	9.5	46.2	0.4	3.6	Peres, 1993
	P. pithecia		28	2	7	61	1		Kinzey and Norconk, 1992
Atelidae	*Alouatta palliata*	Folivore/ Frugivore	28.5	22.5	49				Chapman, 1988
	A. fusca		16	9	71				Mendes, 1985
	A. seniculus		25.5	12.6	57		1.5	0.4	Julliot and Sabatier, 1993
	Lagothrix cana	Frugivore	80.7	3.1	16.2				Peres, 1994
	L. lagotricha		78.9	0.1	11.4	4.3	4.9	0.4	Defler and Defler, 1996
	L. poeppigii		76.7	3.5	7.4	0.54	9.16	2.7	Di Fiore, 2004
	Ateles geoffroyi	Frugivore	77.7	9.8	11.1		1.3	0	Chapman, 1988
			82.2	1	17.2		0.6		Campbell, 2000
	A. belzebuth		78.8	3.2	7.7			10.3	Suarez, 2006
	Brachyteles arachnoides	Folivore/ Frugivore	32	11	51			6	Strier, 1991
			59.1	4.1	33.2			3.6	de Carvalho et al., 2004

Table 3.01. Diet in Extant Platyrrhines.

[1] includes fruit and seeds

[2] includes prey

MATERIALS AND METHODS

The sample was drawn from 208 extant platyrrhine mandibular tooth rows (Table 3.02), and 22 extinct platyrrhine tooth rows or isolated M_2s (Table 3.03). Taxa were chosen to represent a variety of dietary profiles and taxonomic groups across the platyrrhine primates, but sampling was not exhaustive. All of the extant primate teeth had negligible wear. Teeth were rejected if cusp tips showed dentin or significant flattening. The extant sample was collected from museum specimens in the American Museum of Natural History, National Museum of Natural History, Museu Nacional, Rio de Janeiro, Brazil, and the Museu de Zoologia de Universidade de São Paulo, Brazil. Each tooth row was cleaned with acetone to remove debris and was molded using President Jet Microsystem ployvinylsiloxane medium body (Coltène/Whaledent). The molds were reinforced with President Putty Soft (Coltène/Whaledent) and then cast using F-82 epoxy with a TP-41 hardener (Eastpoint Fiberglass, Eastpoint Michigan). To prepare for laser scanning, all casts were painted with a thin layer of matte water-based acrylic paint to correct for glare. The sample of extinct primates was composed of casts made from original specimens in the same manner detailed above or from casts obtained from museums or other researchers. The extinct sample includes representatives from the three major geographic areas were platyrrhine fossils have been found: Patagonia, La Venta, Colombia, and the Greater Antilles. Specimens chosen for inclusion in this study exhibit a variety of dental morphologies and phylogenetic affinities.

The cast tooth rows and M_2s were laser scanned using an LDI Surveyor AM-66RR laser scanner with an RPS 120 sensor at 25 μm interpoint distances. This process created three dimensional point clouds, which were then surface rendered in Geomagic Studio 11 (Geomagic, Inc.) to create virtual three-dimensional dental models. In instances where the entire tooth row was scanned, the M_2 was isolated using the editing functions in Geomagic Studio 11 (Geomagic, Inc.).

Because these cropped specimens lacked the mesial and distal tooth surfaces in the interstitial region, no landmarks were located in this area.

Landmark Editor (Wiley *et al.*, 2005) was used to place 23 *x,y,z* coordinate landmarks on the occlusal surface and sidewalls of M_2. Landmarks were chosen to outline major dental features on the occlusal surface including cusp apices, basin low points, points of intersection between two crests, and the mesial and distal-most points on the occlusal surface. Landmarks placed on the sidewall of the tooth included points of maximum curvature and the CEJ (Table 3.04, Fig. 3.01). Landmarks were chosen based on their repeatability and functional significance. Error tests performed indicated a low error rate (Appendix B).

After landmark placement, the *x,y,z* coordinate points were exported from Landmark editor (Wiley *et al.*, 2005). The points were aligned using generalized Procrustes analysis (GPA) (*morphologika*^{2}, O'Higgins and Jones, 2006). GPA is a statistical technique used to minimize the least squares distance between sets of landmark points by scaling, rotation, transposition, and translation (Gower, 1975; Rolf and Slice, 1990). Principal components analysis (PCA) was performed in *PAST* (Hammer *et al.*, 2001) on the GPA-aligned landmark points to explore overall shape variation in the sample (Fig. 3.02 – 3.04).

Finally, the living species were assigned dietary categories based on annual patterns of consumption, culled from the literature (Table 3.01). Dietary categories include both the major food source contributing 40% to the annual diet and the major protein source or fallback food if a clear one exists (following Anapol and Lee, 1994). *Alouatta* and *Brachyteles* were classified as folivore/frugivores, *Saimiri* as a frugivore/insectivore, *Callicebus*, *Aotus, Ateles*, and *Lagothrix* as frugivores, *Pithecia* as a frugivore/seed predator and *Cebus* as a frugivore/omnivore. Here, the frugivore category is fairly broad and encompasses the highly frugivorous *Ateles* and *Lagothrix* as well as the seasonally frugivorous *Callicebus* and *Aotus*.

To test the efficacy of landmark data for diet prediction in fossil taxa, discriminant function analysis (DFA) (SPSS, Rel. 11.01, SPSS, Inc.) (Tables 3.05, 3.06) was performed on PC 1, PC 1 and centroid size, and the GPA aligned landmarks. The analysis was conducted entering the independent variables together, and with prior probabilities calculated from the group size. Extant forms were grouped by diet, and fossils were left ungrouped. Cross-validation of the models was performed in SPSS. To do this, one sample was removed from the dataset to determine the new discriminant rule. The removed sample was then classified using the new discriminant rule to determine the rate of correct classification by diet.

Species	**N**	
Cebus capucinus	25	
Saimiri boliviensis	27	
Aotus sp.	29	
-*A. brumbacki*		1
-*A. lemurinus*		4
-*A. trivirgatus*		4
-*A. vociferans*		9
-*A. azarae*		1
-*A. infulatus*		6
-*A. nigriceps*		4
Callicebus sp.	27	
-*C. caligatus*		2
-*C. cupreus*		23
-*C. personatus*		2
Pithecia sp.	19	
-*P. aequatorialis*		2
-*P. irrorata*		10
-*P. pithecia*		7
Alouatta sp.	22	
-*A. palliata*		14
-*A. seniculus*		8
Lagothrix sp.	23	
-*L. cana*		7
-*L. lagotricha*		12
-*L. lugens*		1
-*L. poepigii*		2
-*L.* sp.		1
Ateles geoffroyi	19	
Brachyteles arachnoides	17	
Total		208

Table 3.02. Extant Platyrrhine Sample

Graph Symbol	Species		Age	Sites, Localities, or Formations	Family Relationship
A	*Antillothrix bernensis*	MDH 01	Holocene	La Jeringa, Parque del Este, Dominican Republic	Cebidae ?
B	*Insulacebus toussaintiana*	UF 11417	Holocene	Trouing Jérémie no. 5, Haiti	Pitheciidae
C	*Xenothrix mcgregori*	AMNHM 148198 (type)	Holocene	Long Mile Cave, Jamaica	Pitheciidae
D1	*Paralouatta varonai*	MHNH Cueva Alta 1996	Pleistocene	Cueva Alta, Cuba	Atelidae
D2	*Paralouatta varonai*	MNNH V123	Pleistocene	Cueva del Mono Fósil, Cuba	Atelidae
E	*Caipora bambuiorum*	IGC-UFMG 05 (type)	Pleistocene	Toca da Boa Vista, Bahia, Brazil	Atelidae
F1	*Neosaimiri fieldsi*	UCMP 39205 (type)	Miocene	La Venta, Colombia	Cebidae
F2	*Neosaimiri fieldsi*	IGM-KU 89002	Miocene	La Venta, Colombia	Cebidae
F3	*Neosaimiri fieldsi*	IGM-KU 89034	Miocene	La Venta, Colombia	Cebidae
G	*Laventiana annectens*	IGM-KU 8801a	Miocene	La Venta, Colombia	Cebidae
H	*Mohanimico hershkovitzi*	IGM 181500	Miocene	La Venta, Colombia	Cebidae
I	*Patasola magdalenae*	IGM 184332	Miocene	La Venta, Colombia	Cebidae
J	*Aotus dindensis*	IGM-KU 8601 (type)	Miocene	La Venta, Colombia	Cebidae
K	*Cebupithecia sarmientoi*[1]	UCMP 38762	Miocene	La Venta, Colombia	Pitheciidae
L1	*Stirtonia tatacoensis*	IGM-KU 8102	Miocene	La Venta, Colombia	Atelidae
L2	*Stirtonia tatacoensis*	IGM-KU 8215	Miocene	La Venta, Colombia	Atelidae
M	*Dolichocebus gaimanesis*	MPEF 5146	Miocene	Chubut, Argentina	Cebidae ?
N1	*Carlocebus carmenensis*	MACN-SC 43	Miocene	Santa Cruz, Argentina	Pitheciidae ?
N2	*Carlocebus carmenensis*	MACN-SC 250	Miocene	Santa Cruz, Argentina	Pitheciidae ?
N3	*Carlocebus carmenensis*	MACN-SC 63	Miocene	Santa Cruz, Argentina	Pitheciidae ?
P1	*Soriacebus ameghinorum*	MACN-SC 2 (type)	Miocene	Santa Cruz, Argentina	Pitheciidae ?
P2	*Soriacebus ameghinorum*	MACN-SC 379	Miocene	Santa Cruz, Argentina	Pitheciidae ?

Table 3.03. Extinct Platyrrhine Sample.

[1] m1

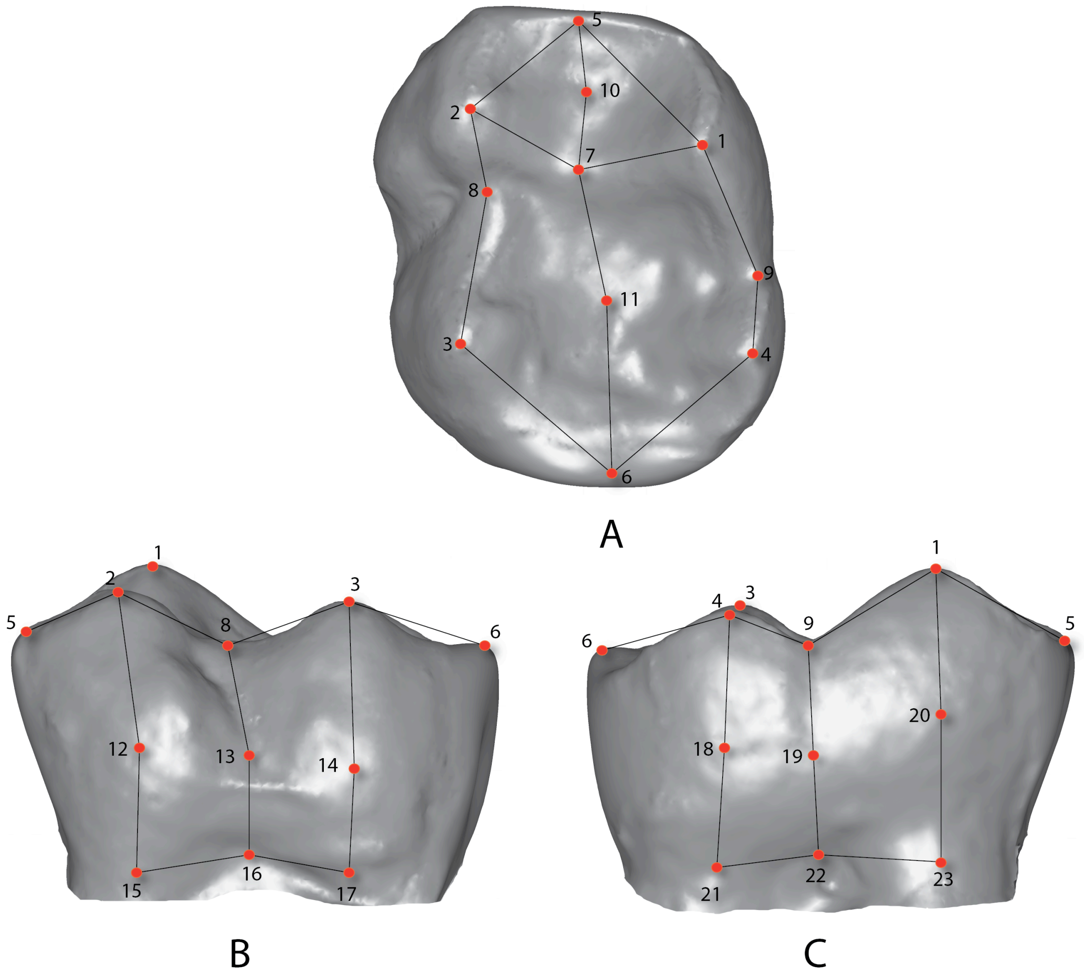


Figure 3.01. A) Occlusal view of left M_2 of *Callicebus cupreus* (AMNH 98370) with landmarks, B) Buccal view, mesial to the right. C) Lingual view, mesial to the left. Points are connected with wireframes generated in *morphologika*^{2} (O'Higgins and Jones, 2006).

Occlusal Surface Landmarks	
1	Metaconid apex
2	Protoconid apex
3	Hypoconid apex
4	Entoconid apex
5	Mesial-most point on occlusal surface
6	Distal-most point on occlusal surface
7	Lowest point on the protocristid - usually at the midline
8	Lowest point on the cristid obliquid
9	Point at which the preentocristid and postmetacristid meet
10	Lowest point in the trigonid basin
11	Lowest point in the talonid basin

Sidewall Landmarks	
12	Point of maximum curvature directly below the protoconid
13	Point of intersection of the ectoflexid with the buccal wall
14	Point of maximum curvature directly below the hypoconid
15	The cemento-enamel junction (CEJ) directly below the protoconid
16	The CEJ directly below the intersection of the ectoflexid with the buccal wall
17	The CEJ directly below the hypoconid
18	Point of maximum curvature directly below the entoconid
19	Point of maximum curvature directly below where the preentocristid and postmetacristid meet
20	Point of maximum curvature directly below the metaconid
21	The CEJ directly below the entoconid
22	The CEJ directly below the below where the preentocristid and postmetacristid meet
23	The CEJ directly below the metaconid

Table 3.04. Mandibular M_2 landmarks

RESULTS

Principal components analyses

Figure 2 shows a PCA of landmarks 1-23. Variation along PC 1 (21.6% of total variance) is primarily driven by cusp height in combination with basin depth. The species showing the most extreme version of high dental relief (relative height of the cusps above the tooth basin) are the folivorous/frugivorous *Alouatta* and *Brachyteles* and the frugivorous/insectivorous *Saimiri.* The largely frugivorous species *Ateles, Lagothrix, Aotus,* and *Callicebus* have less dental relief and lower flatter crowns. The most extreme variations in this latter pattern are found in the frugivorous/seed predacious *Pithecia* and frugivorous/omnivorous *Cebus*, which have nearly flat crowns with little delineation between the trigonid and talonid basins, abbreviated crests, and overall low cusp height.

Among the fossils forms, *Paralouatta varonai, Patasola magdalenae*, *Laventiana annectens,* and the three *Neosaimiri fieldsi* individuals fall within the range of frugivorous/insectivorous *Saimiri* and the folivore/frugivores along PC 1. The remainder of the extinct platyrrhines fall within the large region of overlap along PC 1, but several alignments are worth noting: *Caipora bambuiorum*, a Pleistocene ateline, is remarkable for its similarity to *Ateles*, and *Aotus dindensis* consistently groups with extant *Aotus*, though the *Aotus* distribution along PC 1 does primarily fall within a large region of overlap. *Cebupithecia sarmientoi*, considered a Miocene pitheciin, falls outside of the range of *Pithecia*, but within the range of *Callicebus*. The alouattin, *Stirtonia tatacoensis*, falls just outside the range of modern *Alouatta*. *Carlocebus carmenensis* specimens show a wide degree of variability along PC 1, with MACN SC 205 (N2) within the range of *Alouatta*, *Brachyteles*, and *Saimiri*, and MACN SC 43 (N1) falling with the platyrrhines having far less dental relief.

PC 2 (Fig. 3.02, 3.03) shows significant overlap for most taxa, and there is a weak allometric component to the shape. In a regression of PC 2 against centroid size, the R^2 value is 0.39. Variation along this axis is largely governed by the relative position of the hypoconid, the relative length of the trigonid, and the degree of wasting at the CEJ. While there is substantial overlap for most taxa, PC 2 does differentiate the large-bodied folivore/frugivores *Alouatta* and *Brachyteles* from the frugivore/insectivore *Saimiri*. The fossil alouattin, *Stirtonia*, demonstrates similar morphology to *Alouatta* as does *Paralouatta* along PC 2, though *Stirtonia* is separated from *Alouatta* along PC 3. *Xenothrix mcgregori* also falls near the position of *Alouatta* at the edge of the range of modern variation, but is distinct when comparing PC 2 and PC 3 (Fig. 3.03). Again, *Aotus dindensis* clusters within the *Aotus* group, and *Caipora* groups with *Ateles*. *Carlocebus* shows a wide range of variation along this axis, also.

Variation along PC 3 (Fig. 3.03, 3.04) is accounted for by the relative length of the M_2, the degree of waisting at the CEJ, and height of the point of maximum curvature on the tooth sidewall in combination with the degree of separation of the cusp tips on the crown surface. There is considerable overlap among the living genera with only *Cebus* falling outside the confidence limits of *Aotus* and *Ateles* along this axis. Most of the fossil platyrrhines fall within the large area of overlap, but on the whole tend to have a much lower point of maximum curvature and greater sidewall flare than do the living forms. The Caribbean platyrrhines, *Xenothrix* and *Insulacebus*, are extreme in this morphology*,* a trait that has been noted previously as one of the distinctive features of these taxa (Rosenberger, 1977; Cooke *et al.*, 2011).

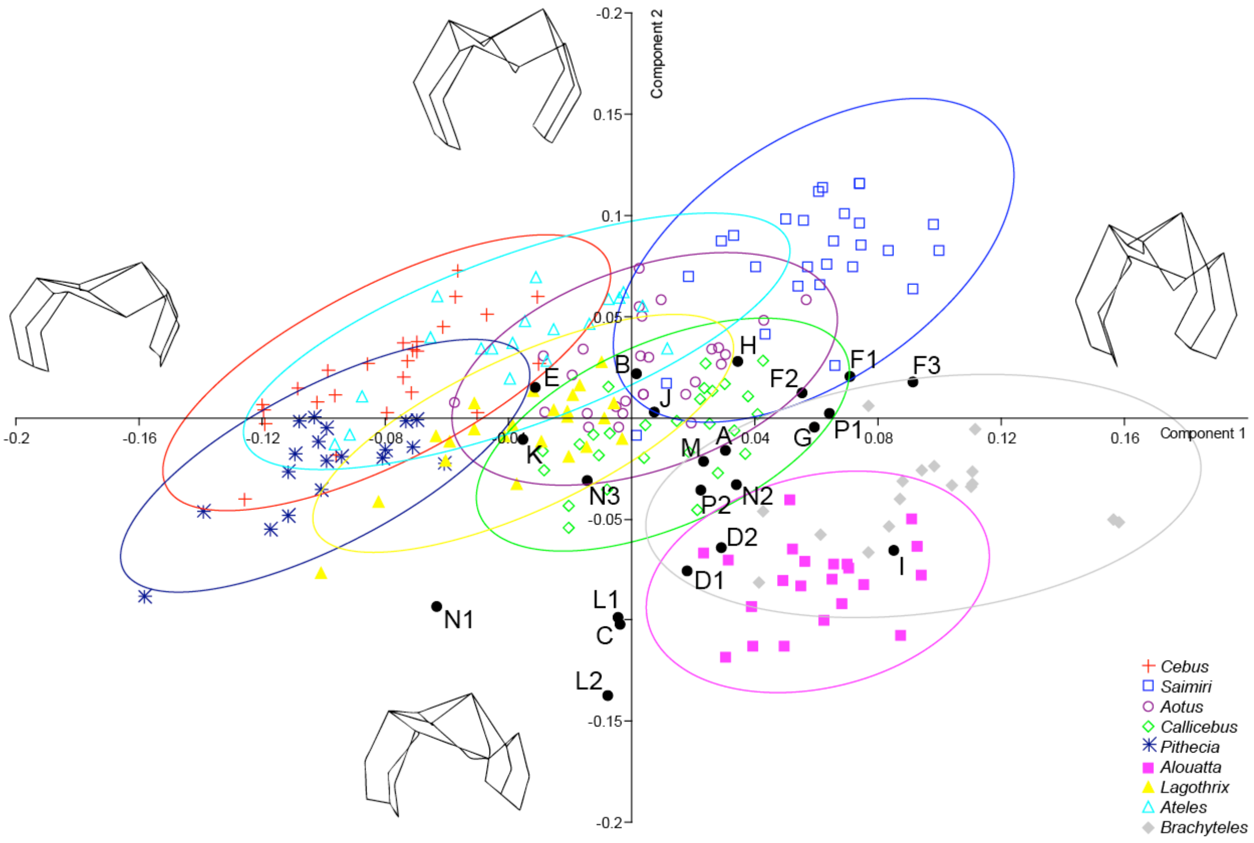


Figure 3.02. Plot of PC 1 vs. PC 2 with 95% equal frequency ellipses. Extinct species are lettered with the key given below. PC 1 represents 21.6% of the total variance, and PC 2 accounts for 14.0% of the total variance. Wireframe deformations (from a distolingual view) show shape changes at the extremes of the axes.

Species		Symbol	Species		Symbol
Antillothrix bernensis	MDH 01	A	*Patasola magdalenae*	IGM 184332	I
Insulacebus toussaintiana	UF 11417	B	*Aotus dindensis*	IGM-KU 8601 (type)	J
Xenothrix mcgregori	AMNHM 148198 (type)	C	*Cebupithecia sarmientoi*	UCMP 38762	K
Paralouatta varonai	MHNH Cueva Alta 1996	D1	*Stirtonia tatacoensis*	IGM-KU 8102	L1
Paralouatta varonai	MNNH V123	D2	*S. tatacoensis*	IGM-KU 8215	L2
Caipora bambuiorum	IGC-UFMG 05 (type)	E	*Dolichocebus gaimanesis*	MPEF 5146	M
Neosaimiri fieldsi	UCMP 39205 (type)	F1	*Carlocebus carmenensis*	MACN-SC 43	N1
N. fieldsi	IGM-KU 89002	F2	*C. carmenensis*	MACN-SC 250	N2
N. fieldsi	IGM-KU 89034	F3	*C. carmenensis*	MACN-SC 63	N3
Laventiana annectens	IGM-KU 8801a	G	*Soriacebus ameghinorum*	MACN-SC 2 (type)	P1
Mohanimico hershkovitzi	IGM 181500	H	*S. ameghinorum*	MACN-SC 379	P2

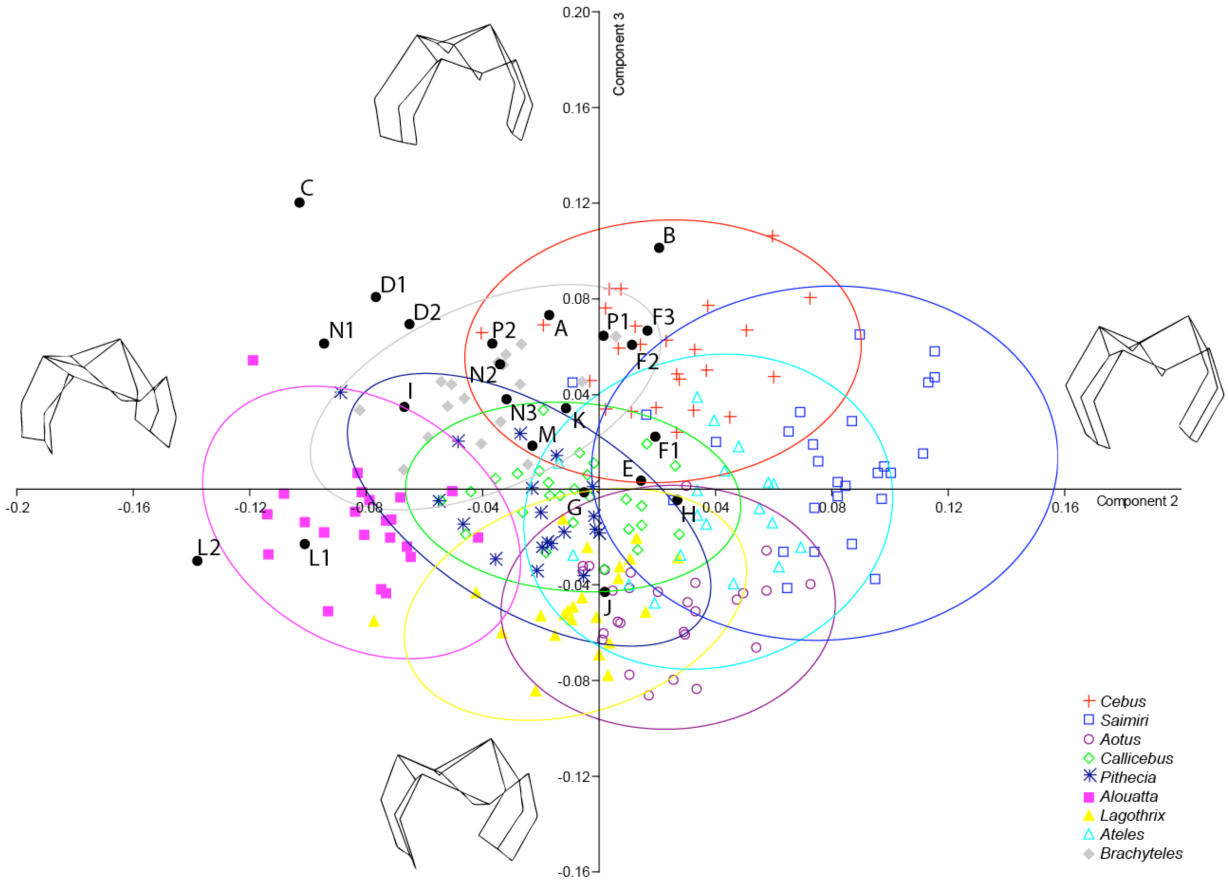


Figure 3.03. Plot of PC 2 vs. PC 3 with 95% equal frequency ellipses. PC 2 represents 14.0% of the total variance, and PC 3 accounts for 9.5% of the total variance. Wireframes deformations (from a distolingual view) show shape changes at the extremes of the axes.

Species		**Symbol**	**Species**		**Symbol**
Antillothrix bernensis	MDH 01	A	*Patasola magdalenae*	IGM 184332	I
Insulacebus toussaintiana	UF 11417	B	*Aotus dindensis*	IGM-KU 8601 (type)	J
Xenothrix mcgregori	AMNHM 148198 (type)	C	*Cebupithecia sarmientoi*	UCMP 38762	K
Paralouatta varonai	MHNH Cueva Alta 1996	D1	*Stirtonia tatacoensis*	IGM-KU 8102	L1
Paralouatta varonai	MNNH V123	D2	*S. tatacoensis*	IGM-KU 8215	L2
Caipora bambuiorum	IGC-UFMG 05 (type)	E	*Dolichocebus gaimanesis*	MPEF 5146	M
Neosaimiri fieldsi	UCMP 39205 (type)	F1	*Carlocebus carmenensis*	MACN-SC 43	N1
N. fieldsi	IGM-KU 89002	F2	*C. carmenensis*	MACN-SC 250	N2
N. fieldsi	IGM-KU 89034	F3	*C. carmenensis*	MACN-SC 63	N3
Laventiana annectens	IGM-KU 8801a	G	*Soriacebus ameghinorum*	MACN-SC 2 (type)	P1
Mohanimico hershkovitzi	IGM 181500	H	*S. ameghinorum*	MACN-SC 379	P2

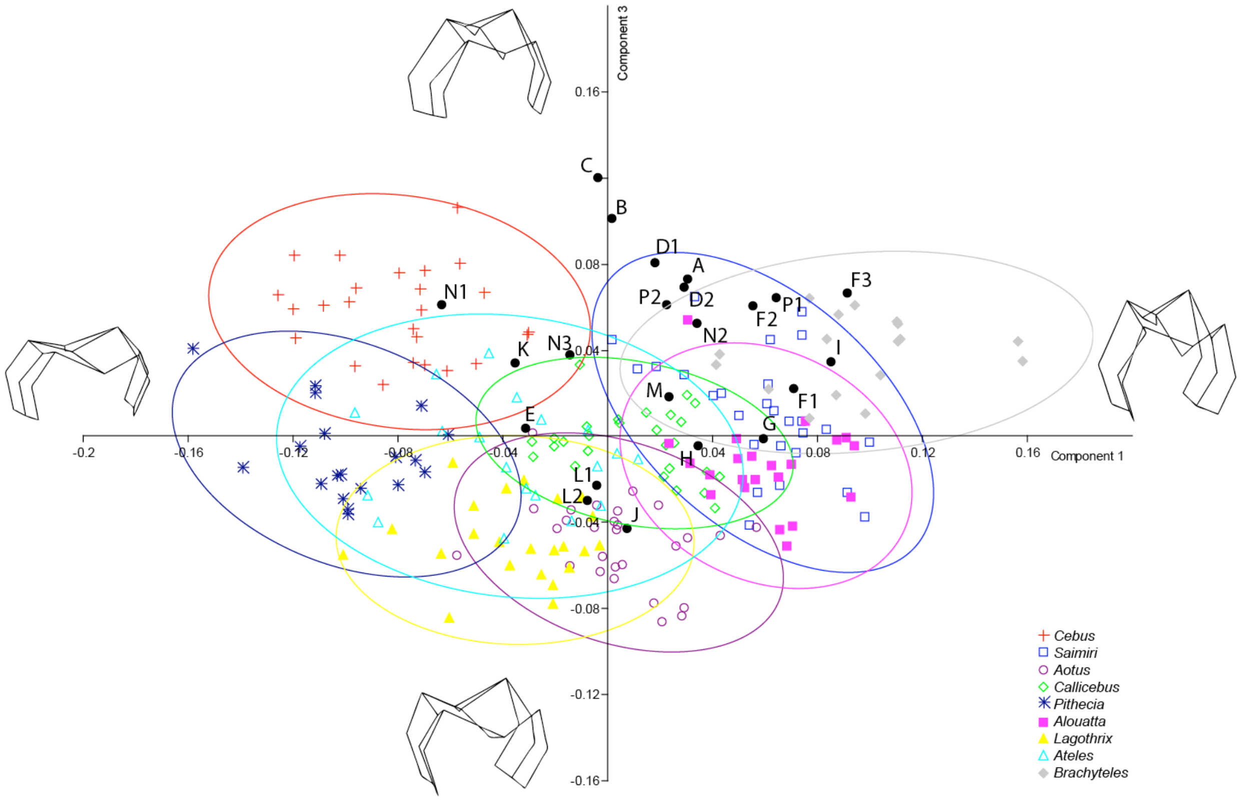


Figure 3.04. Plot of PC 1 vs. PC 3. PC 1 represents 21.6% of the total variance, and PC 3 accounts for 9.5% of the total variance. Extinct species are lettered (Table 3.03). Wireframes deformations (from a distolingual view) show shape changes at the extremes of the axes.

Species		Symbol	Species		Symbol
Antillothrix bernensis	MDH 01	A	*Patasola magdalenae*	IGM 184332	I
Insulacebus toussaintiana	UF 11417	B	*Aotus dindensis*	IGM-KU 8601 (type)	J
Xenothrix mcgregori	AMNHM 148198 (type)	C	*Cebupithecia sarmientoi*	UCMP 38762	K
Paralouatta varonai	MHNH Cueva Alta 1996	D1	*Stirtonia tatacoensis*	IGM-KU 8102	L1
Paralouatta varonai	MNNH V123	D2	*S. tatacoensis*	IGM-KU 8215	L2
Caipora bambuiorum	IGC-UFMG 05 (type)	E	*Dolichocebus gaimanesis*	MPEF 5146	M
Neosaimiri fieldsi	UCMP 39205 (type)	F1	*Carlocebus carmenensis*	MACN-SC 43	N1
N. fieldsi	IGM-KU 89002	F2	*C. carmenensis*	MACN-SC 250	N2
N. fieldsi	IGM-KU 89034	F3	*C. carmenensis*	MACN-SC 63	N3
Laventiana annectens	IGM-KU 8801a	G	*Soriacebus ameghinorum*	MACN-SC 2 (type)	P1
Mohanimico hershkovitzi	IGM 181500	H	*S. ameghinorum*	MACN-SC 379	P2

Discriminant function analyses

Discriminant function analysis successfully grouped living taxa of known dietary profile into dietary groups at a rate better than chance. A DFA using only PC 1 scores classified 67.6% of platyrrhines into the correct dietary category (Table 3.05A). The majority of misclassifications occurred between folivorous/frugivorous *Alouatta* and *Brachyteles* and frugivorous/insectivorous *Saimiri,* and between the frugivorous/seed predacious *Pithecia* and frugivorous/omnivorous *Cebus.* The addition of centroid size yielded much better results with 96.6% correctly classified (Table 3.05B), and made distinguishing between the large bodied folivore/frugivores and the smaller frugivorous/insectivorous *Saimiri* possible. A DFA of the GPA aligned complete landmark set yielded 100% correct classification (Table 3.05C). In cross-validation studies, PC 1 and centroid size fared best with 87.4% of classifications correctly classified. The other two approaches cross-validated poorly with PC 1 and the complete landmark set, both classifying 46.9% of cases correctly.

To predict the hypothetical diet, the fossil forms were left ungrouped in the DFA. Results of predicted dietary groups are shown in Table 3.06. Most fossil platyrrhines were classified with the frugivores in all analyses, but classification did vary across analyses for several taxa. The alouattins *Stirtonia* and *Paralouatta* were classified as frugivores when using PC 1 or PC 1 and centroid size, but were classified as folivore/frugivores when using the landmark set. The position of *Neosaimiri* was also equivocal. Using only PC 1, *Neosaimiri* specimens were classified as folivore/frugivores or frugivore/insectivores, but the addition of centroid size resulted in their classification as frugivore/insectivores with the exception of UCMP 39205, which also had the largest centroid size. The landmark data placed *Neosaimiri* with the frugivores. Both *Patasola* and *Laventiana* also were classified as folivore/frugivores (PC 1) or frugivore/insectivores (PC 1 and centroid size), but like *Neosaimiri* were grouped as frugivores using the complete landmark set. One species, *Xenothrix,* was categorized as a frugivore/omnivore in the complete landmark analysis, but elsewhere fell with the frugivores. Differences in specimen allocation were also encountered with *Carlocebus*. One (MACN SC 43) was classified as a frugivore/seed predator using the landmark set and as a frugivore in the other analysis; the other two *Carlocebus* specimens were always grouped with the frugivores.

A

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	26	8	5	0	0
	Frugivore/ Insectivore	16	5	6	0	0
	Frugivore	0	3	88	2	4
	Frugivore/ Seed predator	0	0	1	12	6
	Frugivore/ Omnivore	0	0	7	9	9

67.6% of original grouped cases correctly classified. 46.9% of cross-validated cases were correctly classified.

B

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	39	0	0	0	0
	Frugivore/ Insectivore	0	26	1	0	0
	Frugivore	0	0	96	0	1
	Frugivore/ Seed predator	0	0	0	17	2
	Frugivore/ Omnivore	0	0	3	0	22

96.6% of original grouped cases correctly classified. 87.4% of cross-validated cases were correctly classified.

C

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	39	0	0	0	0
	Frugivore/ Insectivore	0	27	0	0	0
	Frugivore	0	0	97	0	0
	Frugivore/ Seed predator	0	0	0	19	0
	Frugivore/ Omnivore	0	0	0	0	25

100.0% of original grouped cases correctly classified. 46.9% of cross-validated cases were correctly classified.

Table 3.05. Discriminant Function Analyses (DFA) of PC 1 Score, B) PC 1 Score and Centroid Size, C) GPA aligned landmarks.

		PC 1 Score	PC 1 Score and Centroid Size	GPA aligned Landmarks
Greater Antilles				
Antillothrix bernensis	MDH 01	Frugivore	Frugivore	Frugivore
Insulacebus toussaintiana	UF 11417	Frugivore	Frugivore	Frugivore
Xenothrix mcgregori	AMNHM 148198 (type sp.)	Frugivore	Frugivore	Frugivore/ Omnivore
Paralouatta varonai	MHNH Cueva Alta 1996	Frugivore	Frugivore	Folivore/ Frugivore
P. varonai	MNNH V123	Frugivore	Frugivore	Folivore/ Frugivore
Brazil				
Caipora bambuiorum	IGC-UFMG 05 (type sp.)	Frugivore	Frugivore	Frugivore
La Venta, Colombia				
Neosaimiri fieldsi	UCMP 39205 (type sp.)	Frugivore/ Insectivore	Frugivore	Frugivore
N. fieldsi	IGM-KU 89002	Frugivore/ Insectivore	Frugivore/ Insectivore	Frugivore
N. fieldsi	IGM-KU 89034	Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore
Laventiana annectens	IGM-KU 8801a	Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore
Mohanimico hershkovitzi	IGM 181500	Frugivore	Frugivore	Frugivore
Patasola magdalenae	IGM 184332	Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore
Aotus dindensis	IGM-KU 8601 (type sp.)	Frugivore	Frugivore	Frugivore
Cebupithecia sarmientoi	UCMP 38762	Frugivore	Frugivore	Frugivore
Stirtonia tatcoensis	IGM-KU 8102	Frugivore	Frugivore	Folivore/ Frugivore
S. tatcoensis	IGM-KU 8215	Frugivore	Frugivore	Folivore/ Frugivore
Patagonia, Argentina				
Dolichocebus gaimanesis	MPEF5146	Frugivore	Frugivore	Frugivore
Carlocebus carmenensis	MACN-SC 43	Frugivore	Frugivore	Frugivore/ Seed predator
C. carmenensis	MACN-SC 250	Frugivore	Frugivore	Frugivore
C. carmenensis	MACN-SC 63	Frugivore	Frugivore	Frugivore
Soriacebus ameghinorum	MACN-SC 2 (type sp.)	Folivore/ Frugivore	Frugivore	Frugivore
S. ameghinorum	MACN-SC 379	Frugivore	Frugivore	Frugivore

Table 3.06. Discriminant Function Analysis (DFA) Dietary Classification of Extinct Platyrrhines.

Discussion

Molar morphology and diet in the extant platyrrhines

Principal component 1 largely differentiated genera based on diet (Fig. 3.05). The greatest separation existed between clusters containing: 1) the folivore/frugivores, *Alouatta* and *Brachyteles* and the frugivore/insectivore, *Saimiri,* 2) the largely frugivorous primates, *Ateles*, *Lagothrix*, *Aotus*, and *Callicebus*, and 3) the frugivore/seed predator, *Pithecia*, and the frugivore/omnivore *Cebus*. This distribution largely mirrors the abilities of Kay's shearing quotient (Kay 1978, 1984) to distinguish platyrrhines of different dietary guilds. The landmark-based data does provide additional information about the exact shape changes that occur across this distribution, however. This method was least successful at differentiating primates specializing in frugivory, frugivory/seed predation and frugivory/omnivory (Table 3.05).

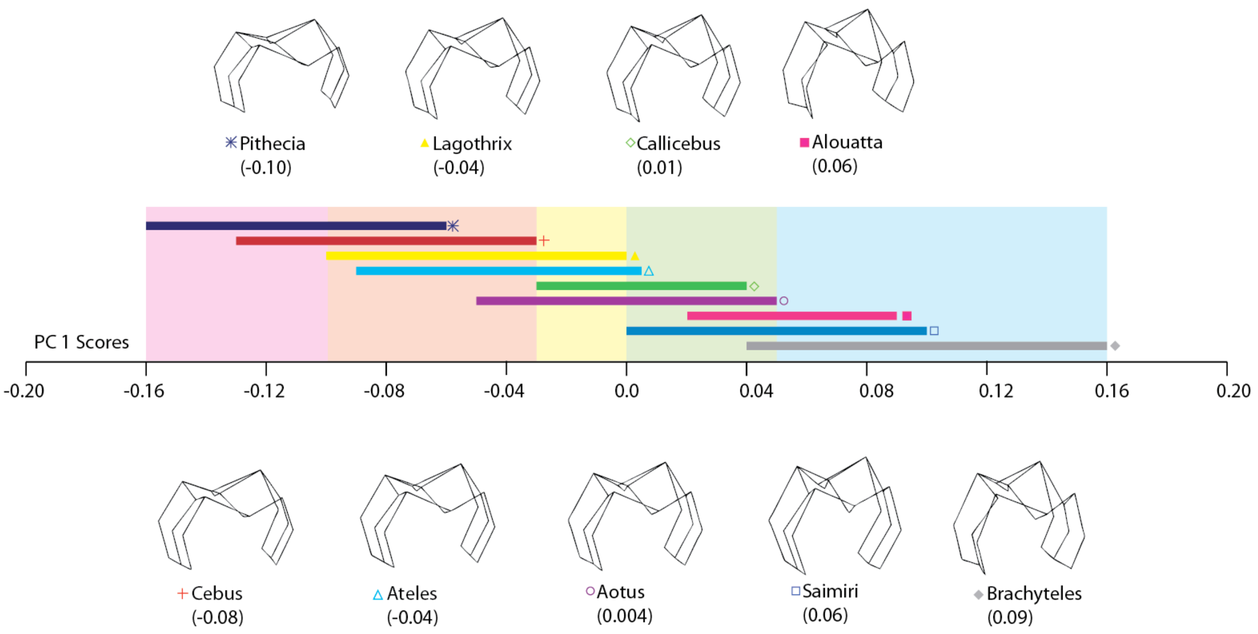


Figure 3.05. PC 1 scores of extant taxa. Average PC 1 score for each genus is shown below the form's wireframe. Diet is represented by the color blocks: light blue represents folivore/frugivores and frugivore/insectivores, yellow represents frugivores, and pink represents frugivore/seed predator and frugivore/omnivores. The regions of dietary overlap are shown in green and orange.

The folivorous/frugivorous platyrrhines *Brachyteles* and *Alouatta*, have a distinct morphology marked by high crowns, deep basins, deep intercuspal notches on the buccal and lingual sides of the crown, and a long cristid obliqua. While both have similarities in molar form, genetic (*e.g.,* Schneider *et al.*, 2001; Opazo *et al.*, 2006; Herke *et al.*, 2007; Wildman *et al.*, 2009) and postcranial evidence (*e.g.*, Rosenberger and Strier, 1989), as well as subtle morphological differences in dentition (Rosenberger, 1992; Anthony and Kay, 1993) indicate parallel adaptation to a leafy diet. The diets of both of these species contain a significant quantity of leaves (Table 3.01), which have specific processing demands. The toughness or resistance to crack propagation of cellulose is considerable and requires long blades to process (Kay, 1975; Rosenberger and Kinzey, 1976; Lucas, 2004). Additionally, some leaves consumed by *Alouatta*, and by extension other leaf-eating platyrrhines, contain mechanical defenses such as silica (Teaford *et al.*, 2006), which will wear teeth down very quickly, necessitating high crowns to prolong the life of the tooth.

The frugivorous/insectivorous *Saimiri boliviensis* falls within the range of the folivorous/frugivorous primates along PC 1. Mischaracterizations in the DFA included the classification of *Saimiri* within the folivore/frugivore group and vice versa. These are unsurprising results that have been supported in other functional studies. Mastication of insects requires biomechanical adaptations similar to those necessary for leaf eating, and specialists in both soft-bodied and hard-bodied insects have been found to have significant shearing crest development. Hard-bodied insects tend to be tough and brittle, while soft-bodied insects are subject to ductile deformations and must be sliced through completely in order to break them down (Strait, 1993; Lucas, 2004). Consequently, primates that derive a substantial portion of their diet from insects have been difficult to distinguish from leaf-eating primates using functional measures of shearing crest length. Primarily, researchers have relied on body size as a way of separating the folivorous from the insectivorous, as the energy requirements of small-bodied primates (<500 g) preclude reliance on leaves as a major food source (Kay, 1975). While *Saimiri* was statistically indistinguishable from *Alouatta* along PC 1 (ANOVA, p=0.99), it could be differentiated from the folivore/frugivores along PC 2, a principal component that does have a weak correlation with size. Additionally, the DFA of PC 1 scores and centroid size had much more success in classifying these groups than did PC 1 scores alone. Morphologically, the landmarks along PC 2 that separate *Saimiri* from *Alouatta* and *Brachyteles* include those that outline its relatively shorter trigonid, and more distally placed hypoconid. This likely maximizes the length of the cristid obliquid as each of its endpoints are moved further away from each other.

In contrast, the molars of primates that do not rely on leaves or insects for an important portion of their diets are marked by relatively larger basin areas, lower crown relief, and an overall squarer molar outline, which largely correlates with reduced shearing ability, lower resistance to wear, and increased surface area for crushing. This pattern exists across platyrrhines ranging in body size from *Aotus* (800-900 grams) to the very large *Lagothrix* and *Ateles* (6000-10,000 grams) (average weights compiled by Ford and Davis, 1992). Of this group, the least frugivorous are *Callicebus* and *Aotus*, which exploit a greater variety of food types than do the most committed soft-fruit frugivores, *Ateles* and *Lagothrix* (Table 3.01). Most of this dietary variation appears to be seasonal (Wright, 1989), and when availability allows it, fruit can be consumed in proportions similar to those observed in *Ateles* and *Lagothrix* (Kinzey, 1978; Terborgh, 1983; Wright, 1989; Herrera and Heymann, 2004). Along PC 1, *Aotus* and *Callicebus* are statistically indistinguishable from each other (ANOVA, p=0.99); both genera maintain a greater degree of dental relief than the committed soft-fruit frugivores – a likely adaptation to this more flexible dietary profile. *Lagothrix* and *Ateles* also show significant overlap along PC 1 (ANOVA, p=0.99).

The most extreme in the trend toward low levels of relief, and consequently the most positive PC 1 scores, are evident in the frugivorous/seed predacious *Pithecia* and the frugivorous/omnivorous *Cebus*. Along PC 1 they were statistically indistinguishable (ANOVA, p=0.19) and were misclassified in the DFA of PC 1 most frequently; *Cebus* was classified as *Pithecia* 36% of the time and *Pithecia* was classified as *Cebus* 32% of the time (Table 3.05A, Fig. 3.05). Their molars have a wide basin, low cusps, and are square in outline, resulting in enlarged area for crushing food items. While *Pithecia* and *Cebus* have different dietary profiles, they both incorporate hard objects into their feeding behavior, though the species of *Cebus* included in this analysis, *C. capucinus*, is a less committed hard object consumer than *Cebus apella* (Table 3.01). *Pithecia* initially breaches the hard outer covering of seeds with its anterior teeth before crushing them with the cheek teeth. Its molars have a unique enamel structure that makes them very resistant to crack propagation when crushing hard seeds (Martin, Olejniczak, and Maas, 2003). Very little of their diet is composed of leaves or insects.

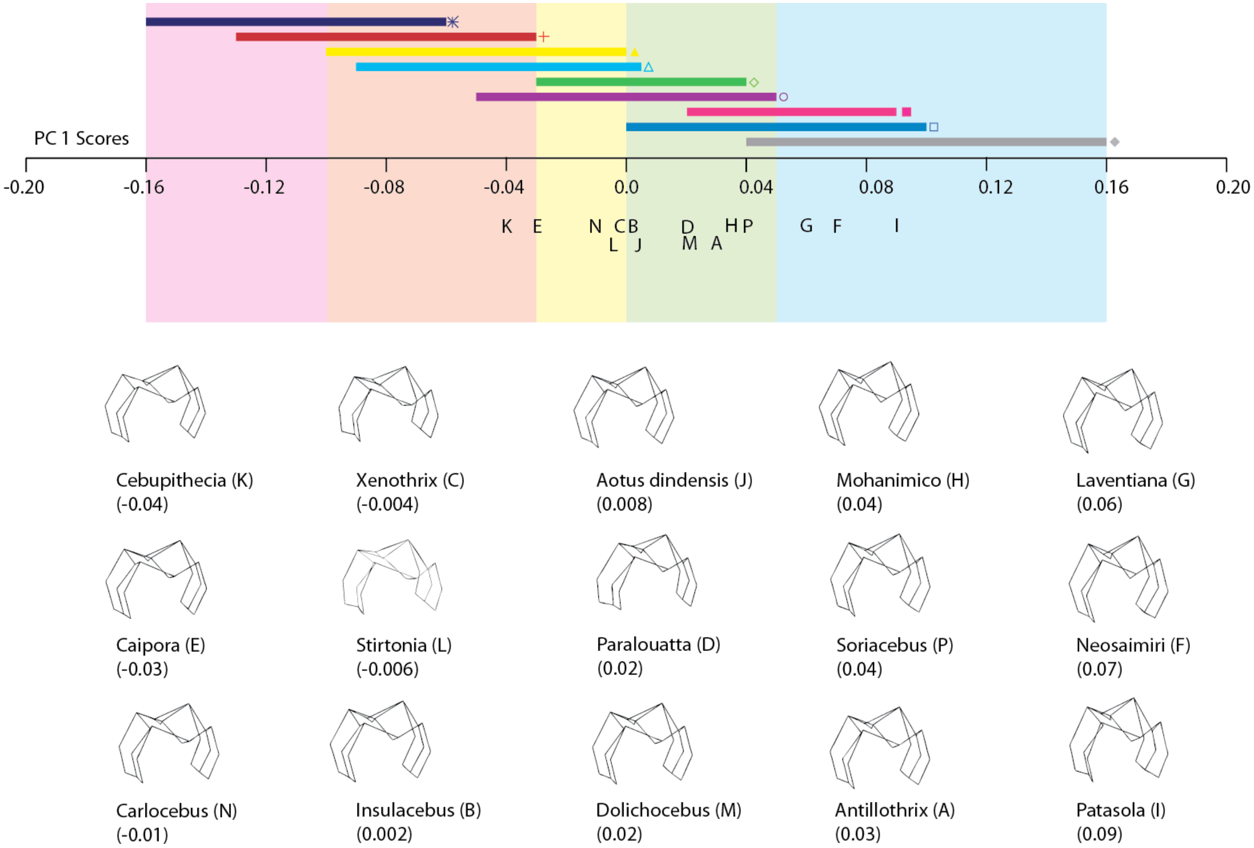
Like *Saimiri*, *Cebus* includes invertebrate prey (including insects) as a sizeable portion of its diet during certain times of the year (Tomblin and Cranford, 1994; Janson and Boinski, 1992), though the types of invertebrate prey exploited by the two cebines differ. At localities surveyed by Janson and Boinski (1992), *Cebus* tended to consume social insects and snails as their primary invertebrate prey, while *Saimiri* specialized in grasshoppers and caterpillars. Functionally, the delicate cusps and crests that are usually the hallmark of a committed insectivore are incompatible with the processing of hard fruit and nuts, which *Cebus* also does. The great diversity of the *Cebus* diet likely explains its lack of specialization for insectivory despite its inclusion of this resource in its diet.

Dietary prediction in the continental extinct platyrrhines

The platyrrhine fossil record begins with the 26 Ma Bolivian platyrrhines *Branisella boliviana* (Hoffstetter, 1969) and *Szalatavus attricuspis* (Rosenberger *et al.*, 1991a), though this paper is largely concerned with the later platyrrhines of the Miocene and does not include these primates in the analysis. The Bolivan fossils provide a brief glimpse into the earliest period of platyrrhine evolution, but these small-bodied monkeys remain phylogenetically enigmatic (Fleagle and Tejedor, 2002), though some researchers have argued for a special relationship with callitrichines (Horovitz, 1999; Takai *et al.*, 2000). Between the Oligocene Bolivian deposits and the rich fossil localities of the Patagonian Colhuehuapian and Santacrucian South American Land Mammal Ages there is only one other primate known: *Chilicebus carrascoensis* from the early Miocene Abanico Formation of Chile. It is represented by a well-preserved skull (Flynn *et al.*, 1995).

From the Argentine Patagonian Miocene several primates are known including *Dolichocebus gaimanensis, Mazzonicebus aimendrae* dating to approximately 20 Ma (Kay *et al.,* 1999; Kay 2010) *Soriacebus ameghinorum, S. adrianae, Carlocebus carmenensis*, *C. intermedius, Killikaike blakei*, *Tremacebus harringtoni* and *Homunculus patagonicus*. These have been alternately hypothesized to be stem platyrrhines not monophyletically related to the modern radiation (Kay, 1990; Fleagle *et al.*, 1997; Kay *et al.*, 2008; Hodgson *et al.*, 2009; Kay and Fleagle, 2010) or allied with members of the modern radiation (Rosenberger, 1979; Rosenberger, 2002; Tejedor *et al.*, 2006; Rosenberger *et al.*, 2009; Rosenberger, 2010). Within the latter phylogenetic scheme, *Dolichocebus* and *Killikaike* are considered as cebids, and *Soriacebus*, *Carlocebus*, and *Homunculus* fall with the pitheciids, and *Tremacebus* is considered a relative of owl monkeys. One additional form, *Proteopithecia neuquenensis*, is 15.7 ± 0.07 Ma old and has been described as a pitheciid (Kay *et al.*, 1998).

The fossils included in this study, *Soriacebus*, *Carlocebus*, and *Dolichocebus*, fell within the large cluster of frugivorous platyrrhines in the principal components analysis and were mostly classified as frugivores in the DFA (Table 3.06, Fig. 3.06). They are morphologically similar to each other with elevated trigonids, distinct ectoflexids, cusps of moderate height – not as extreme in dental relief as the committed folivore/frugivores and frugivore/insectivores nor as flat as *Pithecia* and *Cebus*. *Soriacebus* and *Carlocebus* also shared a lower point of maximum curvature on the tooth sidewall.



Cebupithecia (K)
(-0.04)

Xenothrix (C)
(-0.004)

Aotus dindensis (J)
(0.008)

Mohanimico (H)
(0.04)

Laventiana (G)
(0.06)

Caipora (E)
(-0.03)

Stirtonia (L)
(-0.006)

Paralouatta (D)
(0.02)

Soriacebus (P)
(0.04)

Neosaimiri (F)
(0.07)

Carlocebus (N)
(-0.01)

Insulacebus (B)
(0.002)

Dolichocebus (M)
(0.02)

Antillothrix (A)
(0.03)

Patasola (I)
(0.09)

Figure 3.06. PC 1 scores of extinct taxa. The key is as follows: *Cebus* red cross, *Saimiri* blue square, *Aotus* purple circle, *Callicebus* green diamond, *Pithecia* blue star, *Alouatta* pink filled square, *Lagothrix* yellow filled triangle, *Ateles* light blue triangle, *Brachyteles* grey filled diamond. For extinct species for which there is more than one individual an average shape and average PC 1 score was generated. PC 1 score for each genus is shown below the form's wireframe. Diet is represented by the color blocks: light blue represents folivore/frugivores and frugivore/insectivores, yellow represents frugivores, and pink represents frugivore/seed predator and frugivore/omnivores. The regions of dietary overlap are shown in green and orange.

Dentally, *Soriacebus* is particularly intriguing; its anterior dentition consists of elongate incisors in combination with large canines, which favorably compare with the modern pitheciins *Pithecia*, *Chiropotes*, and *Cacajao* (Fleagle *et al.,* 1987; Fleagle, 1990). The molars, however, are not at all similar to any modern forms, and both *Soriacebus* specimens fall within the range of overlap of the frugivores and folivore/frugivores along PC 1. This mosaicism may indicate that the anterior dentition evolved a more modern morphology well before the typically low relief molars seen in modern pitheciins (Rosenberger, 1992).

Carlocebus shows a larger degree of variation across its distribution than in other fossil species for which 2-3 specimens were included. This calls into question the inclusion of one specimen (MACN SC 43) within this species. While two of the fossils cluster closely together in all analyses and are classified by DFA as frugivores, MACN SC 43 exhibits lower dental relief and falls with the frugivore/seed predators in one analysis (Table 3.06). The range of the *Carlocebus* distribution does mirror the extremes of the distributions for *Callicebus cupreus*, but it is worth considering the possibility that a mixed assemblage of multiple species might be included within the *Carlocebus* material. As additional specimens are found, a better understanding of the natural distribution of this group will likely develop.

Dolichocebus, here tentatively considered a cebid (but see Kay *et al.*, 2008 and Kay and Fleagle, 2010 for an alternate view), falls within the region of overlap between the frugivores and *Saimiri* and the folivore/frugivores. In the DFA, it was classified as a frugivore, indicating that this form, if closely related to *Saimiri* or the cebines, as Rosenberger holds (1979, 2002, 2010), is more primitive and not as committed to partial insectivory. Compared with *Saimiri*, *Dolichocebus* has larger basins, an overall lower dental profile, and like the other Patagonian primates more closely approximated cusps in the trigonid, such that the width of the tooth anteriorly is largely a result of a buccal flaring. A diet of mixed resources is predicted for this form, which is in keeping with the paleoecology of the Patagonian region (Fleagle *et al.*, 1997).

Patagonia represents the furthest reaches of the platyrrhine radiation at latitudes around 50 degrees south, and the environment would have been subject to significant seasonal fluctuations in temperature and light (Fleagle *et al.*, 1997; Rosenberger *et al.*, 2009). Isotopic and faunal evidence suggest that grasslands had already begun to establish themselves over much of South America with grazers and browsers present in the same localities as the primates (Flynn and Wyss, 1998; Jacobs *et al.*, 1999; MacFadden, 2000). The primates of this region likely inhabited marginal environments of dry or gallery forests (Fleagle *et al.*, 1997; Rosenberger *et al.*, 2009; Perry *et al.*, 2010), and many fossils show significant dental wear (Perry *et al.*, 2010). The fact that this region exhibits much lower primate species diversity than is found in later fossil assemblages from more humid tropical environments equates well with this paleoecological reconstruction. The primates included in this study from this period fall within the range of *Callicebus* and *Aotus* – two primates, which while frugivorous, maintain a certain amount of dietary flexibility. In the seasonal marginal environments of Miocene Patagonia, dietary flexibility would have been likely with *Soriacebus*, *Carlocebus*, and *Dolichocebus* exploiting a variety of food types (see Rosenberger *et al.*, 2009). These primates maintain a certain degree of shearing ability but clearly are neither committed insectivores nor folivores.

A large gap in the platyrrhine fossil record occurs between the Patagonian deposits and the site of La Venta in Colombia, dated to 13.5-11.8 Ma (Guerrero, 1997). The fauna includes twelve platyrrhine species, many of which can be definitively associated with modern groups. La Venta represents a faunal community with similar levels of ecological diversity as modern platyrrhine communities (Wheeler, 2010). Seven species representing all three platyrrhine families are included in this analysis: the alouattin *Stirtonia tatacoensis*, the cebids *Neosaimiri fieldsi*, *Laventiana annectens, Mohanimico hershkovitzi*, *Patasola magdalenae*, *Aotus dindensis*, and the pitheciid *Cebupithecia sarmientoi.*

Stirtonia, *Neosaimiri*, and *Cebupithecia* have been recognized as being phylogenetically linked with *Alouatta*, *Saimiri*, and the pitheciins, respectively, but the relationships of the other taxa have been a matter of some debate. Kay (1990) has argued that *Mohanimico hershkovitzi* and *Aotus dindensis* are conspecific while Rosenberger *et al.* (1990) have advocated for their separate generic status and a different classification. They suggested that *Mohanimico* may be a callitrichine and *Aotus dindensis* a pitheciid, but most importantly they hold that *Aotus dindensis* is a representative of the modern genus. Here, the inclusion of *A. dindensis* within the modern genus is accepted, but *Aotus* is classified in the Family Cebidae following the genetic evidence (Schneider *et al.*, 2001; Opazo *et al.*, 2006; Herke *et al.*, 2007; Wildman *et al.*, 2009). *Laventiana* was originally described as a primitive cebid possibly located at the point of divergence between the calltrichines and the cebines (Rosenberger *et al.*, 1991b). There is general agreement on the placement of *Laventiana* within Cebidae, but some have advocated its inclusion either within *Neosaimiri fieldsi* (Takai, 1994) or as a separate *Neosaimiri* species (Kay and Meldrum, 1997).

Within the analyses conducted here, several interesting dietary trends emerge. First, *Stirtonia* is morphologically similar to modern *Alouatta*, so much so that an ancestor-descendent relationship has been argued as a possibility for the two forms (Delson and Rosenberger, 1984), but it displays a less extreme version of the alouattin dentition. Along PC 1, *Stirtonia* falls outside of the range of *Alouatta*, but does group with it along PC 2 and PC 3. This is largely as a result of the relative positions of the cusps on the crown surface, particularly the hypoconid, the degree of waisting at the CEJ, and the location of maximum curvature on the tooth sidewall. In the DFA including only PC 1 scores or PC 1 scores and centroid size, *Stirtonia* was classified with the frugivores, a result that mirrors previous analyses on the shearing crest lengths of this species (Kay *et al.*, 1987; Fleagle *et al.*, 1997). Interestingly, in the DFA of the GPA aligned landmarks, *Stirtonia* was classified with the folivore/frugivores. These mixed results seem to indicate that *Stirtonia* had evolved the cusp placement and overall dental shape of the alouattins – as captured by the complete landmark set – but did not possess the extreme degree of dental relief which accounts for variation along PC 1. Arguably, the complete landmark set contains much more phylogenetic information that is not functional than does PC 1, which is perhaps driving this result. On the other hand, there are interspecific differences in feeding within modern genera and we should not expect *Stirtonia* to precisely mirror any modern *Alouatta* in its feeding behavior.

Several extinct La Venta platyrrhines have been classified as having a diet that is at least partially insectivorous. The small-bodied *Patasola magdalenae* falls within the range of the frugivore/insectivore and folivore/frugivore cluster along PC 1 and within the range of *Alouatta* and *Brachyteles* along PC 2 (Fig. 3.02). *Patasola* has been reconstructed as having a body size of around 350-550 grams (Cooke *et al.*, 2011) and is phylogenetically linked with callitrichines (Kay and Meldrum, 1997). Metabolic constraints would have made a predominantly leafy diet unlikely at that size, and an at least partially insectivorous diet would best explain the morphology. This indicates that the separation along PC 2 between the modern folivorous/frugivorous and frugivorous/insectivorous platyrrhines is likely not a result of a functional adaptation to processing insects. In the DFA, *Patasola* is classified as a folivore/frugivore when only PC 1 scores are employed, but with the addition of centroid size it is falls with the frugivore/insectivores. This result is at odds with another analysis utilizing shearing crests, which suggested *Patasola* had a frugivorous diet (Fleagle *et al.*, 1997). While landmark analyses show *Patasola* has dental relief within the range of the frugivore/insectivore *Saimiri*, these analyses do not incorporate callitrichines. Their addition would include morphological variation not analyzed here and might refine the placement of *Patasola*.

Two other cebines, *Neosaimiri* and *Laventiana*, fall in close proximity to each other in the PCA and within the broad cluster of folivore/frugivores and frugivore/insectivores along PC 1 (Fig. 3.02). They too were classified as frugivore/insectivores in the DFA. Along PC 2, both species fall at the edge or outside of the distribution of modern *Saimiri*, indicating that while there is evidence that *Neosaimiri* and *Laventiana* may have had a similar dietary profile as the modern genus, other morphological differences exist. Along PC 2, *Neosaimiri* and *Laventiana* differ from *Saimiri* in the relative length of the trigonid (shorter in *Saimiri*), and their more mesially positioned hypoconid. In studies of relative shearing crest lengths, *Neosaimiri* and *Laventiana* were found to have somewhat shorter crests than modern *Saimiri* indicating a more mixed diet (Fleagle *et al.*, 1997), a result replicated here.

Aotus dindensis falls within the distribution of modern *Aotus* in plots of the first three principal components, though it also falls within the range of *Lagothrix* in several analysis – highlighting some of the morphological similarities of molar form between the two frugivorous species if size is discarded. While there are other extinct platyrrhines which also fall in the range of *Aotus* along some axes (notably *Mohanimico*), none is as consistent in its grouping with extant *Aotus*. *Aotus*-like morphology has been argued to be present at a very early date in the fossil record based on cranial (Fleagle and Rosenberger, 1983) and cranio-dental (Setoguchi and Rosenberger, 1987; Takai, 2009) fossil material. It seems that fully *Aotus*-like molar morphology was present by the mid-Miocene. In all DFA, *Aotus dindensis* is classified as a frugivore, and may have had a similar ecological niche as modern *Aotus* based on these analyses as well as research on a facial fragment and tali (Setoguchi and Rosenberger, 1987; Gebo *et al.,* 1990). *Mohanimico*, which exhibits similar molar morphology to *Aotus dindensis*, falls within this range as well and is consistently classified as a frugivore.

The pitheciine *Cebupithecia sarmientoi* has dental morphology that compares favorably with the modern pitheciins including molars with low relief and canines showing a triangular cross sectional outline. It does maintain some primitive characteristics including smooth enamel (Fleagle *et al.*, 1997) and smaller unmolarized premolars. Previous analyses have hypothesized a diet of fruit with the potential for some seed predation (Fleagle *et al.*, 1997). These analyses support that conclusion. *Cebupithecia* falls within the range of *Callicebus* along PC 1. Within the DFA, *Cebupithecia* groups with the frugivores and not *Pithecia*, though two of the pitheciin genera, *Chiropotes*, and *Cacajao,* were not included. It should be noted that a *Cebupithecia* M_1 was used. While pitheciin M_1s and M_2s are morphologically quite similar some differences exist – particularly greater differentiation between the trigonid and talonid and a somewhat more closely spaced metaconid and protoconid. The possibility that these results may be driven by the subtle differences in M_1 and M_2 morphology should be considered.

The La Venta platyrrhines included in this analysis exhibit a much larger range of dietary profiles than do the Patagonian forms (Fig. 3.06), indicating more dietary differentiation and an increase in available ecological niches. Overall, the variation observed in the La Venta sample mirrors the extant sample, but the La Venta primates do not show the extremes of dental relief (very low and very high), though that certainly could be due to sampling error. Paleoecological studies have reconstructed La Venta as a riparian mosaic with significant forest cover (Kay and Madden, 1997a, b) that may have followed meandering rivers (Guerrero, 1997; Kay and Madden, 1997a, b). The region received a significant amount of rain (1500-2000 mm per year), but much less than the amount received by the closed canopy forests of modern Amazonia (Kay and Madden, 1997a, b). It would have been broadly similar to the western Amazonian lowlands of today and the primates had a similar ecological diversity (Wheeler, 2010).

Very little fossil evidence for the platyrrhines exists between the middle Miocene forms from La Venta and the Pleistocene and Holocene subfossils from Brazil and the Caribbean. Two species, a cebid, *Acrecebus fraileyi,* and an atelid, *Solimoea acrensis*, have been described from the Huyaquerian (9-6.8 Ma) of Brazil (Kay and Cozzuol, 2006), but these are not included here.

In the 1990s, two large-bodied Pleistocene platyrrhines were recovered from the Brazilian cave site Toca da Boa Vista in Bahia, *Caipora bambuiorum* and *Protopithecus brasiliensis*. *Caipora* bore a striking resemblance to *Ateles*, despite being nearly twice its size. The second primate, *Protopithecus,* resembled *Alouatta* in cranial, though not dental morphology and was also very large-bodied, leading researchers to suggest that these two primates represented Pleistocene megafauna (Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996; Cooke *et al.*, 2007). The *Protopithecus* skull has no preserved lower molars so it was not included in this study. *Caipora*, however, has a well-preserved dentition and in analyses it falls well within the *Ateles* distribution along PC 1 and PC 2 and clusters with the frugivores in all DFAs. It has the low dental relief, wide basins, and low crowns that are the hallmark of frugivorous forms. Except for its much larger size, the molars of *Caipora* fit comfortably within the variation of *Ateles*. Based on the molar morphology, this platyrrhine exploited a similar feeding niche to the modern frugivorous atelines, indicating that the large body size radiation of atelid primates that exists today also once included large-bodied forms that survived well into the Plesitocene.

Dietary prediction in the extinct Caribbean platyrrhines

The final group of platyrrhines includes the subfossil forms from the Greater Antillean islands Jamaica, Hispaniola, and Cuba. These five species, *Xenothrix mcgregori*, *Antillothrix bernensis*, *Insulacebus toussaintiana*, and *Paralouatta varonai* and *P. marianae* (the latter represented by a single talus) have been considered to be a monophyletic group most closely related to modern *Callicebus* (MacPhee *et al.*, 1995; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004), members of different extant clades (Rosenberger, 1977; Rímoli, 1977; Ford, 1990; Rivero and Arredondo, 1991; Rosenberger, 2002; Rosenberger *et al.*, 2011; Cooke *et al.*, 2011), or most recently, Kay *et al.* (2011) have hypothesized that *Antillothrix* might be a stem platyrrhine. Overall, these primates are marked by unique dental morphologies that more closely resemble the Miocene Patagonian forms than the modern mainland radiation (Rosenberger *et al.*, 2010; Cooke *et al.*, 2011). Nearly all of the Greater Antillean material is Pleistocene or Holocene in age, but it is likely that these primates entered the Caribbean during the Miocene or perhaps before (Rosenberger, 1978; MacPhee *et al.*, 1995; Iturralde-Vinent and MacPhee, 1999). The earliest evidence of endemic Greater Antillean platyrrhines comes from Cuban Miocene deposits dating to 17.5-18.5 Ma, in which the type specimen for *P. marianae* was found (MacPhee *et al.*, 2003).

The endemic Cuban primate, *Paralouatta varonai*, a hypothesized alouattin (Rivero and Arredondo, 1991; Rosenberger *et al.*, 2009, but see MacPhee *et al.*, 1995 and Horovitz and MacPhee, 1999 for an alternate view), is dentally distinctive from the other alouattins in some aspects of its morphology. The species falls within the range of *Alouatta* and *Brachyteles* along PC 1 and PC 2. Since this analysis only considers lower molar morphology, it is worth noting that the maxillary molars of *Paralouatta* are morphologically quite distinct from *Alouatta* and have a prominent cingulum from which the hypocone arises (Fig. 3.07). Cranially, it has the long, low, small-brained airorhynchous skull of the other alouattins (Rivero and Arredondo, 1991).

Dietarily, *Paralouatta* is classified with the frugivorous primates except in the DFA of the landmark set where it fell with the folivorous/frugivorous forms. While the overall shape outlined by this landmark set resembles the modern folivorous/frugivorous primates, the M_2 is far more bunodont than in *Alouatta* or *Brachyteles*. *Paralouatta* likely represents an early branch of the alouattin lineage prior to the evolution of committed folivorous/frugivorous habits. Additional evidence for frugivorous or partially frugivorous alouttins exists in the Brazilian *Protopithecus* (not included in this analysis), which has the characteristic cranial morphology of the alouattins, but like *Paralouatta* does not exhibit a lower anterior dentition adapted to a folivorous/frugivorous diet (Cooke *et al.*, 2007; Rosenberger *et al.*, in press). While the possibility of adaptation to a unique island environment and re-evolution of bunodonty from a more-alouattin like ancestor theoretically exists, given the other primitive aspects of the *Paralouatta* dentition it seems very unlikely.

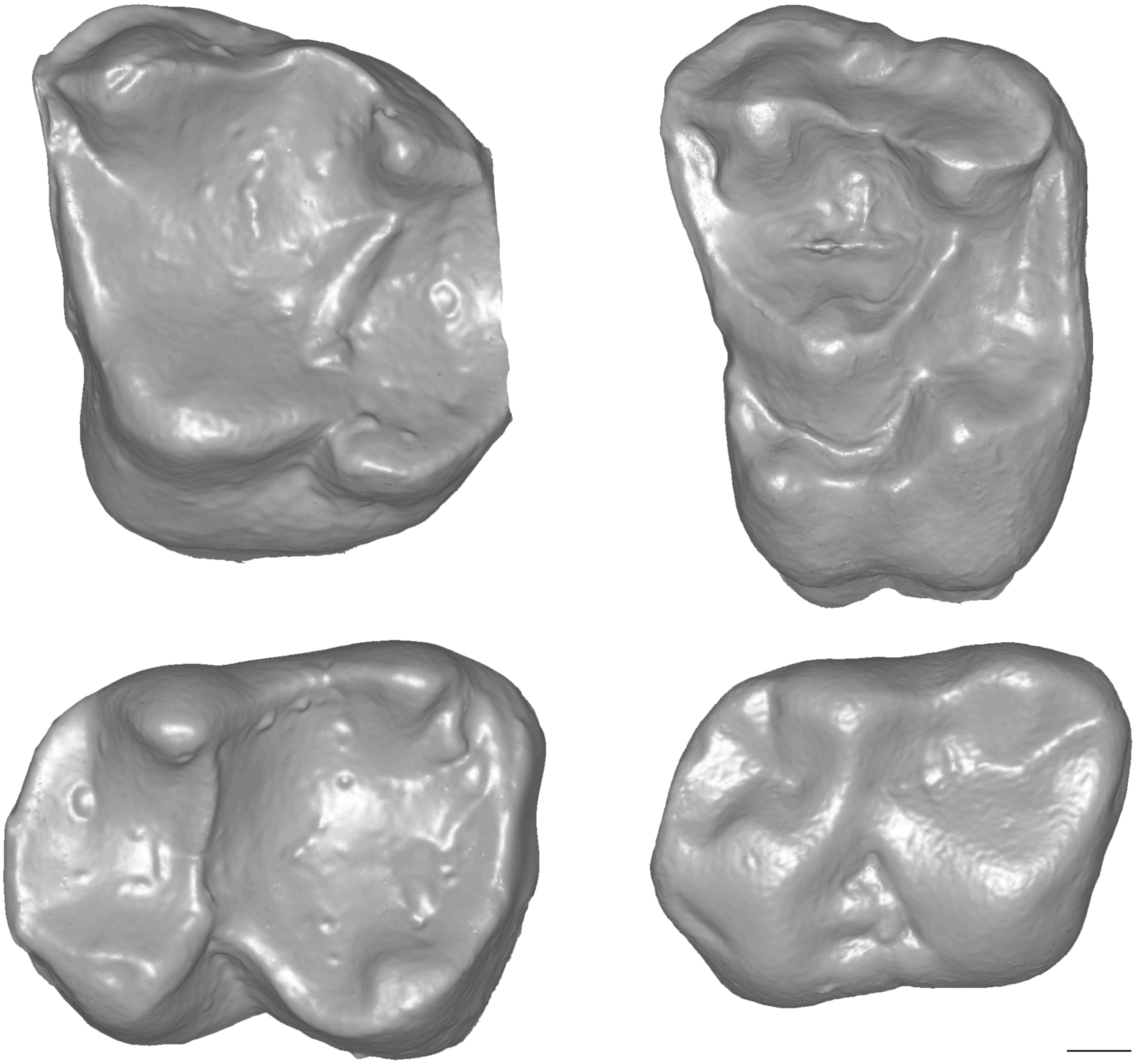


Figure 3.07. Maxillary (above) and mandibular (below) left second molars of *Alouatta seniculus* (left) and *Paralouatta varonai* (right). Scale bar indicates 1 mm. Mesial is to the left.

The two Hispaniolan taxa, *Antillothrix* and *Insulacebus*, bear a close morphological resemblance to each other. *Insulacebus* is considered a pitheciid (Cooke *et al.*, 2011), and new fossil evidence is causing a re-evaluation of the phylogenetic placement of *Antillothrix*. Like the Patagonian platyrrhines, these species exhibit a distinct flaring ectoloph, elevated trigonids, and a moderate degree of dental relief. *Insulacebus* has the bucco-lingually compressed mesial cusps present in several Patagonian forms (Cooke *et al.*, 2011). *Insulacebus* and *Antillothrix* differ from the Patagonian primates in size; they are both much larger, estimated to be around 4000 grams (Rosenberger *et al.*, 2011; Cooke *et al.*, 2011). Along PC 1 and PC 2, both *Insulacebus* and *Antillothrix* fall broadly within the range of *Callicebus* and both are classified as frugivores in the DFA.

The Jamaican platyrrhine *Xenothrix* has been variously linked with *Callicebus* (Rosenberger, 1977; MacPhee and Horovitz, 2004) and *Aotus* (Rosenberger, 2002), but demonstrates a unique morphology unknown elsewhere in the platyrrhine radiation. It lacks a third molar, but analyses have shown that it likely lost this tooth independently of the callitrichine primates (Rosenberger, 1977). Additionally, it is fairly large-bodied – around 5000-6000 g (MacPhee and Meldrum, 2006; Cooke *et al.*, 2011). It has closely approximated cusps, a high degree of buccal flare, a low point of maximum curvature on the tooth sidewall, and a relatively long trigonid. Its molars are somewhat polycuspate. While additional analyses including other two-molared forms might be warranted, it seems most likely that *Xenothrix* occupied an ecological niche unique to its island habitat. In the DFA, it is variously reconstructed as a frugivore or frugivore/omnivore – a reflection of its low dental relief – but the possibility that it exploited resources untapped by the comparative sample is certainly worth considering. Additional evidence for this may be found in its unusual postcranial adaptations (Fleagle and MacPhee, 1982; MacPhee and Meldrum, 2006). Isotopic studies of this form might be particularly enlightening as they could potentially provide a different line of evidence for its dietary profile.

Little is known of the paleoecology of the Caribbean prior to the Pleistocene when primates entered the region and became isolated from the mainland radiation of platyrrhines. Today, the Greater Antilles show a remarkable degree of ecological diversity. Hispaniola alone has rainforest, dry lowlands dominated by cacti and scrub, montane cloud forest, and high mountain pine forest. While it is unknown if this ecological diversity existed in the past, faunal distributions on Hispaniola do indicate some areas were highly endemic (Cooke *et al.*, 2011).

To date, we do not have more than one species of primate from any one site or larger ecological region on any of the Greater Antillean islands. Two species of primate are known from different regions on Cuba and Hispaniola, and the two primate skulls (Rosenberger *et al.*, 2011; Kay *et al.*, 2011) from the southeastern Dominican Republic have yet to be compared with each other to confirm that they are conspecifics. Thus far, in the Caribbean, we do not have evidence of a "primate community" in the sense that we do in La Venta or even (to a lesser extent) Patagonia. It remains to be seen whether or not the Greater Antillean islands will each harbor a community of primates jointly sharing habitats as with the continental fauna, or if the monkeys will be organized as narrowly adapted individual species living in separate ecological zones.

CONCLUSIONS

Landmark-based 3DGM is successful in differentiating extant platyrrhines with different dietary profiles, and can be employed as one of the methodologies used in reconstructing paleodiet in extinct forms. In discriminant function analyses, PC 1 scores combined with centroid size can differentiate primates with different dietary profiles and can be used to reconstruct hypothetical diets of extinct platyrrhine primates. Without centroid size less definition between folivores/frugivores and frugivore/insectivores is obtained, as studies of shearing crest length have also concluded. The predominantly frugivorous, but somewhat eclectic feeders, *Aotus* and *Callicebus*, bridge the gap between the frugivorous/insectivorous and folivorous/frugivorous forms and the committed frugivores (*Ateles* and *Lagothrix*), frugivore/seed predators (*Pithecia*) and frugivore/omnivores (*Cebus*).

The extinct forms of Miocene Patagonia cluster close to the distribution of *Aotus* and *Callicebus* – two platyrrhines who, while predominantly frugivorous, do exploit other food sources seasonally. This feeding niche would have been compatible with the paleoecological reconstructions from this region. In such marginal environments, maintenance of some degree of shearing ability would be advantageous in order to allow dietary flexibility in medium-sized platyrrhines. However, one form, *Proteropithecia neuquenensis*, not analyzed here, may have occupied a more specialized dietary niche. In the more humid tropical environment of La Venta, Colombia where there was a wider array of dietary niches available, the fossil platyrrhines show a greater range of dental morphology from frugivore/insectivores to primates who may have been exploiting fruit and hard seeds. The dental morphologies of the primates of La Venta more closely resemble the variation seen in the Amazonian platyrrhine communities of today than do either of the other two regions explored in this analysis. The Greater Antilles harbored a unique fauna, which more closely matched the morphologies seen in the Patagonian forms than the continental forms from La Venta or the modern period. All the Caribbean forms, but *Xenothrix*, maintained a modern degree of dental relief also falling within the range of *Aotus* or *Callicebus*. While paleoecological information on this region is scant, like the primates of Patagonia the Caribbean forms likely inhabited marginal niches where dietary flexibility was essential.

CHAPTER 4

MEASURES OF DENTAL RELIEF ON PLATYRRHINE LOWER SECOND MOLARS

INTRODUCTION

The three-dimensional modeling of teeth for the purposes of surface analysis and data collection initially began with the use of stereogrammetry to collect three-dimensional points (*e.g.,* Savara, 1965; Teaford, 1982; Hartman, 1989). Later, reflex microscopy was employed (Reed, 1997). Since that time, surfaces have been modeled using electromagnetic digitizers (Zuccotti *et al.*, 1998), confocal microscopy (Jernvall and Selanne, 1999), and most recently laser scanning (Ungar and Williamson, 2000; Ungar and M'Kirera, 2003; M'Kirera and Ungar, 2003 *et seq.*; King *et al.*, 2004; Singleton *et al.*, 2010) and CT scanning (Evans *et al.*, 2007; Boyer, 2008; Evans and Jernvall, 2009; Boyer *et al.*, 2010; Bunn *et al.*, 2011; Boyer *et al.*, 2011). CT scan and laser scan data appear to be broadly equivalent, but there can be differences between measures taken depending on the types of scanners used and settings employed (Boyer *et al.*, 2011). While some analyses of dentition have incorporated three-dimensional geometric morphometrics (see Chapter 3 for further discussion), the majority of work has been on functional measures on the overall shape of the crown independent of landmark data. All are less reliant on homologous structures for taking measures, such that animals with radically different morphology (*e.g.*, carnivorans and rodents – see Evans, 2007) can be compared. Less reliance on homologous structures has been argued to be advantageous when analyzing long extinct groups, which may not have morphologies similar to living forms.

Peter Ungar and colleagues, who primarily employed GIS software in their analyses of primate dentition, pioneered much of this work. Using measures of slope and angularity, they found taxon specific trends that they have proposed correlate with dietary differences in chimpanzees and gorillas (Ungar and M'Kirera, 2003). M'Kirera and Ungar (2003) expanded on this work by introducing a measure of occlusal relief, which the authors suggested was a three-dimensional version of Kay's (1978, 1984) shearing quotient (SQ). To calculate occlusal relief, a tooth was oriented in the occlusal plane and cropped below the lowest z value in the talonid basin and a three dimensional surface area was taken. The surface area was then divided by the two dimensional area of the outline of the tooth projected onto a plane. Since SQ is based on lengths of shearing crests along the edges of cusps relative to the mesiodistal length of a tooth, M'Kirera and Ungar (2003) argued that their measure of occlusal relief was essentially a 3D version of SQ. They proposed that dental topographic analysis had advantages over measures of shearing crests because it could continue to be used even after a tooth was worn, while SQ was more limited in its application since measurements are reliant on the researcher's ability to identify cusp tips. In additional studies, dental relief was used to examine the effects of wear on the molars of different groups of *Alouatta* inhabiting dissimilar environments (Dennis *et al.*, 2004), and it was employed in studies of hominin molars (Ungar, 2004). In the latter study, Ungar used measures of slope and relief to reconstruct the different dietary profiles of *Australopithecus afarensis* and early *Homo*. These methods were also used by Ulhaas *et al.* (2004) to examine relief differences in colobine and cercopithecine dentitions, and they found relief differences were maintained throughout different wear stages.

Measures of relief have also been employed by Boyer (2008) on a group of early primates and euarchontan mammals. Boyer measured dental relief slightly differently than did M'Kirera and Ungar (2003) and cropped the molar at the cemento-enemal junction (CEJ), as some of the taxa included in the study had extremely deep or shallow basins. Boyer suggested that Relief Index (RFI) was better at predicting diet than SQ in fossil taxa and was not as subject to differences in phylogeny. This assertion was illustrated with the example of *Lepilemur*, a highly folivorous primate, which consistently fell with more frugivorous species in measurement of SQ, but was successfully classified as a folivore using RFI. Boyer also suggests that this measure could differentiate insectivorous and folivorous primates, but cautioned that his results might be a function of sample size and noted that body size or a proxy of body size greatly increased the efficacy of classification.

Two additional measures of three-dimensional molar morphology have been developed since the introduction of relief indices by M'Kirera and Ungar (2003): Orientation patch count (Evans *et al.*, 2007) and Dirichlet energy (Bunn *et al.*, 2011). Orientation patch count (OPC) (Evans *et al.*, 2007) measures surface complexity. The methodology involves treating the crown surface as a spatial map having cardinal directions. Groups of grid points with the same direction are gathered into patches and these patches are counted. The greater the number of patches the greater the complexity of the tooth surface. Evans *et al.* (2007) developed this method and tested it using a sample of carnivoran and rodent tooth rows and found similar levels of complexity in animals with similar dietary profiles. This measure has also been tested using individual teeth of rodents and carnviroans. (Evans and Jernvall, 2009). OPC appears to be less successful at differentiating primates of different dietary guilds in a sample of strepsirhines and tupaiids, however (Bunn *et al.*, 2011).

Most recently, Dirichlet normal energy (DNE) has been put forth as a potentially useful method for dietary differentiation and classification in primates (Bunn *et al.*, 2011). DNE measures the deviation of a surface from a plane with areas expressing more elevation and steepness of slope having different values than lower areas of the tooth crown. Bunn *et al.* (2011) used a sample of strepsirhine primates and *Tupaia* and found that DNE did successfully differentiate primates by dietary category. DNE was most successful at differentiating insectivores from frugivores. Bunn *et al.* also compared the efficacy of DNE to other 2D and 3D measures of relief and shear, and conducted several combined analyses. The use of more than one methodology in a DFA of primate diet showed much higher rates of correct classification than did the use of just one method. Indeed, RFI and DNE alone each returned a successful classification rate of 66.4% and 59.4% respectively, marginally better than chance, but not a very high success rate. In combined analyses, the performance improved with the highest success rate of classification (83.8%) achieved in an analysis that incorporated SQ, RFI, DNE, OPC, and shearing ratios.

Thus far, functionally designed measures of dental relief have almost exclusively been employed in the study of strepsirhines and catarrhines. This chapter seeks to expand the use of measures of dental relief to platyrrhine primates. In the analyses that follow, a variety of metrics will be evaluated for their abilities to differentiate platyrrhines of different dietary profiles. The work is guided by four research questions:

1. Are 3D measures of dental relief successful in differentiating platyrrhines of different dietary profiles?
2. Do these measures of relief correlate with tooth crown morphology as captured by three-dimensional analyses of shape?
3. How do measures of relief perform in comparison to PC 1 scores as an indicator of diet?
4. Can these measures be used to accurately assess the hypothetical diet of extinct platyrrhine primates?

MATERIALS AND METHODS

Sample and specimen preparation

The sample was drawn from 208 extant platyrrhine mandibular tooth rows (Table 3.02), and 22 extinct platyrrhine tooth rows or isolated M_2s (Table 3.03). These taxa were chosen to represent a variety of dietary profiles (table 3.01) and taxonomic groups. Specimens were molded, cast, and then laser scan models were generated following the protocols previously outlined (Chapter 3). Post-processing of the models was completed in Geomagic Studio 11 (Geomagic, Inc.)

Measurements and indices

A variety of surface area measurements were taken on the 3D models of platyrrhine M_2s. All measurements and trimming procedures were completed in Geomagic Studio 11 (Geomagic, Inc.) unless otherwise noted. The measurements included:

1. Total crown surface area – 3D (TSA) (Boyer, 2008): the 3D model of the tooth was trimmed along the CEJ so that only the enamel cap was included (Fig. 4.01). In virtually all scans the boundary between the enamel and the tooth root was readily visible. Error tests indicate a less than 2% error in collecting this measurement (Appendix A).
2. Visible Surface Area – 3D (VSA): For this measure, only the surface area of the crown that was visible from above when the tooth was oriented in occlusal position was selected. This eliminated duplicate z values. This measure is broadly similar to M'Kirera and Ungar's (2003) methodology, which involved using the lowest z values in the talonid basin as the cut off point for the measurement.
3. Projected Surface Area – 2D (PSA) (M'Kirera and Ungar, 2003; Boyer, 2008): The tooth was oriented in occlusal view and the outline was projected onto a 2D surface with a scale grid in

place. The area of this outline was then taken in ImageJ (NIH) after setting the scale against the grid (Fig. 4.02).

From these measures, indices and quotients of relief were calculated. One of the measures has been previously published (RFI, Boyer, 2008).

1. Relief Index (RFI) (Boyer, 2008): A measure of the overall relief of the tooth crown calculated as $\ln(\sqrt{TSA}/\sqrt{PSA})$.
2. Visible Relief Index (VRFI): An alternate measure of relief including only the visible portion of the tooth when viewing the occlusal surface $\ln(\sqrt{VSA}/\sqrt{PSA})$: This measure is largely similar to M'Kirera and Ungar's (2003) measure of tooth relief.
3. Relief Quotient (RQ): Relief Quotient is derived from the residuals of a frugivore linear regression line based on log VSA plotted against the log centroid size of the tooth model. Centroid size acts as a proxy for body size. The RQ is calculated as [100(observed-expected)/expected]. This is calculated in a similar manner as SQ (Kay, 1980, 1984) (Fig. 4.03).

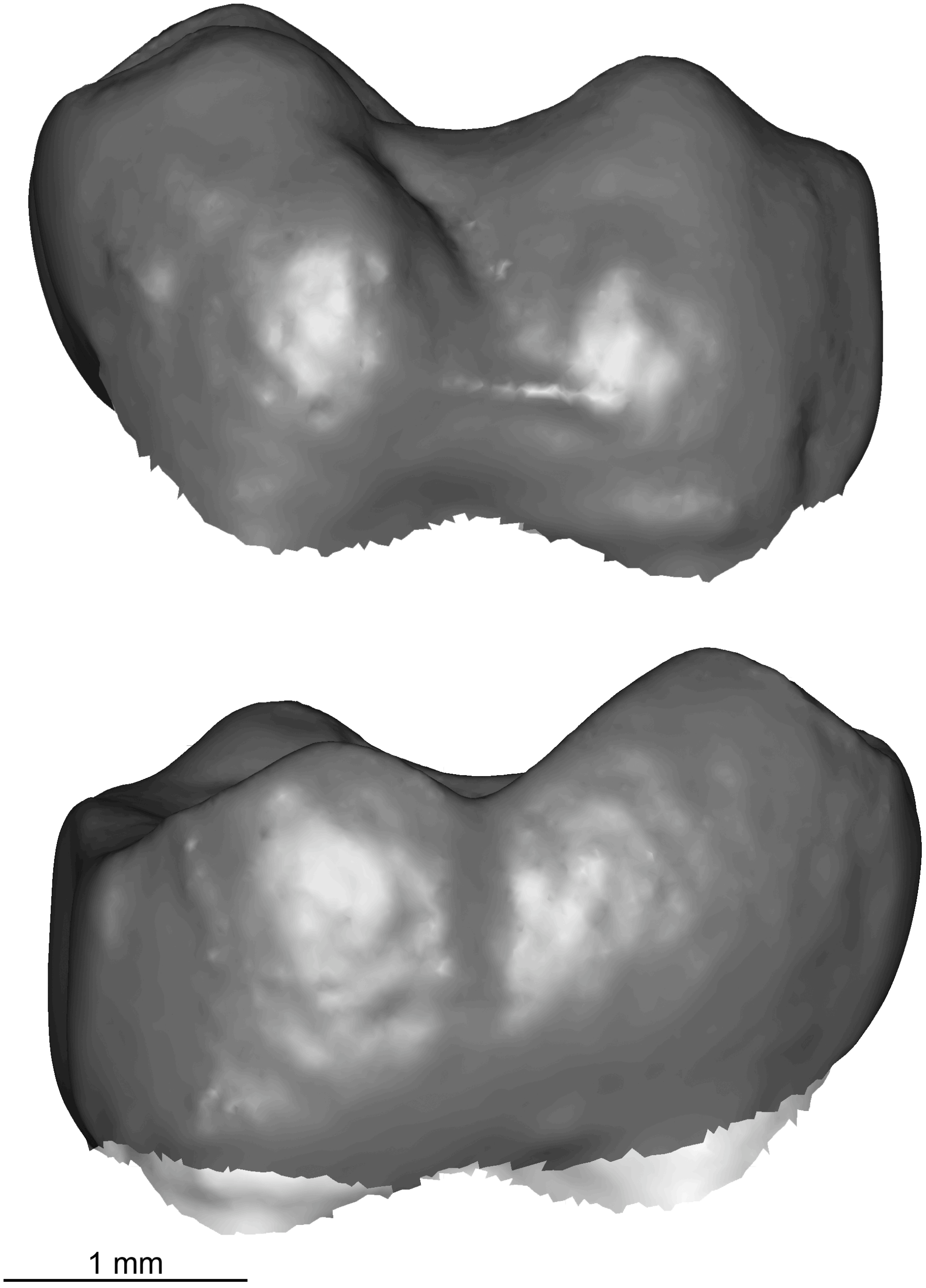


Figure 4.01. Laser scan model of a left M_2 of *Callicebus cupreus* (AMNH 98370) showing trimming along the CEJ from buccal (top) and lingual (bottom) views. Because the models are composed of groups of triangles, the edges of models can appear sharp.

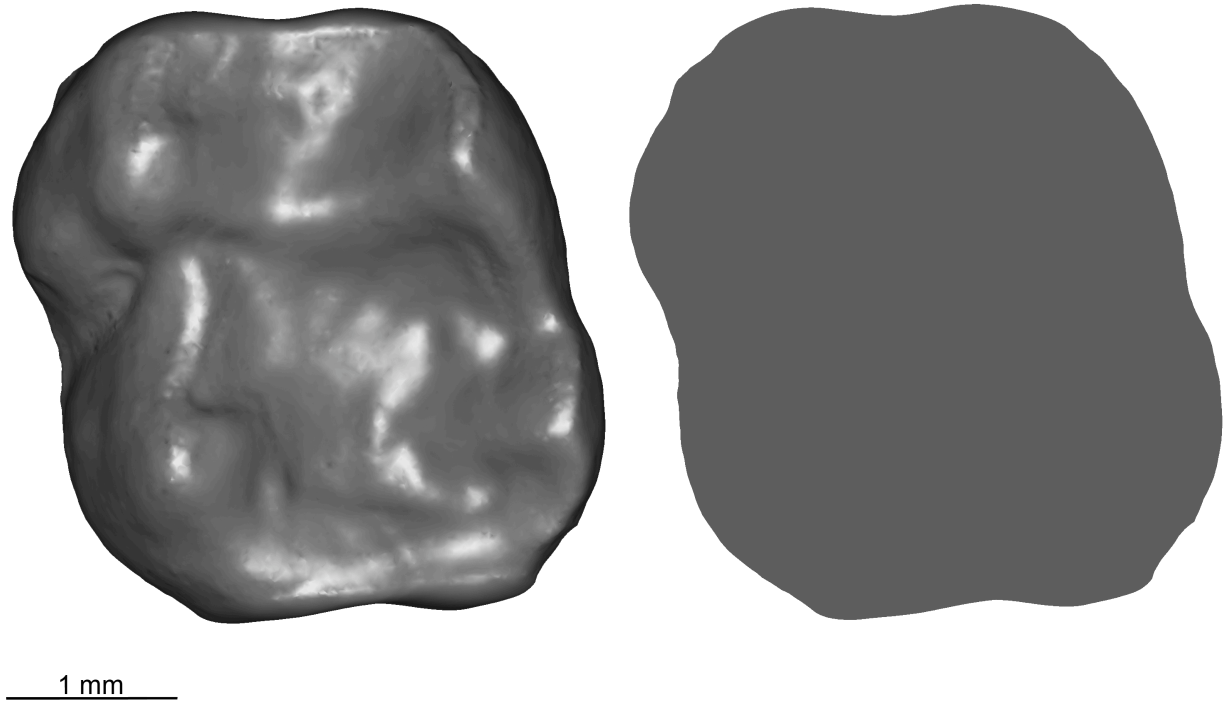


Figure 4.02. Laser scan model of the occlusal surface of left M_2 of *Callicebus cupreus* (AMNH 98370) and an outline (PSA) of the same tooth.

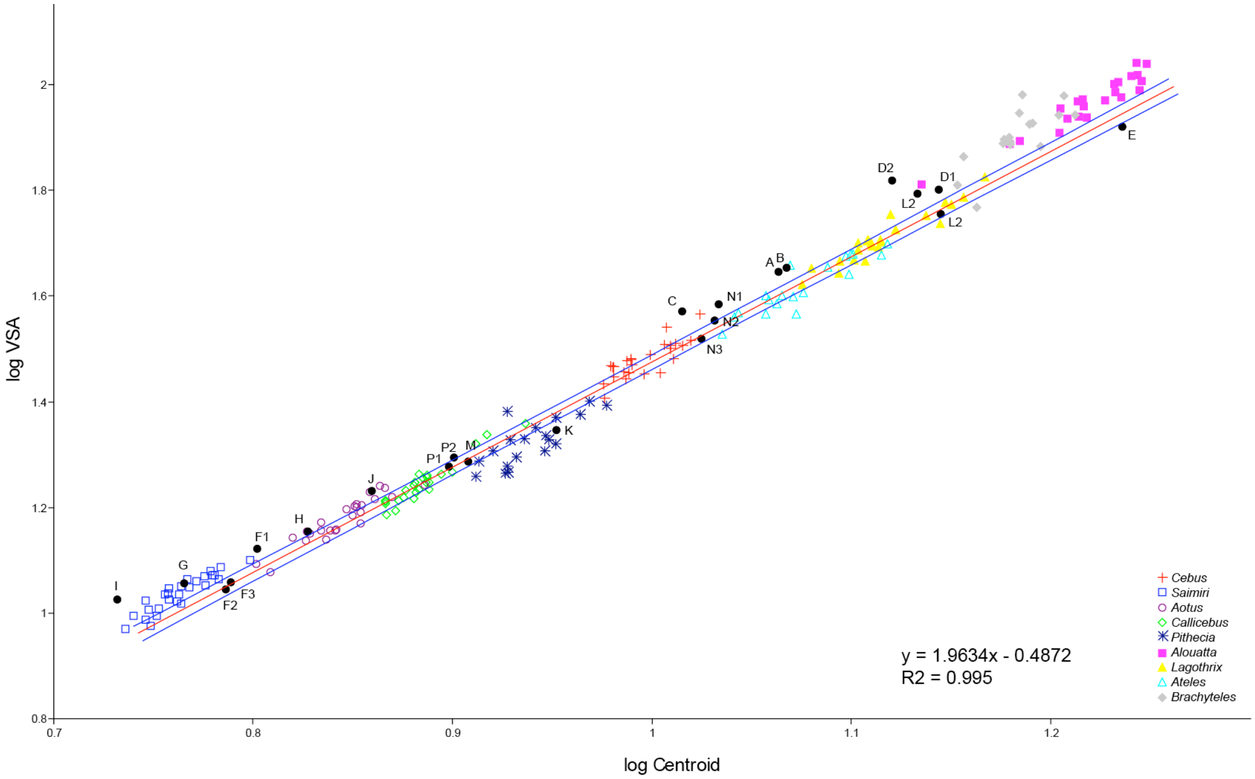


Figure 4.03. Regression of log VSA against log centroid size with 95% confidence intervals. The line was derived from the frugivore VSA values and included *Aotus*, *Callicebus*, *Ateles*, and *Lagothrix*. Fossil taxa are lettered. Note the scale for the x and y axes are different with a 1:4 ratio.

Species		Symbol	Species		Symbol
Antillothrix bernensis	MDH 01	A	*Patasola magdalenae*	IGM 184332	I
Insulacebus toussaintiana	UF 11417	B	*Aotus dindensis*	IGM-KU 8601 (type)	J
Xenothrix mcgregori	AMNHM 148198 (type)	C	*Cebupithecia sarmientoi*	UCMP 38762	K
Paralouatta varonai	MHNH Cueva Alta 1996	D1	*Stirtonia tatacoensis*	IGM-KU 8102	L1
Paralouatta varonai	MNNH V123	D2	*Stirtonia tatacoensis*	IGM-KU 8215	L2
Caipora bambuiorum	IGC-UFMG 05 (type)	E	*Dolichocebus gaimanesis*	MPEF 5146	M
Neosaimiri fieldsi	UCMP 39205 (type)	F1	*Carlocebus carmenensis*	MACN-SC 43	N1
Neosaimiri fieldsi	IGM-KU 89002	F2	*Carlocebus carmenensis*	MACN-SC 250	N2
Neosaimiri fieldsi[1]	IGM-KU 89034	F3	*Carlocebus carmenensis*	MACN-SC 63	N3
Laventiana annectens	IGM-KU 8801a	G	*Soriacebus ameghinorum*	MACN-SC 2 (type)	P1
Mohanimico hershkovitzi	IGM 181500	H	*Soriacebus ameghinorum*	MACN-SC 379	P2

Data acquisition and error testing

For all of the following measures the tooth was first oriented in the occlusal plane. Since, nearly the entire extant sample was taken from complete toothrows, the interstitial regions were missing. These regions were filled using the "fill holes" function of Geomagic Studio 11 (Geomagic, Inc.) using the following settings: hole filling type was "tangent," hole filling method was "fill partial." This resulted in a reasonable approximation of the interstitial area. In order to check for error in this methodology, an individual tooth of *Paralouatta varonai* (MNHNH V123) was artificially cropped so that the interstial region was removed. This area was then filled using Geomagic Studio 11 (Geomagic, Inc.). The true surface area of the tooth was compared with the surface area of the tooth after the cropping and filling procedure was completed. This procedure was repeated on the same specimen on 10 different occasions spaced out over several days. Error rates were found to be less than 1% (Appendix C).

The measure for TSA required the observer to crop the molar along the CEJ. In most specimens this division was readily visible and could be followed easily by the trace tool in Geomagic Studio 11(Geomagic, Inc.). Once the tooth had been cropped, a surface area for the enamel cap was recorded. There was a small amount of error introduced during the cropping procedure, particularly when cropping the interstitial region. To test for the amount of error one molar specimen was cropped 10 times on several different days. Error was found to be less than 2% (Appendix A).

VSA was collected by selecting the visible area of a tooth oriented in the occlusal plane using the "select visible" function in Geomagic Studio 11. The non-selected portion of the tooth was then removed and an area was taken for the remainder. This measure introduced less error than TSA as it is not reliant on the observer's observation of where the CEJ is located. The "select visible" function selected the same area each time it was used.

PSA was collected by removing the lighting of the specimen in Geomagic Studio 11, leaving only the outline of the tooth (Fig. 4.02). An image of this outline was captured using the "snapshot" function of Geomagic Studio 11. The surface area of the tooth outline was measured in ImageJ (NIH).

Statistical treatment

Each index or quotient was initially plotted in standard box and whiskers plot to visualize the distribution of values across different taxa and different dietary groups (Figures 4.04-4.06), and an ANOVA was computed to test for differences between species and dietary categories. Since measures of dental relief have been shown to differentiate primates and euarchontan mammals by diet (M'Kirera and Ungar, 2003; Boyer, 2008; Bunn *et al.*, 2011), discriminant function analysis (DFA) was also employed to examine the efficacy of classifying platyrrhine primates by diet using these measures (see Chapter 3 for additional discussion on discriminant function analysis). If the measure was shown to have a reasonable success rate for living taxa of known dietary profile, it was then used to generate a hypothesized diet for the extant forms.

Additional analyses were performed to examine the correlation between measures of dental relief and 3D molar morphology as captured by 3DGM landmark data. While measures of dental relief have been shown to differentiate primates by diet, a number of conflated aspects of tooth morphology are actually involved. First, there is crown relief, best captured here by VRFI or in previous analyses by M'Kirera and Ungar's occlusal relief (2003). VRFI does not take into account the relative degree of hypsodonty of a tooth, which could significantly add to the estimate of crown area. RFI, on the other hand, includes both crown relief and the overall crown height in one measure; consequently, two important aspects of dental morphology are incorporated into one index. This might obscure a dietary signal. An animal could, for example, have very high crowned teeth with low occlusal relief, or have high occlusal relief with fairly low crown height. These different aspects of molar form may be the result of differences in the selective pressures on primate dentition.

To examine the relationship between these different aspects of dental morphology and measures of relief, multilinear regression analyses were conducted using RFI, VRFI, and RQ as dependent variables regressed against the PC scores 1-4 of the landmark based shape data. The analyses included the first four PCs, as they explained at least 60% of the variation in the principal components analysis. In all cases, PC 5 explained 5% or less of the sample's total variation and separated different taxonomic groups and dietary categories poorly. For this reason, PC scores past this point were not included. RFI was regressed against the PC scores of the complete landmark set, including both the crown and sidewall landmarks, and it was also regressed against reduced landmark sets, including only the molar crown landmarks and only the tooth sidewall landmarks. VRFI and RQ were regressed against a reduced landmark set of the molar crown data (landmarks 1-11), since neither measure incorporated much tooth sidewall data. Correlations were examined between the measures of relief and PC scores for morphological patterns.

RESULTS

Univariate analyses

Since several of the measures of dental relief were employed here for the first time, an ANOVA was computed to test if these measures of relief could differentiate extant platyrrhines of known dietary profiles by species and diet. The results for extant taxa are shown in figures 4.04-4.07, and the fossil taxa are presented in figure 4.07 and table 4.01. An ANOVA of the RFI values indicated that some of the dietary categories did show a significant difference in their means ($p < 0.05$), but several dietary categories could not be differentiated: frugivores and frugivore/omnivores (p=0.09), frugivore and frugivore/insectivore (p=0.27), and folivore/frugivores and frugivore/insectivores (p=0.84). The measure VRFI faired better with all dietary categories statistically significantly different ($p<0.01$) except for frugivores and frugivore/omnivores (p=0.99). For RQ all groups were statistically significantly different ($p<0.001$) except for folivores/frugivores and frugivore/insectivores (p=0.13) and frugivores and frugivore/omnivores (p=0.25).

For RFI, even though there were significant differences in the means between some of the dietary groups, there was substantial overlap in the range of values for these measures between dietary guilds and between taxa. Consequently, the range of RFI values for the folivore/frugivores encompassed a large portion of the range for almost all other groups even after outliers were taken into account (figure 4.05). This is the case for VRFI (Figure 4.06) and RQ (Figure 4.07) as well, though there is a bit more separation for these measures, particularly between the higher relief folivore/frugivore and frugivore/insectivore group and the lower relief other forms.

Species		**RFI**	**VRFI**	**RQ**
Antillothrix bernensis	MDH 01	0.54	0.32	0.03
Insulacebus toussaintiana	UF 11417	0.54	0.32	0.03
Xenothrix mcgregori	AMNHM 148198 (type)	0.47	0.29	0.04
Paralouatta varonai	MNHNH Cueva Alta 1996	0.50	0.34	0.02
P. varonai	MNHNH V123	0.55	0.32	0.06
Caipora bambuiorum	IGC-UFMG 05 (type)	0.55	0.27	-0.01
Neosaimiri fieldsi	UCMP 39205 (type)	0.54	0.33	0.03
N. fieldsi	IGM-KU 89002	0.51	0.32	-0.01
N. fieldsi	IGM-KU 89034	0.54	0.31	0.00
Laventiana annectens	IGM-KU 8801a	0.52	0.32	0.04
Mohanimico hershkovitzi	IGM 181500	0.59	0.29	0.01
Patasola magdalenae	IGM 184332	0.53	0.36	0.08
Aotus dindensis	IGM-KU 8601 (type)	0.51	0.29	0.02
Cebupithecia sarmientoi[1]	UCMP 38762	0.54	0.28	-0.03
Stirtonia tatacoensis[1]	IGM-KU 8102	0.47	0.25	0.00
S. tatacoensis[1]	IGM-KU 8215	0.46	0.29	0.03
Dolichocebus gaimanesis	MPEF 5146	0.48	0.27	-0.01
Carlocebus carmenensis	MACN-SC 43	0.53	0.33	0.03
C. carmenensis	MACN-SC 250	0.47	0.31	0.01
C. carmenensis	MACN-SC 63	0.47	0.25	-0.01
Soriacebus ameghinorum	MACN-SC 2 (type)	0.54	0.31	0.00
S. ameghinorum	MACN-SC 379	0.48	0.31	0.01

Table 4.01. Measures of dental relief in selected fossil platyrrhines.

[1] m1

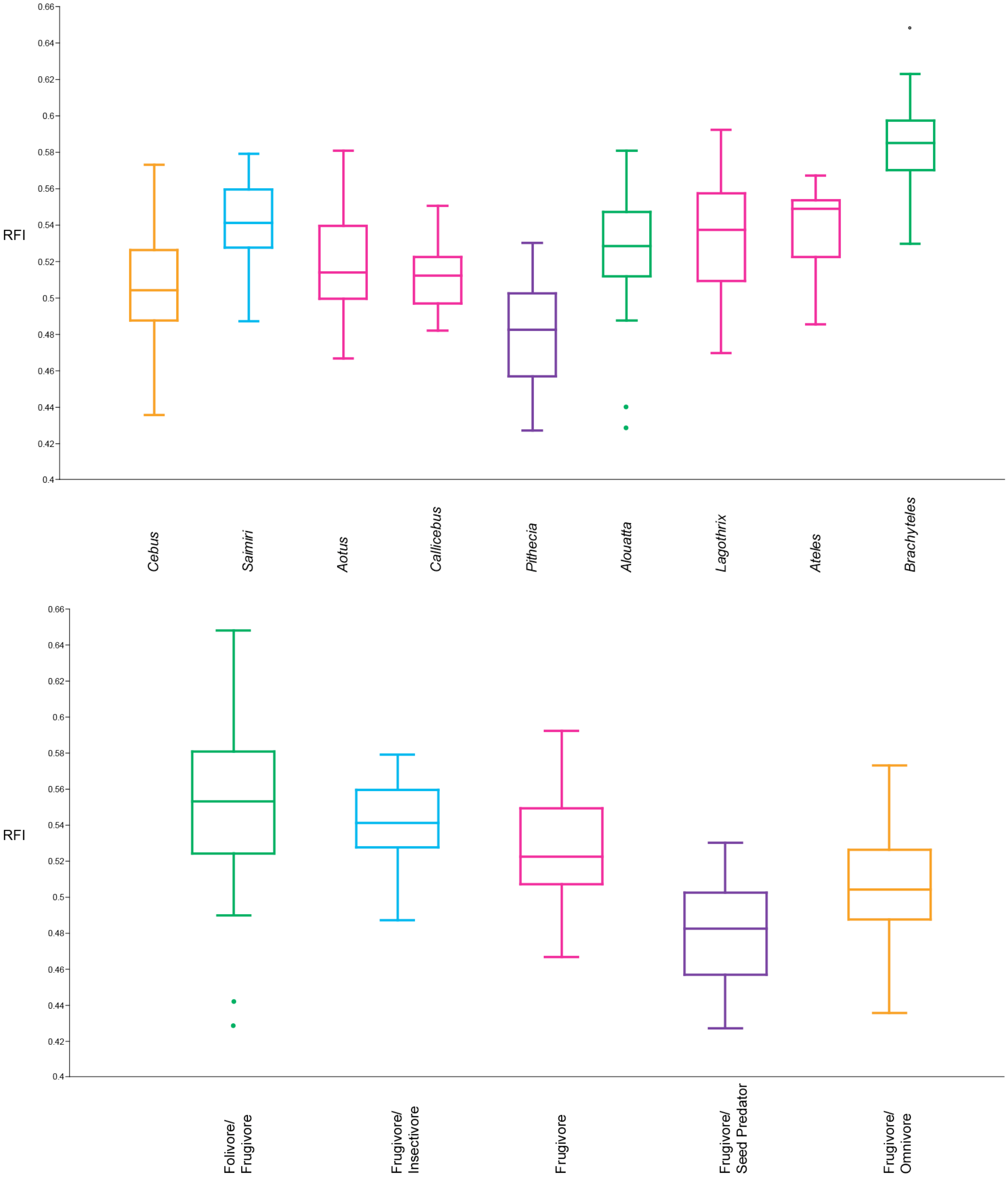
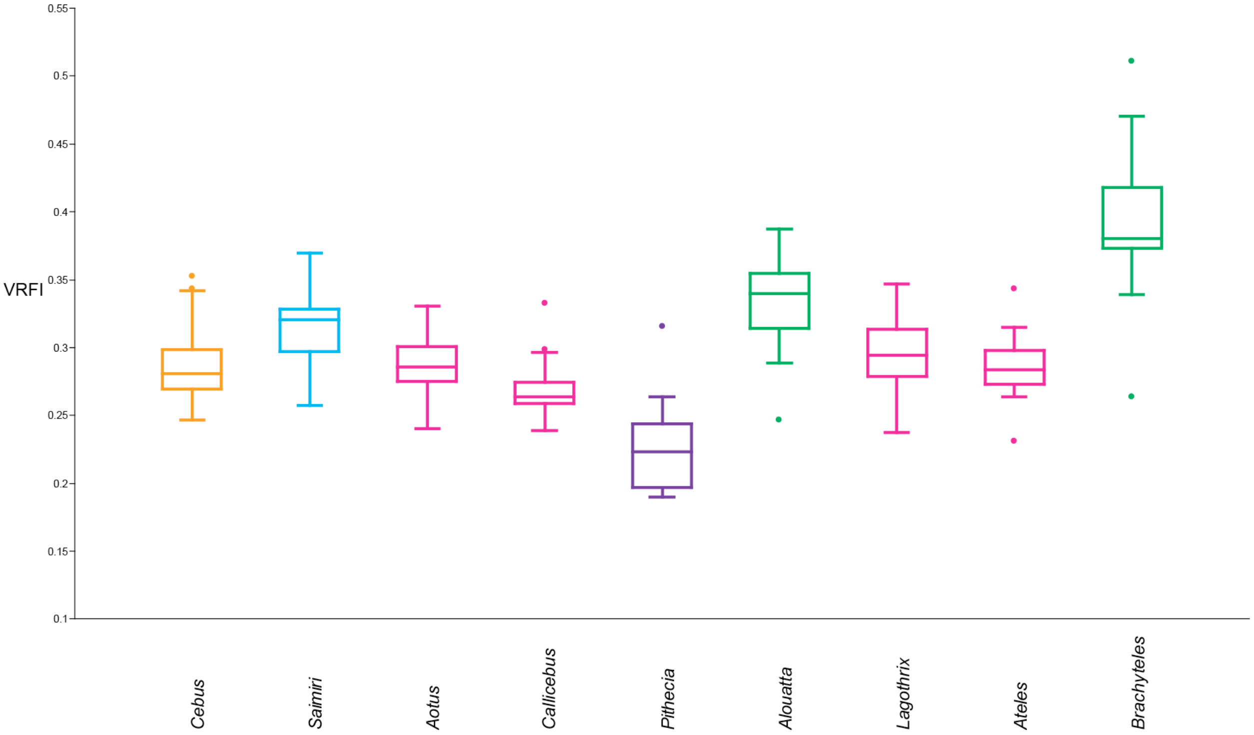


Figure 4.04. RFI distribution across taxa (top) and by dietary category (bottom). Diets are coded by color and outliers are shown as dots.



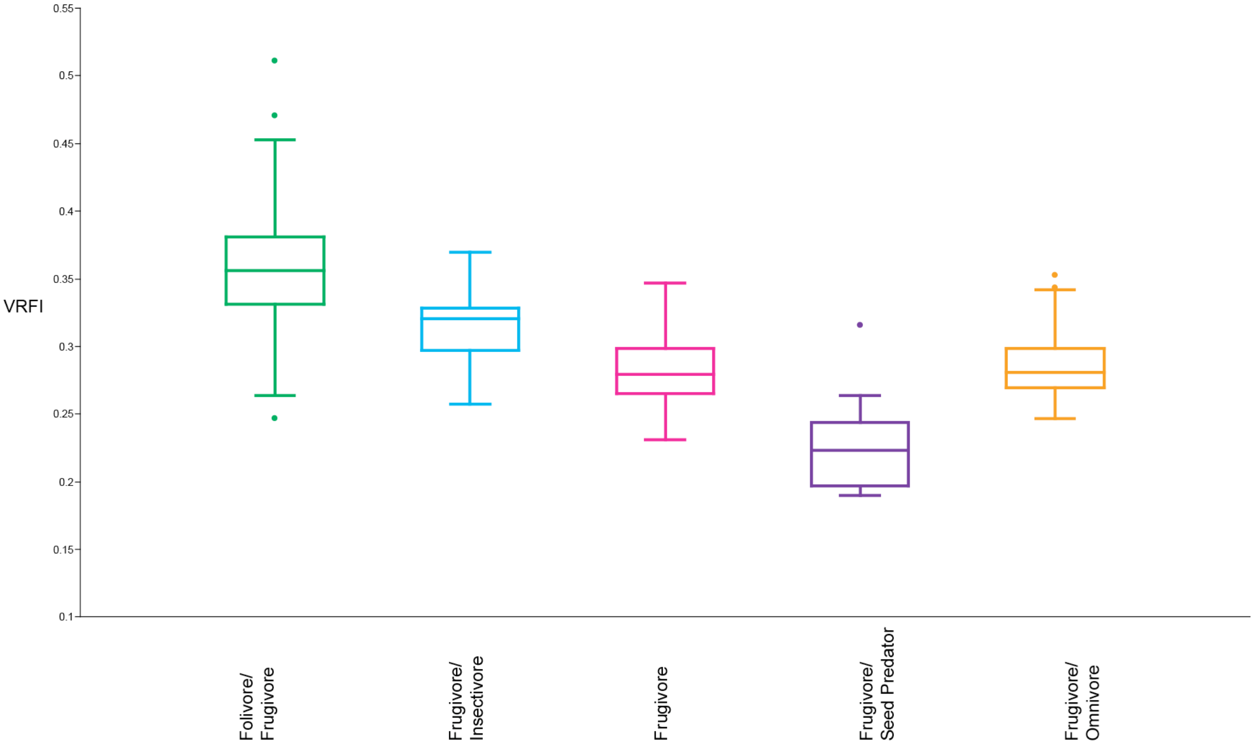


Figure 4.05. VRFI distribution across taxa (top) and by dietary category (bottom).

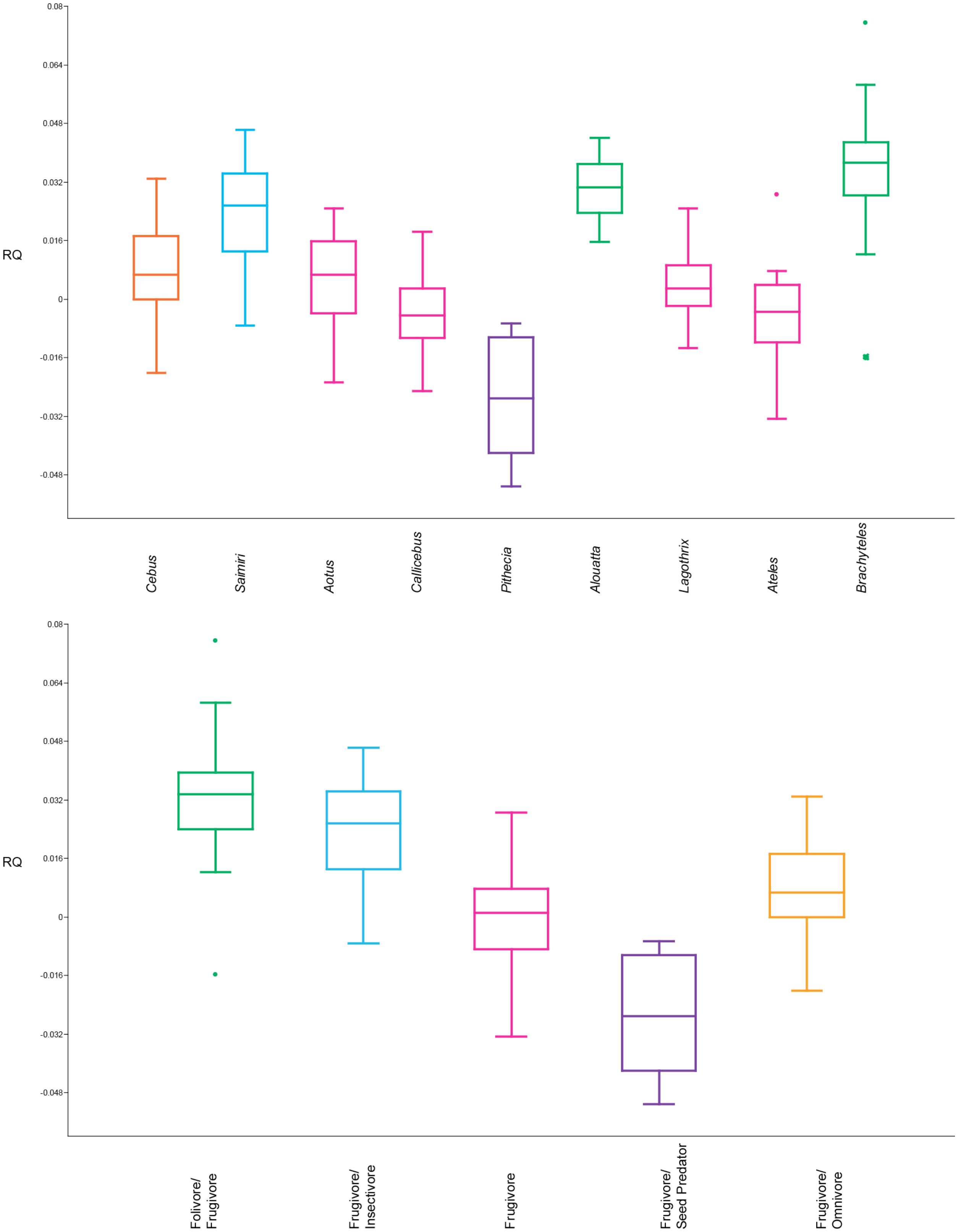


Figure 4.06. RQ distribution across taxa (top) and by dietary category (bottom).

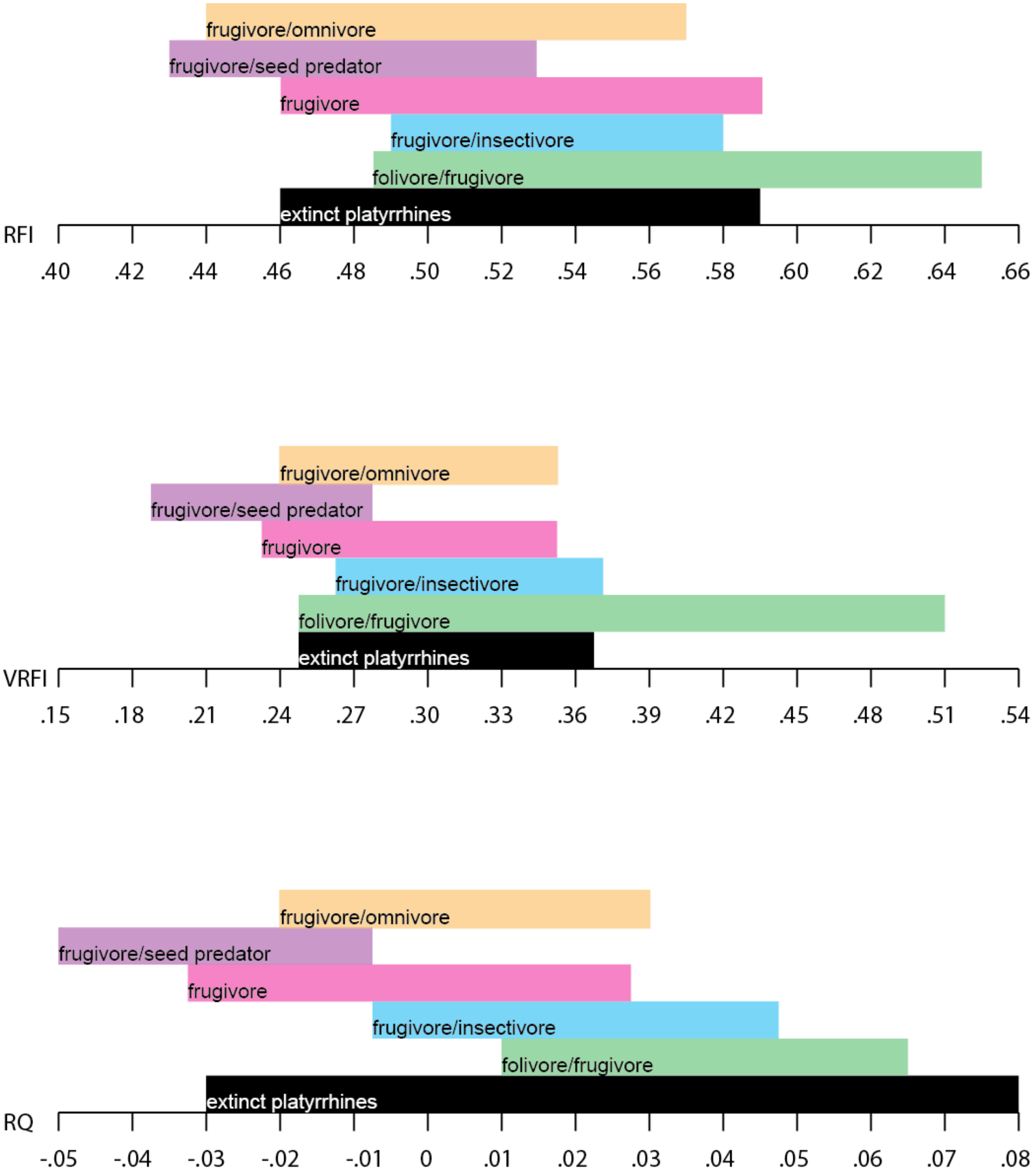


Figure 4.07. Comparative distributions of measures of relief including fossil taxa. Outliers have been removed. Compare with table 4.01.

Discriminant function analyses

To test the efficacy of using measures of relief for separating primates of different dietary guilds a discriminant function analysis was employed for RFI, VRFI, and RQ, and these measures with the addition of centroid size (tables 4.02-4.04). Discriminant function analysis was initially conducted with prior probabilities determined by group size. RFI alone classified extant forms into their correct dietary guild successfully 54.5% of the time; RQ faired somewhat better with a correct classification rate of 63.4%, VRFI was most successful with 64.4%.

Out of all of the dietary categories, RFI classified the frugivores most successfully, but this was largely a result of the prior probability calculation. Since there were more frugivores in the sample, the probability of any one individual being a frugivore was higher. In an additional analyses where equal probabilities of group membership were employed, the rate of correct classification fell substantially to 32.2%– only slightly greater than chance. RQ could best discriminate folivores/frugivores from frugivores, but correct classification fell to 48.5% when groups were considered equal. VRFI faired better with folivore/frugivores and frugivores having the highest success rate for correct classification – 65.3%. With equal probabilities, the success rate fell to 51.5%, but pattern of correct classification remained the same.

When centroid size was included in the analysis the correct classification rate rose, RFI to 75.2%, RQ to 76.2%, and VRFI to 79.2%. None of the models cross-validated well, however; all had an 18.8% rate of correct classification in the cross-validation – approximately the rate of chance if the sample were coded as having an equal probability of falling into any of the groups. In all of these analyses, centroid size was most strongly correlated with the first discriminant function. Centroid size alone had a fairly high rate of correct classification by diet - 46.0%. The first discriminant function accounted for 87.7% of the variance in RFI and centroid analysis, 77.2% in the RQ and centroid analysis, and 83.0% in the VRFI and centroid analysis. Because the cross-validation scores for the DFA were so low, this statistical treatment was considered inadequate for accurately classifying extinct primates by diet.

A

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	15	0	22	1	0
	Frugivore/ Insectivore	4	0	23	0	0
	Frugivore	3	0	89	1	0
	Frugivore/ Seed predator	0	0	13	6	0
	Frugivore/ Omnivore	2	0	20	3	0

54.5% of original grouped cases correctly classified.
18.8% correctly cross validated

B

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	38	0	0	0	0
	Frugivore/ Insectivore	0	27	0	0	0
	Frugivore	7	3	81	1	1
	Frugivore/ Seed predator	0	0	13	6	0
	Frugivore/ Omnivore	0	0	22	3	0

79.2% of original grouped cases correctly classified.
18.8% correctly cross validated

Table 4.02. Discriminant function analyses of A) RFI B) RFI and centroid size

A

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	26	5	7	0	0
	Frugivore/ Insectivore	4	7	16	0	0
	Frugivore	2	3	87	1	0
	Frugivore/ Seed predator	0	0	7	12	0
	Frugivore/ Omnivore	3	0	22	0	0

65.3% of original grouped cases correctly classified.

18.8% correctly cross validated

B

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	37	0	1	0	0
	Frugivore/ Insectivore	0	25	2	0	0
	Frugivore	0	0	92	1	0
	Frugivore/ Seed predator	0	0	3	16	0
	Frugivore/ Omnivore	0	0	6	0	19

93.6% of original grouped cases correctly classified.

18.8% correctly cross validated

Table 4.03. Discriminant function analyses of A) VRFI B) VRFI and centroid size

A

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	31	0	7	0	0
	Frugivore/ Insectivore	17	0	10	0	0
	Frugivore	4	0	87	2	0
	Frugivore/ Seed predator	1	0	8	10	0
	Frugivore/ Omnivore	3	0	22	0	0

65.3% of original grouped cases correctly classified.

18.8% correctly cross validated

B

		Predicted Group Membership				
		Folivore/ Frugivore	Frugivore/ Insectivore	Frugivore	Frugivore/ Seed predator	Frugivore/ Omnivore
Group	Folivore/ Frugivore	37	0	1	0	0
	Frugivore/ Insectivore	0	25	2	0	0
	Frugivore	2	5	82	4	0
	Frugivore/ Seed predator	0	1	8	10	0
	Frugivore/ Omnivore	0	0	25	0	0

93.6% of original grouped cases correctly classified.

18.8% correctly cross validated

Table 4.04. Discriminant function analyses of A) RQ B) RQ and centroid size

Multiple regression analyses

A regression of RFI against PC 1-4 of the complete landmark set yielded significant ($p<0.001$) positive correlations with PC 1 (Pearson correlation, $r=0.548$) and PC 4 ($r=0.431$). The R^2 value for the model overall was 0.527. Morphologically, a higher PC 1 score corresponds to increased crown height in combination with increased cusp-over-basin height. That RFI should be positively correlated with this is an unsurprising result. PC 4 broadly corresponds to the width of the trigonid and the position of the intersection of the prehypocristid and the postprotocristid (landmark 8). Species with higher PC 4 scores and a higher RFI had a relatively wider trigonid and a more lingually placed landmark 8. No significant correlation was found with PC 2 or PC 3. Variation along PC 2 was largely governed by the relative position of the hypoconid and the relative length of the trigonid, and the degree of waisting at the CEJ. This measure separated the frugivore/insectivore, *Saimiri*, from the folivore/frugivores, *Alouatta* and *Brachyteles*. Along PC 3 there was little differentiation among taxa.

To further explore the relationship between RFI and morphology the data set was divided into occlusal surface data (landmarks 1-11) and tooth sidewall data (landmarks 1-4, 12, 14, 15, 17, 18, 20, 21, 23); separate regressions were run. The overall support for the models generated was low. Sidewall data yielded a model with an R^2 of 0.392, and the regression of the occlusal surface landmarks had an R^2 of 0.457, but several morphological patterns could be isolated. In the analysis of the sidewall data, RFI was significantly ($p<0.001$) negatively correlated with PC 1 ($r=-0.515$), weakly negatively correlated with PC 2 ($r=-0.284$), and weakly positively correlated with PC 3 ($r=0.214$). Variation along PC 1 was largely the result of differences in crown heights, with higher PC 1 scores correlating with lower crown height. PC 2 variation was accounted for by differences in the point of maximum curvature and the degree of waisting at the CEJ. Species with higher PC 2 values had lower points of maximum curvature along the sidewall of the tooth, and the tooth was wider at the CEJ. Lower PC 2 values correlated with the tooth having a higher point of maximum curvature and a pinched CEJ. RFI values showed a negative correlation with this trend such that higher RFI values correlated with species that had pinched CEJ and a higher point of maximum curvature. Shape changes along PC 3 involved the position of cusp tip landmarks and how closely spaced they were relative to the landmarks outlining the point of maximum curvature on the tooth sidewall. High RFI values were found in taxa with both more closely approximated cusps and wider points of maximum curvature.

The analysis of the crown data ($R^2=0.449$) showed a significant ($p<0.001$) positive correlation between RFI and PC 1 ($r=0.391$) and PC 4 ($r=0.398$). A significant negative correlation was found for PC 3 ($r=-0.375$). Higher PC 1 scores correlated with a longer narrower crown with higher cusps and higher PC 4 values correlated with higher cusps and a wider trigonid. Variation along PC 3 was also explained by trigonid shape and cusp height. Overall, individuals with higher RFI values had higher cusps and wider rather than longer trigonids.

Since VRFI, as a measure, contained little tooth sidewall data, it was regressed against the PC scores of the reduced landmark set including only the occlusal surface landmarks 1–11. Support for the model was fairly high with an R^2 value of 0.710. There were significant ($p<0.001$) positive correlations with PC 1 ($r=0.653$) and PC 4 ($r=0.484$). A very weak but still significant negative correlation was found for PC 3 ($r=-0.204$). PC 2 and PC 3 were not significantly correlated with VRFI. Variation along PC 1 was largely accounted for by the relative height of the tooth's cusps above the tooth basin. Individuals with higher PC 1 scores have higher cusps. The relative length of the trigonid as compared to the talonid (landmarks 5, 7) explains variation along PC3. Variation along PC 4 is accounted for by the relative width of the trigonid (landmarks 1, 2) as compared to the talonid (landmarks 3, 4) as well as the relative height of the cusps above the basin; species with higher PC 4 scores tend to have a wider trigonid and a greater degree of dental relief.

RQ was regressed against the PC scores 1–4 of the reduced landmark set including only crown landmarks. The results indicated a significant ($p<0.001$) positive correlation with PC 1 ($r=0.644$), and PC 4 ($r=0.370$). PC 2 and PC 3 were not significantly correlated with RQ. The R^2 value for the model was 0.594. These results are similar to those for VRFI.

DISCUSSION

Despite the low success rate for the discriminant function analyses in classifying primates of different dietary guilds into correct categories, and in some instances weak correlations in the regression analyses, some trends in these data can still be identified. As expected, the folivore/frugivores (*Alouatta*, *Brachyteles*) and insectivore/frugivores (*Saimiri*) have higher relief values than the other forms, though *Saimiri* falls completely within the frugivore distribution for RFI. The frugivore/seed predator, *Pithecia*, has the lowest relief for all measures. In the analyses that took crown height into account, forms with higher cusps also tended to have higher crowns. Finally, there was a correlation among higher values for RFI, a higher point of maximum curvature on the sidewall of the tooth, and a greater degree of waisting along the CEJ, though differences in the latter two measures likely affect different measures of relief in different ways. For all of the measures, there was a correlation with an increased trigonid width.

Functionally, some of these morphologies can be argued to have a relationship with adaptation to processing certain food types. Other features are better explained by phylogenetic or other effects. A wider rather than longer trigonid, for example, is found in all of the atelines, and both *Brachyteles* and *Alouatta* have this morphology in combination with taller cusps. It is impossible to completely divorce these morphologies from each other; so, it is likely that the very weak correlation between wider trigonids and higher dental relief is being driven by the fact that the half of the platyrrhines with wider trigonids also have taller cusps and higher crowns. It seems that while this feature *correlates* with increased dental relief, it does not necessarily *cause* increased dental relief (or vice versa).

By far, crown height and the height of the cusps above the basin were most highly correlated with increased dental relief. These morphologies can be tied to measures of dental relief in a causal way. Among the extant forms, *Alouatta, Brachyteles*, and *Saimiri* all have higher crowns and higher cusps – suggesting a morphological complex better adapted to shearing leaves or insects and perhaps to resisting wear. For measures of RFI, though, all of the extinct forms fall within the range of three or more dietary categories except for *Mohanimico hershkovitzi*, which falls within the range of frugivores and folivore/frugivores. While the intermediate nature of the relief values of the extinct forms is not out of accord with the largely frugivorous dietary reconstructions hypothesized through the use of landmark data (Chapter 3), the lack of resolution and significant overlap of RFI values in general is troubling and suggests that this measure is not particularly valuable for inferring diet in the fossil platyrrhines.

For VRFI and RQ, where there was somewhat more differentiation between dietary groups, the high cusped *Patasola magdalenae* did consistently show high values for relief, corroborating previous results that suggest this Miocene form may have relied on an at least partially insectivorous diet. The relief values for *Patasola* are actually higher than those found in the frugivorous/insectivorous *Saimiri*. In addition to *Patasola*, several other extinct, somewhat high cusped primates that may have incorporated some insect material in their diet had high relief values for RQ, including one specimen of *Neosaimiri* and *Laventiana*. There are several forms, however, where the crown morphology and the value of RQ seem to be out of step. The causes of this potential source of misclassification will be discussed below.

There is a very weak correlation between higher RFI and a more waisted CEJ and lower point of maximum curvature, but variation in this morphology exists among the higher relief forms, *Saimiri*, *Alouatta*, and *Brachyteles*. *Saimiri* has a more waisted CEJ and higher point of maximum curvature than does either *Alouatta* or *Brachyteles*. In general, a greater degree of waisting is more common among the extant platyrrhines than among the fossil forms. Of the living forms, *Brachyteles* is the least waisted, but also has some of the highest values for RFI. The extremely high cusps largely drive these high relief values. It is interesting to consider the functional implications of a wide molar base, however. Folivore/frugivores are generally subject to a significant degree of molar wear as a result the presence of grit in their diets in dry forests and mechanical defenses in leaves (Teaford and Glander, 1991; Ungar *et al.*, 1995; Teaford *et al.*, 2006). If a tooth maintains its width at the base, as it wears, more surface area will be exposed than in a primate with a narrower CEJ. This may be advantageous for primates that incorporate more leaves into their diets, and is an interesting morphological point of departure between *Saimiri* and the folivore/frugivores.

If one includes the extinct forms, the species with the lowest points of maximum curvature and the least waisting at the CEJ are the Caribbean forms. The Patagonian form, *Soriacebus ameghinorum* also has relatively little waisting and a low point of maximum curvature, but it does fall within the range of some of the living forms for this feature. For RFI values, the Caribbean platyrrhines fall within the area of overlap for most dietary categories (Table, 4.01; Fig. 4.07) and indeed *Xenothrix* with its very low point of maximum curvature also has one of the lowest values for RFI. For VRFI values, the results were not significantly different than for RFI, but for RQ, *Antillothrix*, *Insulacebus*, *Xenothrix* and one of the two *Paralouatta varonai* specimens all fell within the range of the higher relief folivore/frugivores (Fig. 4.08), though to be fair, *Antillothrix* and *Insulacebus* only narrowly miss the range of the frugivores.

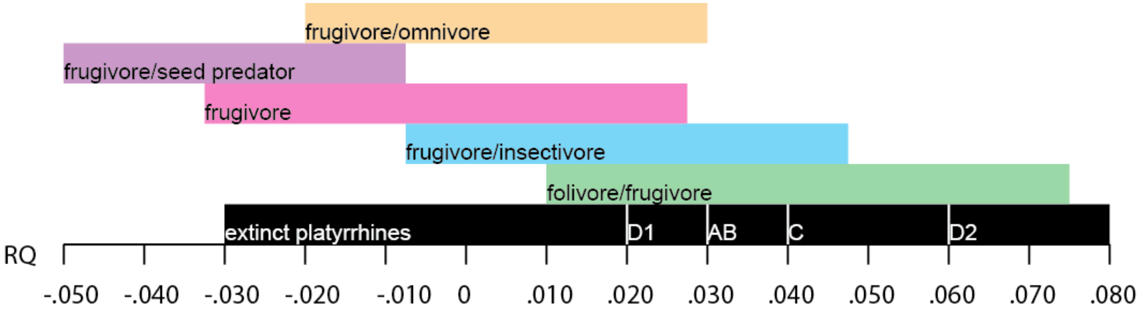


Figure 4.08. Comparative distributions of measures of relief including Caribbean fossil taxa: A) *Antillothrix bernensis*, B) *Insulacebus toussaintiana* C) *Xenothrix mcgregori* D1) *Paralouatta varonai* (MNHNH Cueva Alta 1996) D2) *P. varonai* (MNHNH V123).

This is a particularly perplexing result when considering *Xenothrix*, which has relatively low cusps when compared to basins and which is classified as either a frugivore or seed predator by the well-supported DFAs using PC scores or landmark data, and which has fairly low values of relief for RFI and VRFI. While RQ is a measure of relief, it is, in fact, measuring something somewhat different than either RFI or VRFI. RFI and VRFI each use a ratio of true 3D surface area to projected 2D surface area. RQ, on the other hand, examines the relationship between VSA and centroid size as determined by morphological measurements using landmark data and surface area. Consequently, a positive value for RQ means that a tooth has more exposed surface area in occlusal position than would be expected for a frugivore. Ultimately, the best explanation for these higher values for *Xenothrix* and the other Caribbean platyrrhines may have to do with the morphology at and below the point of maximum curvature of the tooth. In a form like *Xenothrix,* with a very low point of maximum curvature, much more of the surface area of the tooth is exposed in occlusal view, which may ultimately throw off RQ. Indeed, if the area below the point of maximum curvature is expressed as a percentage of the total surface area (Fig. 4.09) *Xenothrix* has a much lower value than the extant frugivorous primates, and the other Caribbean forms fall at the edge of the frugivorous distribution. While *Xenothrix* is, by all accounts, a unique form, perhaps filling a dietary and ecological niche with no modern analogue, it serves as a cautionary tale against using measures of relief without a clear understanding of the morphologies that give rise to the relief value.

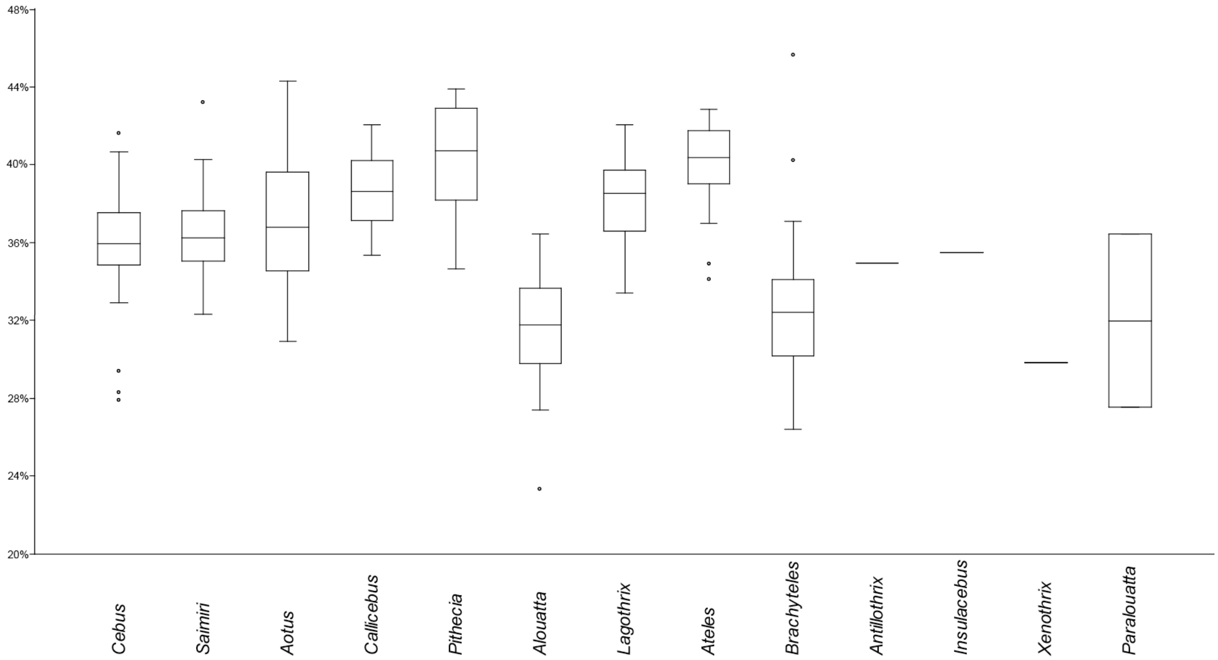


Figure 4.09. Plot of the percentage of the surface area of an M_2 below the point of maximum curvature ((TSA-VSA)/TSA *100) in selected extant platyrrhine primates and the extinct Caribbean platyrrhines. An ANOVA was conducted on these values and results are shown below. Significant p values are bold.

	Cebus	*Saimiri*	*Aotus*	*Callicebus*	*Pithecia*	*Alouatta*	*Lagothrix*	*Ateles*	*Brachyteles*
Cebus		0.988	0.800	**0.030**	**0.000**	**0.004**	0.099	**0.000**	**0.015**
Saimiri	0.988		0.999	0.999	**0.002**	**0.002**	0.624	**0.009**	**0.000**
Aotus	0.800	0.999		0.774	**0.017**	**0.000**	0.946	0.072	**0.000**
Callicebus	**0.030**	0.999	0.774		0.694	**0.000**	1.000	0.925	**0.000**
Pithecia	**0.000**	**0.002**	**0.017**	0.694		**0.000**	0.412	1.000	**0.000**
Alouatta	**0.004**	**0.002**	**0.000**	**0.000**	**0.000**		**0.000**	**0.000**	1.000
Lagothrix	0.099	0.624	0.946	1.000	0.412	**0.000**		0.729	**0.000**
Ateles	**0.000**	**0.009**	0.072	0.925	1.000	**0.000**	0.729		**0.000**
Brachyteles	**0.015**	**0.000**	**0.000**	**0.000**	**0.000**	1.000	**0.000**	**0.000**	

The low point of maximum curvature on all of the Caribbean platyrrhines may be an adaptation to resisting dental wear. For *Antillothrix* and *Insulacebus*, the sample sizes are so small that no conclusions can be drawn about the degree of dental wear that an individual might have had over its lifetime, but sampling is better for *Xenothrix* and *Paralouatta*. Of the thirteen known M_1 or M_2s of *Paralouatta varonai*, eleven were too worn to use in this sample, though several of these likely came from the same individual. They wore nearly flat before exposing dentin and several teeth showed large dentin lakes. *Xenothrix* also had substantial wear on the known fossil material. While the limited nature of the sample sizes prevents drawing firm conclusions about the extent of the dental wear that these species might have encountered, these remains and results are suggestive.

Finally, another interesting aspect of these results involves the morphologies with which RFI, VRFI, and RQ were not correlated. For the occlusal morphology landmark set, variation along PC 2 concerned the relative position of the hypoconid and entoconid and the position of landmark 8, the lowest point on the cristid obliqua, and landmark 9, the point at which the preentocristid and postmetacristid meet along the lingual edge of the tooth. Along PC 2 there were substantial differences among the living forms, and this axis separated *Alouatta* and *Brachyteles* from *Saimiri* (Fig. 3.02-3.03). *Alouatta* and *Brachyteles* have a mesially placed hypoconid and a more lingually placed landmark 8. This positioning may allow more shearing length along the cristid oblqua through more lingual angling. *Saimiri* has a distally placed hypoconid and a somewhat less angled cristid obliqua, but the entoconid of *Saimiri* is more mesially placed, and the hypoconid more distal. Consequently, there is a rearrangement of the features of the crown, but not necessarily a decrease in overall shearing ability between the folivore/frugivores and the frugivore/insectivores, even though the folivorous/frugivorous primates do seem to have a somewhat higher range of measures of relief. This confirms the long held notion that there is more than one way to increase dental relief and, concomitantly, shearing potential.

CONCLUSIONS

All three measures for dental relief do show some patterning across platyrrhines with different dietary profiles, but the reductionist approach utilized in generating these measures can obscure morphology and ultimately result in inaccurate dietary assessments for certain species. Interestingly, these results are at odds with the most common arguments for the use of these types of measures – that they are more successful at differentiating primates of different dietary guilds than SQ partially *because* they require less judgment of morphological forms by the observer and are subject to less intraobserver error in collecting measurements. Certainly, the reduction of intraobserver error is worthwhile, but M'Kirera and Ungar (2003), Boyer (2008), and Bunn *et al.* (2011) have extended this argument to suggest that automating the process of dietary determination as much as possible is useful. Most recently, Bunn *et al.* (2011, p. 11) stated that orienting a tooth in the occlusal plane,

> "…requires a nontrivial amount of morphological experience. Plyusnin *et al.* (2008) observed the concept of automated phenotype analysis offers a similar promise to the field of morphological research as automated genomics does to genetic research. Reducing the amount of morphological expertise required to implement tools for molar-shape quantification is an important step toward that goal."

This may well be a problematic position to take. Without a careful analysis of morphology, combined with information on locality, habitat, and evolutionary relationships, a taxon like *Xenothrix* may well have been misclassified. Dietary data is available for most living species, so for these primates, morphology can be evaluated in terms of what is actually occurring ecologically. For the extinct forms, this is impossible, and careful assessment of morphology in a larger context is essential for most accurately hypothesizing paleodiet.

These results also indicate that measures of relief are not necessarily equally effective for all primate groups. While Boyer (2008) found fairly good separation among the strepsirhine taxa for RFI, in the analyses conducted here RFI was the least effective measure of dental relief. This seems to indicate a real morphological phenomenon among the platyrrhines rather than a problem with RFI as a measurement per se, but the claim that RFI might be effective for different taxonomic groups does not seem to hold up. Overall, there seems to be less differentiation among platyrrhines in molar relief as captured by RFI than in strepsirhines. The results for VRFI are somewhat better, and do not seem to suffer from the misclassifications present analyses utilizing RQ. There is still a substantial overlap of different dietary categories for VRFI, however. All of the platyrrhines are to some degree frugivorous (Table 3.01) and none are exclusively folivorous or insectivorous, as in some species of strepsirrhine.

In determining measures of diet in the fossil forms, metrics of relief should be used only with caution and perhaps in the context of additional methods of dietary reconstruction. Preliminary studies using Dirichlet energy and OPC seem to show poor resolution for platyrrhines as well (Boyer *et al.*, 2011), but PC 1 scores and centroid size were able to differentiate the platyrrhines by diet quite successfully, as do measures of shearing crest length (Kay, 1978). Above all, however, a clear understanding of the dental morphology that results in these measures is essential for accurately interpreting results.

CHAPTER 5

CONCLUSIONS

Biogeographical scenarios and Caribbean primate adaptations

The endemic Caribbean monkeys represent an enigmatic radiation that likely entered and became isolated in the Greater Antilles early in the evolutionary history of the platyrrhine lineage. The analyses completed here aimed to expand our knowledge of their paleobiology through the description of new fossil material and through the analysis of their dietary profiles. The methodologies employed three-dimensional measures of molar morphology. Some of these techniques had been previously used to examine the morphological adaptation to diet in strepsirhine and catarrhine primates (*e.g.*, M'Kirera and Ungar, 2003; Boyer 2008; Skinner *et al.*, 2008; Singleton *et al.*, 2010), but with the exception of *Alouatta* (Dennis *et al.*, 2004), platyrrhines were not included in these studies. This dissertation is the only systematic exploration of platyrrhine dental morphology employing three-dimensional geometric morphometric techniques and three-dimensional measures of platyrrhine molar function through the use of relief indices. Additionally, I gathered far larger sample sizes of members of different species than were used in any previous studies and included a greater number of total species. This work both expands our knowledge of the molar morphology of platyrrhines generally, the Caribbean forms specifically, and examines the efficacy of different techniques employed for purposes of dietary reconstruction in fossil forms.

Much of the initial work on the Greater Antillean primates and indeed the Caribbean mammals more generally concerned patterns of biogeography both within and between islands and between the Greater Antilles and mainland South America. Explanations for the presence of mammals on these isolated islands today fall into one of two main camps: supporters of colonization via land bridge or overwater dispersal. This argument is not new (*e.g.,* Barbour, 1914, 1916; Matthew, 1915, 1918; Darlington, 1938, 1957; Simpson, 1940, 1952, 1958, 1965), but modern theories of plate tectonics and sea floor spreading have resulted in profoundly different reconstructions of what the early Caribbean land bridges might have looked like (Williams, 1989; Iturralde-Vinent and MacPhee, 1999 Iturralde-Vinent, 2006). Influential in this realm is the GAARlandia landspan model proposed by Iturralde-Vinent and MacPhee (1999). While it had been previously suggested that the Aves Ridge might have once been a series of closely spaced islands (see Holcombe and Moore, 1977; Pindell and Barrett, 1988; Pindell, 1994), the idea of a continuous subaerial connection between the Greater Antilles and the mainland at the Eocene-Oligocene boundary was new. If this landspan provided a path for the Antillean platyrrhines to enter the islands, close phylogenetic relationships between the Antillean platyrrhines and any of the modern platyrrhine families would be eliminated based on current molecular divergence date data (*e.g.,* Perelman *et al.*, 2011). The analyses here suggest a Miocene entry via overwater dispersal, perhaps during a period of low sea levels, as the most likely explanation for the entrance of the Caribbean platyrrhines. This pattern is echoed in other mammalian taxa with molecular divergence dates for bats and some rodent species also occurring in the Miocene. It should be noted however, that sloth remains have been recovered from Puerto Rico that date to the Early Oligocene (MacPhee and Iturralde-Vinent, 1995; White and MacPhee, 2001) suggesting a much earlier entry into the region for the megalonychids.

Part and parcel with much of the original research on GAARlandia is the hypothesis of Caribbean platyrrhine monophyly originally proposed with a close phylogenetic link with *Callicebus* (MacPhee *et al.*, 1995 *et seq.*). This hypothesis of relationship has been called into question (*e.g.* Rosenberger, 2002; Rosenberger *et al.*, 2011; Cooke *et al.*, 2011) with the proposal that the Caribbean platyrrhines might be related to a number of different mainland groups, including a link between *Alouatta* and *Paralouatta* and a possible relationship between *Xenothrix* and *Callicebus* or *Aotus*. The hypothesis of multiple origins for the Antillean platyrrhines would accord well with a Miocene entry, as the modern platyrrhine families were established on the mainland by this juncture.

While the current genetic evidence eliminates the possibility of both a dispersal into the Antilles via the GAARlandia landspan and a close relationship with mainland *Callicebus* for the Antillean primates, as MacPhee *et al.* (1995, *et seq.*) have previously proposed, it remains a valid hypothesis that the Caribbean forms may have entered the Caribbean earlier than the Miocene and may not be monophyletically linked with a member of the modern platyrrhine radiation. This idea has been proposed by Kay *et al.* (2011) and is now supported by MacPhee (pers. comm.). In his analysis of the recently recovered *Antillothrix* cranium from the Dominican Republic, Kay *et al.* (2011) found few features that they felt definitively united *Antillothrix* with a member of the modern platyrrhine radiation. This scenario is in keeping with Kay's proposal that the Patagonia primates are also stem platyrrhines. Given the combination of primitive features with some truly derived morphology in the Greater Antillean primates, this hypothesis of relationship is worth considering as additional fossil evidence is recovered from the Caribbean region.

Of all of the Antillean platyrrhines, *Xenothrix mcgregori* stands out as being most unlike other living and extinct New World Monkeys. This taxon possesses a suite of unusual morphological characteristics. In initial descriptions of the fossil mandible, Williams and Koopman (1952) remained circumspect about its phylogenetic placement and noted similarities with a number of different platyrrhine groups. It wasn't until more than fifty years after its initial discovery in the 1920s that a thorough review was undertaken with the purpose of evaluating phylogenetic affinities (Rosenberger, 1977). In this analysis, *Xenothrix* was linked with *Callicebus* or *Aotus* both considered pitheciids. Since that time, additional material has been described, which Rosenberger (2002) believes links the Jamaican monkey more firmly with *Aotus*, though others have suggested that there is little evidence for this relationship (Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004).

Most recently, *Xenothrix* has been phylogenetically allied with the newly described Hispaniolan primate, *Insulacebus toussaintiana* (Cooke *et al.*, 2011; Chapter 2).

Regardless of its kinship, *Xenothrix* appears to have unique dental as well as postcranial adaptations. Most notably, *Xenothrix* has two molars rather than three. While this may seem suggestive of a relationship with the callitrichine primates, differences in molar proportions between *Xenothrix* and the callitrichines indicate that they are not closely related (Rosenberger, 1977). Incidentally, this may be the third time in the platyrrhine radiation that a lineage has lost a molar if the nesting of the three-molar *Callimico goeldii* within the Callitrichinae continues to be supported (Schneider *et al.*, 2001; Opazo *et al.*, 2006; Wildman *et al.*, 2009; Osterholz *et al.*, 2009; Perelman *et al.*, 2011), and *Callimico* is assumed not to have re-evolved a third molar. Third molar loss results in unusual molar proportions. *Xenothrix* has relatively long lower molars with M_1 larger than M_2 and upper molars that are bucco-lingually broad with a large M^1 and a greatly reduced M^2 (Fig. 2.01).

The morphology of the molars themselves is also unusual, and *Xenothrix* was an outlier in virtually all analyses conducted herein. In landmark-based analyses of molar shape, *Xenothrix* had fairly low crown relief, but not, in fact, as low as the omnivorous *Cebus* or seed-predacious *Pithecia*. Most notable were the buccolingually closely approximated cusps in combination with very small occlusal basins (Fig. 2.10-2.11). This is a feature shared amongst the Antillean primates generally, but is most extreme in *Xenothrix* and its likely relative *Insulacebus*. The close approximation of the cusps may correspond with a relatively low point of curvature on the sidewall of the tooth, a feature also shared by the other Antillean platyrrhines. Postcranially, *Xenothrix* is distinct and was likely a slow climber, though here too, it showed little resemblance to modern forms (Ford and Morgan, 1986; Fleagle and MacPhee, 1991; MacPhee and Meldrum, 2006).

Biogeographically, *Xenothrix* was perhaps the most isolated of the Caribbean platyrrhines. Jamaica itself was unconnected to Hispaniola, Cuba, and Puerto Rico during most of the evolution of the modern Caribbean basin even during periods of low sea level, except for a brief time during the Eocene – Oligocene transition when the eastern Blue Mountains Block may have been congruent with the southwestern portion of what today makes up Hispaniola (Iturrlade-Vinent and MacPhee, 1999). Based on current fossil evidence, Jamaica seems to be set apart faunally from the other Caribbean islands, and lacks some of the major mammal groups known elsewhere, such as the sloths, insectivores, and some groups of rodents (Dávalos, 2004).

The Cuban platyrrhine *Paralouatta varonai* shows strong cranial resemblance to the modern *Alouatta*, but dentally it is far more primitive (Horovitz and MacPhee, 1999; Chapter 3, 4). The maxillary first and second molars maintain a prominent hypocone-bearing cingulum and do not have the shearing adaptations present in the modern representatives of the alouattin lineage. In prior studies (Horovitz and MacPhee, 1999), mandibular molars compare poorly with the modern alouattins in terms of shearing adaptations. Cusp placement on the lower second molar, however, is more similar to the folivore/frugivore, *Alouatta*, than to other forms. In a discriminant function analysis (DFA) of all landmark points in this study, *P. varonai* falls with the folivore/frugivores. This species is likely an early representative of a lineage that may not have yet evolved strong adaptations toward a partially folivorous diet. Indeed, even the Miocene alouattin, *Stirtonia tatacoensis*, is not consistently classified with the folivore/frugivores in DFA of landmark data. Another representative of Alouattini, which also lacks strong adaptations toward a partially folivorous diet is *Protopithecus brasiliensis* from the Late Pleistocene of Brazil (Hartwig and Cartelle, 1996; Cooke *et al.*, 2007; Rosenberger *et al.*, in press). The presence of these two forms indicates that there were at least two members of this group, which showed *Alouatta*-like cranial adaptations but remained distinctive and far more primitive dentally (Cooke *et al.*, 2007; Rosenberger *et al.*, in press).

Postcranially, *P. varonai* has some morphological adaptations that MacPhee and Meldrum (2006) have agued may be consistent with a semi-terrestrial mode of locomotion. If true, this would be the first example of a platyrrhine primate descending from the trees, so to speak. There has been speculation about why the platyrrhines did not ever colonize this ecological niche, despite South America having extensive grasslands (see Rosenberger *et al.*, 2009), with a possible explanation being that the evolution of many of the modern platyrrhines occurred in the context of flooded forests. Perhaps, though, as *P. varonai* or its ancestors entered the Greater Antilles conditions were favorable for a semi-terrestrial existence for a fairly large bodied primate. Dentally, the substantial degree of wear observed on the dentition of *P. varonai* is not inconsistent with such a locomotor profile.

It is unclear when *Paralouatta* or its ancestors might have first entered Cuba, but the island does have the distinction of having the oldest platyrrhine remains in the Caribbean, *Paralouatta marianae,* which is dated to the Early Miocene (16.3-18.8 Ma) (MacPhee *et al.*, 2003). Given the scant nature of this material (a single bone), the phylogenetic affinities of *P. marianae* had cannot be stated for certain. Molecular evidence indicates that *Alouatta* split from the other atelids around 16 MA (Opazo, 2006; Perelman *et al.*, 2011), a date not entirely incompatible with the fossil evidence. Though, if *P. marianae* is indeed a close relative of *P. varonai* and an alouattin, it would mean that primates entered the Greater Antilles just at the point of divergence. Additionally, the youngest possible range of the date estimates for *P. marianae*, and the oldest molecular divergence dates would have to be accepted. Clearly, there is a significant amount of uncertainty in this scenario, but with current fossil evidence there is no way of knowing exactly how *P. marianae* might have been related to *P. varonai.*

Another scenario purporting to explain the relationships of *Paralouatta* exists, however. MacPhee and colleagues (MacPhee *et al.*, 1995 *et seq.*) have proposed a monophyletic clade for the Greater Antillean primates. In this model, similarities between *Paralouatta* and the alouattins are interpreted as homoplasies. While this model cannot be excluded based on current fossil evidence, the presence of an additional alouattin lacking in the folivorous dentition of the crown groups suggests that the lineage may have included primates with a wider degree of morphological adaptations than previously thought. Given the great similarities cranially between *Paralouatta* and modern *Alouatta*, I remain skeptical that these are not shared derived traits.

The two extinct forms from Hispaniola, *Insulacebus toussaintiana* and *Antillothrix bernensis*, have been found on opposite ends of the island. This pattern is in accordance with biogeographical reconstructions of the history of Hispaniola, which is composed of two paleoislands, one to the east and one to the west (Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2006). Few specimens are known of either species, though, so it is unclear if the current distribution of fossil material is a real pattern or a result of poor sampling. The type specimen of *Insulacebus* includes a complete dentition and some gnathic fragments. Morphologically, the molars share features in common with the dentally aberrant *Xenothrix* including a tendency toward polycupate final lower molars, and closely approximated molar cups – particularly exaggerated on the trigonid. Its upper molars are fairly primitive with a large cingulum and a clearly delineated trigon. *Insulacebus* can be differentiated from *Antillothrix* by its unique premolar proportions and M^2 morphology. In the multivariate analyses, it was found to group with the frugivores like the other Caribbean platyrrhines.

For many years, *Antillothrix* was only known from a maxillary fragment containing P^4-M^2, but recent paleontological work has recovered two skulls and many postcranial elements (Rosenberger *et al.*, 2011; Kay *et al.*, 2011). Study of most of this material is ongoing, but analyses on dental morphology conducted here indicate a frugivorous diet. Morphologically, the lower molars of *Antillothrix* resemble *Insulacebus*, but the upper dentition shows distinct differences. Postcranially, *Antillothrix* seems to have limb proportions different from all living platyrrhines sampled (Rosenbeger *et al.*, 2011). Recent fossil evidence may confirm this pattern. At the present time, study of this material is too incomplete to hypothesize possible locomotor patterns.

Dietary reconstruction methodologies: successes and pitfalls

Paleodietary reconstruction of the Caribbean platyrrhines as well as the other mainland fossil forms was best accomplished using landmark-based three-dimensional geometric morphometric techniques. Measures of dental relief were only able to provide a very limited degree of differentiation between platyrrhines of disparate dietary categories. In applying these techniques for dietary reconstruction the upper and lower tooth rows of a sample of platyrrhine primates were first molded and cast to create a library of dental replicas. The casts were then laser scanned to create virtual models. All measurements were taken from these virtual specimens using two programs, Geomagic Studio 11 (Geomagic, Inc.) and Landmark Editor (Wiley *et al.*, 2005). Geomagic Studio 11 was used to edit the models and to collect surface area measurements; Landmark Editor allowed the collection of *x,z,y* coordinate landmarks on the occlusal surface and sidewalls of the tooth. Surface area and coordinate data were analyzed using *PAST* (Hammer *et al.*, 2001) and SPSS (Rel. 11.01, SPSS, Inc.). Some additional analyses on the coordinate data were performed in *morphologika*^{2}, (O'Higgins and Jones, 2006).

Landmark data were analyzed using principal components analysis. PC 1 was largely explained by dietary differences with the folivous/frugivous *Alouatta*, *Brachyteles*, and the frugivorous/insectivorous *Saimiri* having larger positive PC 1 values and the lower crowned omnivorous *Cebus* and seed predacious *Pithecia* having negative PC 1 values (Fig. 3.02-3.04). The remaining largely frugivorous platyrrhines fell in the middle of the distribution. Interestingly, PC 1 was not correlated with size nor did there appear to be a substantial phylogenetic affect to the distribution.

PC 1 scores were then used to classify extinct forms by diet using discriminant function analysis (SPSS, Rel. 11.01, SPSS, Inc.), and correct classification was most successful if centroid size was included in the analysis. Using PC 1 scores alone folivorous/frugivorous and frugivorous/insectivorous forms were difficult to distinguish from each other. There was considerable overlap amongst the frugivorous forms with *Aotus* and *Callicebus* consistently falling in the center of the principal component distribution plots. While sample size for the extinct forms was very small, for the most part the extinct platyrrhines fell in the middle of the distribution

Using PC 1 scores and centroid size, all of the Caribbean forms were classified as frugivores in DFA, as were the Patagonian forms. The Middle Miocene Laventan platyrrhines showed more dietary variability, however, indicating a more diverse platyrrhine community than was present in either Patagonia or the Caribbean based on current fossil evidence. Both Patagonia and the Caribbean were at the extremes of the geographic distribution of the platyrrhine primates. Patagonia in particular would have experienced seasonality both in temperature and in day light throughout the year. While not all platyrrhine primates present in the region were sampled in this study, they all show dental morphology which would indicate a frugivorous diet, but with the maintenance of some degree of dental relief. None of the Patagonian species sampled showed the extreme of dental relief observed in the living forms or in the LaVenta sample.

La Venta has been shown to have a similar level of species richness and diversity as modern tropical forest platyrrhine communities (Wheeler, 2010), and in these dietary reconstructions there are representatives of several different dietary groups including both frugivores and frugivore/insectivores. While the DFA did not classify it as a seed predator, the PC 1 values of *Cebupithecia* fall within the range of the modern seed-predacious genus *Pithecia*, indicating that by this point in time the dental morphology of the crown pitheciins had begun to establish itself. Many of the fossil representatives of the La Venta fauna are small-bodied platyrrhines likely allied with the cebines and callitrichines. *Patasola*, *Laventiana*, and *Neosaimiri* have all been classified as frugivore/insectivores. Finally, the alouttin, *Stirtonia tatacoensis,* shows similar dental morphology as

Alouatta, but has far less dental relief than the modern form, indicating that the strong commitment to an at least partially folivorous diet was not yet entrenched in its dental morphology.

In addition to the landmark-based analyses conducted in this dissertation, a variety of indices of molar relief were also employed. By and large these were far less effective for dietary reconstruction than the landmark based analyses. Relief indices are a measure of the elevation of the tooth crown constructed by taking a ratio of the true three dimensional area of a tooth or tooth surface to a two dimensional projection of the outline of the tooth onto a plane. Essentially, if the tooth crown were completely flat it would be equal in area to the two-dimensional projection – as the height of the dental topography increases the ratio will change. While relief indices have been successfully used to classify strepsirhine primates (*e.g.*, Boyer, 2008) into different dietary categories using DFA, this statistical technique was unsuccessful at classifying platyrrhine primates by diet with any measure of accuracy.

This result was unexpected and further analyses were undertaken to examine how relief indices changed in relation to the true dental morphology as articulated through PC scores. Overall there were weak correlations between PC scores and relief indices with higher (positive) PC 1 scores correlating with higher indices of relief, as expected. One of the more interesting results concerned the sidewall data, which affected the relief indices in unexpected ways. This was most clearly demonstrated in the Caribbean platyrrhines. All of the species had relatively closely approximated cusps on the second molar in combination with a low point of maximum curvature on the sidewall of the tooth. This morphology in its most extreme form is exhibited in *Xenothrix*. This results in a greater amount of surface area exposed on the occlusal surface of the tooth, which ultimately increased the relief indices despite *Xenothrix* having a relatively low cusp-to-basin relief.

It is possible that these unique morphologies were an adaptation to maintaining molar function in the face of a high degree of dental wear. Both *Xenothrix* and *P. varonai* seem to have been subject to significant dental wear, though, as a caveat, it should be noted that this assessment is based on a relatively small sample of specimens. Interestingly, a low point of maximum curvature is also shared by the Miocene Patagonian forms *Soriacebus ameghinorum* and *Carlocebus carmenensis*. Is it possible that this feature in combination with the buccolingual compression of cusps might have been present in incipient form among the Early Miocene primates, which gave rise to some or all of the Caribbean platyrrhines. Certainly, *Soriacebus* shows some resemblances in its mandibular dentition to both *Insulacebus* and to *Xenothrix*. It is unknown how far north the Patagonian species might have ranged, but the presence of the Paranaian Sea (Aceñolaza, 2000; Alonso, 2000; Cozzuol, 2006) would likely have meant that a direct connection to the Caribbean was unlikely. Ecologically, however, both the Patagonian and the Caribbean platyrrhines might have encountered similar ecological stressors including significant seasonality. And both groups have molar adaptations that would allow dietary flexibility.

The Greater Antillean platyrrhines have always been an enigmatic fauna that show a variety of derived and primitive features. Their unique morphologies have made them difficult to classify and the subject of a number of phylogenetic studies (*e.g.*, Rosenberger, 1977; Ford 1990b, Horovitz and MacPhee, 1999; Rosenberger, 2002; MacPhee and Horovitz, 2004). From the analyses on dental morphology presented here, and from previous analyses on postcranial material (Ford, 1986; Ford and Morgan, 1986; Ford, 1990 a, b; Fleagle and MacPhee, 1991; MacPhee and Meldrum, 2006) it is becoming increasingly clear that several of the species may have occupied ecological niches for which there is no modern analogue. As work continues on recently described fossil material (*e.g.*, Rosenberger *et al.*, 2011; Kay *et al.*, 2011; Cooke *et al.*, 2011), we will be better able to understand the adaptations of these platyrrhines.

APPENDIX A

ERROR STUDIES ON SURFACE AREA MEASURES (TSA AND OTSA)

Error tests were undertaken to evaluate the effect that intraobserver error might have on the measurements total crown surface area (TSA; Chapters 2 and 4) and occlusal table surface area (OTSA; Chapter 2). Ten trials were conducted on a specimen of *Callicebus cupreus* (AMNH 97370). The measurements were completed over the course of several days and no measurements were collected back to back. Percentage error was calculated as [100 (trial *n* – mean)/mean]. Results and univariate statistics of the ten trials are presented below.

Occlusal Table Surface Area (OTSA)

Trial Number	OTSA Value	Percentage Error
Trial 1	9.0592	1.29
Trial 2	8.9286	0.17
Trial 3	9.0013	0.64
Trial 4	8.8360	1.21
Trial 5	8.8390	1.17
Trial 6	8.9607	0.19
Trial 7	8.9877	0.49
Trial 8	8.9375	0.07
Trial 9	8.8836	0.67
Trial 10	9.0053	0.69

Min	8.8360
Max	9.0592
Mean	8.9439
Std. error	0.0234
Variance	0.0055

Surface Area of the Molar Crown (TSA)

Trial Number	TSA Value	Percentage Error
Trial 1	30.2590	0.07
Trial 2	30.3347	0.18
Trial 3	30.8018	1.72
Trial 4	29.9829	0.98
Trial 5	30.2928	0.04
Trial 6	30.3097	0.10
Trial 7	29.9587	1.06
Trial 8	30.3187	0.13
Trial 9	30.2850	0.02
Trial 10	30.2603	0.07

Min	29.9587
Max	30.8018
Mean	30.2804
Std. error	0.0723
Variance	0.0522

APPENDIX B

ERROR STUDIES ON THREE-DIMENSIONAL LANDMARK DATA

Error tests were undertaken to evaluate the effect that intraobserver error might have on the collection of landmark data. Ten trials were conducted on the lower second mandibular molar of a female specimen of *Callicebus cupreus* (AMNH 97370). The landmarks were collected in Landmark Editor (Wiley *et al.*, 2005) according to protocols outlined in Chapter 3. Landmarks were collected over the course of several days and no measurements were collected back to back. The landmarks were subjected to generalized Procrustes analysis (GPA), and a consensus configuration was calculated. The Procrustes chord distance between each trial and the consensus configuration was calculated.

Ten additional *Callicebus cupreus* individuals were then selected at random from the larger *Callicebus cupreus* sample. Effort was made to include only individuals of the same subspecies, however, this was not possible for all individuals, though no morphological patterning was observed along subspecific lines in the complete sample. Landmarks were placed on the M_2, a consensus configuration was generated, and the Procrustes chord distances between each individual and the consensus configuration were calculated.

Results are displayed below. The Procrustes chord distances between the consensus configuration and the trials were significantly smaller ($p<0.0001$) than the distances between each individual and the consensus configuration indicating that population variability is far larger than intraobserver error.

Trial	Distance
1	0.0395
2	0.0493
3	0.0356
4	0.0366
5	0.0458
6	0.0328
7	0.0333
8	0.0311
9	0.0313
10	0.0410
Average	0.0376

Individual	Distance
AMNH 76419	0.0886
AMNH 76420	0.1123
AMNH 76590	0.0743
AMNH 142275	0.1200
AMNH 72146	0.0880
AMNH 72156	0.0613
AMNH 73412	0.0861
AMNH 73414	0.0744
AMNH 73415	0.0936
AMNH 76588	0.0719
Average	0.0870

APPENDIX C

ERROR STUDIES ON DATA COLLECTION IN THE INTERSTITIAL REGION

Because the living platyrrhine dentitions were laser scanned as an entire tooth row, the interstitial region was missing in all laser scans. These regions were filled using the "fill holes" function of Geomagic Studio 11 (Geomagic, Inc.). This resulted in a reasonable approximation of the interstitial area. In order to check for error in this methodology, an individual tooth of *Paralouatta varonai* (MNHNH V123) was artificially cropped so that the interstial region was removed. This area was then filled using Geomagic Studio 11 (Geomagic, Inc.). The true surface area of the tooth was compared with the surface area of the tooth after the cropping and filling procedure was completed. This procedure was repeated on the same specimen on 10 different occasions spaced out over several days. The results are presented below.

True surface area of MNHNH V123 was 98.7946 mm^2

Trial Number	Value	Percentage Error
Trial 1	99.3805	0.59
Trial 2	99.4396	0.65
Trial 3	99.1896	0.40
Trial 4	99.2078	0.42
Trial 5	99.1792	0.39
Trial 6	99.2098	0.42
Trial 7	99.1355	0.35
Trial 8	99.1912	0.40
Trial 9	99.2559	0.47
Trial 10	99.3639	0.58

Min	99.1355
Max	99.4396
Mean	99.2553
Std. error	0.0324
Variance	0.0105

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