An extinct monkey from Haiti and the origins of the Greater Antillean primates

Siobhán B. Cooke[a,b,c,1], Alfred L. Rosenberger[a,b,d,e], and Samuel Turvey[f]

[a]Graduate Center, City University of New York, New York, NY 10016; [b]New York Consortium in Evolutionary Primatology, New York, NY 10016; [c]Department of Evolutionary Anthropology, Duke University, Durham, NC 27708; [d]Department of Anthropology and Archaeology, Brooklyn College, City University of New York, Brooklyn, NY 11210; [e]Department of Mammalogy, American Museum of Natural History, New York, NY 10024; and [f]Institute of Zoology, Zoological Society of London, London NW1 4RY, United Kingdom

A new extinct Late Quaternary platyrrhine from Haiti, *Insulacebus toussaintiana*, is described here from the most complete Caribbean subfossil primate dentition yet recorded, demonstrating the likely coexistence of two primate species on Hispaniola. Like other Caribbean platyrrhines, *I. toussaintiana* exhibits primitive features resembling early Middle Miocene Patagonian fossils, reflecting an early derivation before the Amazonian community of modern New World anthropoids was configured. This, in combination with the young age of the fossils, provides a unique opportunity to examine a different parallel radiation of platyrrhines that survived into modern times, but is only distantly related to extant mainland forms. Their ecological novelty is indicated by their unique dental proportions, and by their relatively large estimated body weights, possibly an island effect, which places the group in a size class not exploited by mainland South American monkeys. Several features tie the new species to the extinct Jamaican monkey *Xenothrix mcgregori*, perhaps providing additional evidence for an inter-Antillean clade.

Platyrrhini | island biogeography | paleoprimatology | fossil primate

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) was first demonstrated definitively with the description of *Xenothrix mcgregori* (Fig. S1) from Jamaica in 1952 (2). Two other genera, each one confined to a different island, have since been reported: in Hispaniola, *Antillothrix bernensis* (Fig. S1) (3,4,5), and in Cuba, *Paralouatta varonai* and *Paralouatta marianae* (6,7). 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 million years old (7). The youngest associated dates are late Holocene, with *X. mcgregori* dated to 2,145 ± 220 ^{14}C years before present (8), and this species may have persisted into the European-era historical period (9,10). Two ^{14}C dates pertaining to material from Hispaniola are 3,850 ± 135 (3) and 9,550 ± 150 (11). *Insulacebus toussaintiana* represents the newest addition to this enigmatic fauna. Although the remains have not been dated thus far, the condition of the material would suggest a recent age in line with the other Holocene fossils known from the area.

Systematic Paleontology

The classification of *Insulacebus toussaintiana* is as follows: Order Primates (Linnaeus, 1758); Suborder Anthropoidea (Mivart, 1864); Parvorder Platyrrhini (Geoffroy, 1812); Superfamily Ateloidea (Gray, 1825); Tribe Aotini (Poche, 1904); *I. toussaintiana* gen. et sp. nov.

Note that there are two contrasting views on the taxonomic placement of *Aotus*, with the molecular studies indicating an affinity with the Cebinae (12,13) and morphological evidence suggesting a relationship with Pithecinae (14).

Holotype

UF 114714 (Florida Museum of Natural History) is 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 and Table 1). The latter preserves alveoli from left P_4 to the right canine.

Etymology

Insula (L.) means island, and *cebus* (Gr.) means monkey; The species name, *toussaintiana*, is 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 no. 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). This excavation was one of a series conducted from February through August in 1984 by the University of Florida under the direction of Charles Woods (15). Trouing Jérémie no. 5 is also the type locality for the extinct rodent *Rhizoplagiodontia lemkei* and the extinct sloth *Neocnus toupiti* (15,16).

Diagnosis of Genus and Species

I. toussaintiana, a large platyrrhine comparable in body size to a very large Tufted Capuchin, *Cebus apella*, 4.6 to 4.7 kg (Table 2 and Table S1) (17–28), is distinguished from all other platyrrhine primates by the following combination of traits: large spatulate central incisors in tandem with smaller conical lateral incisors; maxillary and mandibular canines are low-crowned and stout; maxillary premolars are heteromorphic, increasing dramatically posteriorly in crown size and complexity, with $P^{2–3}$ small, single-rooted, and lacking lingual cingula, whereas 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; $P_{3–4}$ possess a protoconid and metaconid of equal height, closely spaced together but lacking a clear protocristid; $M_{1–2}$ with restricted trigonid and talonid basins as a result of narrowly spaced protoconid–metaconid and hypoconid–entoconid, and a basally wide trigonid as a result of 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

I. toussaintiana is described from the nearly complete dentition (Fig. 2 and Table 1), 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
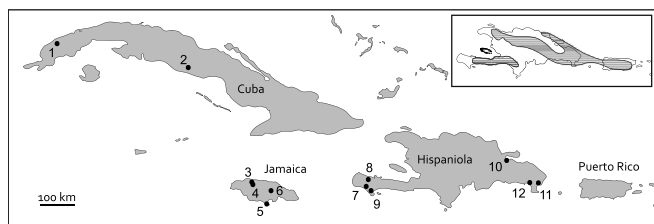
ANTHROPOLOGY

Fig. 1. Schematic map of primate localities in the Greater Antilles. 1: *Paralouatta varonai*, Cueva de Mono Fósil, Cueva Alta; 2: *P. marianae*, Domo de Zaza; 3: Primate femur, Sheep Pen Cave; 4: *Xenothrix mcgregori*, Long Mile Cave; 5: *X. mcgregori*, Jackson's Bay Caves; 6: Primate femur, Coco Ree Cave; 7: *Insulacebus toussaintiana*, Trouing Jérémie no. 5; 8: Primate humerus and femur, Trouing Lanj Genti no. 1; 9: Primate mandible, Trou Woch Sa Wo; 10: Primate tibia, Samaná Bay; 11: *Antillothrix bernensis*, Cueva de Berna, Boca de Yuma; 12: *A. bernensis*, La Jeringa Cave. *Inset*: Hypothetical subaerial landmass of Hispaniola and Puerto Rico during the mid-Miocene (1).

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. 3). 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 (29), may be comparable in completeness and quality of preservation.

The upper central incisors are broad and spatulate with an inconspicuous lingual cingulum, whereas the lateral incisor, whose crown is slightly damaged, is conical in shape, and small in comparison with I^1 (Fig. S2). Among extant platyrrhines, in which incisor morphology is often clade-specific (30), comparable crown morphology, is found in *Aotus* and to a somewhat lesser degree in *Saimiri*. Among the extinct Caribbean forms, this combination has also been hypothesized for *X. mcgregori* based on relative alveolar size (31), although this interpretation has met with resistance (32). In the absence of *X. mcgregori* specimens with intact incisors, the relative crown size remains unknown. Although *I. toussaintiana* 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 compared with molars. In all living taxa that have relatively broad spatulate incisors, there is a concomitant decrease in molar area. 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 (33). In *I. toussaintiana* 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. S3). In the absence of nondental 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 platyrrhine taxa.

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 extant platyrrhines. In the Caribbean, relatively small canines are thought to be present in the Cuban *P. varonai* and Jamaican *X. mcgregori*. The mandibular canine of *I. toussaintiana* is distinctive, as a strongly developed, bluntly pointed tooth with several features resembling *Aotus* and select Miocene forms including *Soriacebus ameghinorum*, *Cebupithecia sarmientoi*, and *Nuciruptor rubricae* (Figs. S4 and S5). It presents a somewhat triangular cross-section near the base largely as a result of 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 lower canine of *C. sarmientoi*. On the lingual surface, the crown is reinforced by a rounded torus running from tip to cingulum. It offsets the distal surface and contributes to forming the triangular cross-sectional shape. The canine apex, 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 *C. sarmientoi*. 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. Although 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 aotins or within the pithecine clade (*SI Text*).

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. S6) and an unusual anatomical mosaic (*SI Text*). Although the anterior premolars ex-

Fig. 2. Laser scan-generated images of the *I. toussaintiana* dentition. Individual teeth were scanned at 25 μm interpoint distances using an LDI RPS 120 laser scanner. The images were edited and rendered in Geomagic Studio 11. Dark gray teeth are part of the original UF 114714 assemblage, whereas light gray teeth are mirror images used to reconstruct a complete dental arcade. The exact shape of the palate is unknown and *X. mcgregori* was used as a guide in creating this image.

Table 1. Maximum mesiodistal lengths and buccolingual breadths of *I. toussaintiana* (UF 114714)

Specimen	Right, mm		Left, mm	
	Length (MD)	Breadth (BL)	Length (MD)	Breadth (BL)
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
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

BL, buccolingual; MD, mesiodistal.

Table 2. Body size in extant and extinct Caribbean and Laventan platyrrhine primates

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										
I. toussaintiana	1	5.1	5.5	27.8	3.3	5,443	5,443	4,788	4,805	4,159–5,443
X. mcgregori (19)[†]	1	5.1	6.1	31.1	3.4	6,477	6,483	5,840	5,720	4,881–6,483
Trou Woch Sa Wo mandible (19)[†]	1	4.9	5.5	27.0	3.3	5,177	5,175	4,521	4,569	3,971–5,177
P. varonai (19)*[†]	5	5.7	7.0	39.9	3.7	9,551	9,582	9,104	8,444	6,981–9,582
La Venta, Colombia, primates										
Neosaimiri fieldsi (20)	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
A. dindensis (IGM-KU 8601) (21)*	1	3.5	3.0	10.6	2.4	1,199	1,189	850	1,054	850–1,199
Mohanamico hershkovitzi (IGM 181500) (22)*	1	2.7	3.3	8.9	2.2	919	909	627	807	627–919
Micodon kiotensis (IGM-KU 8401) (23)[†]	—	—	—	—	—	—	—	—	—	"Saguinus or Callithrix sized"
Patasola magdalenae (IGM 184332) (24)*	1	2.3	2.7	6.4	1.9	547	540	347	480	347–547
L. conclucatus (IGM 184531) (24)*	1	2.5	2.9	7.3	2.0	677	669	443	595	650–1,206
Miocallicebus villaviejai (IGM-KU 97001) (25)[†]	—	—	—	—	—	—	—	—	—	"Cebus sized"
C. sarmientoi (UMCP 38762)	1	3.7	3.7	13.8	2.6	1,821	1,810	1,370	1,603	1,370–1,821
N. rubricae (IGM 251074) (26)*	1	3.9	3.9	15.5	2.7	2,180	2,168	1,682	1,919	1,682–2,180
S. tatacoensis	2	5.2	5.9	30.4	3.4	6,243	6,247	5,600	5,513	5,513–6,247
S. victoriae (27)[†]	—	—	—	—	—	—	—	—	—	10,000

The body weights were calculated using published regression equations (17, 18) based on M1 area. BL, buccolingual; MD, mesiodistal.

*Molar measurements were taken from published sources and the body weight was calculated here.

[†]Published body weight estimate.

hibit an *Aotus*-like pattern in simplicity and overall morphology, the P^4 is reminiscent of the Squirrel Monkey, *Saimiri*, in its width relative to M^1 and the well developed cingulum. This morphology contrasts with *A. bernensis*, which has premolars of all approximately equal breadth that lack prominent cingula (5). The mandibular premolars are also heteromorphic in size, shape, and cusp and basin development (*SI Text*). Compared with living platyrrhine primates, the morphology of the *Insulacebus* P$_{3–4}$ is unique in two ways: the cusps are close in approximation and lack the protocristid that normally links them. The former feature is mirrored in the mandibular molars.

The upper molars (*SI Text*) of the fossil decrease in size toward the rear, with the prominent M^1 hypocone, talon, and cingulum becoming smaller on the morphologically similar M^2. M^3 is essentially a bicuspid crown with a well formed distolingual cingulum. In contrast to *I. toussaintiana*, the M^1 of *A. bernensis* has a smaller, less prominent lingual cingulum and a smaller hypocone, and the *A. bernensis* 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 *X. mcgregori* appears to lack the strong cristae present in *A. bernensis* and *I. toussaintiana*.

The lower molar pattern of *I. toussaintiana* is unusual in several ways and does not closely match other platyrrhines, except for particular features evident in *X. mcgregori* and, to a lesser extent *S. ameghinorum*. Like the posterior premolars, each molar's protoconid and metaconid are spaced closely together and are sharply divided by a sulcus (Fig. 4). The entoconid and hypoconid cusps are closely approximated relative to the buccolingual breadth of the talonid. Buccally, all three molars present, a flaring of the enamel sidewall near the base of the protoconid. Among the special resemblances shared with *X. mcgregori*, the buccolingually constricted trigonid and talonid basins of M$_{1,2}$ are noteworthy for the cusp approximation ratio value; this ratio is distinctively low in *I. toussaintiana* and even more exaggerated in *X. mcgregori*. Only *S. ameghinorum* matches them. The cross-sectional morphology of platyrrhine crowns suggests that our metric documenting this pattern reflects a complex effect, involving both a narrowing of intercuspal distances and augmen-

tation of the mesial and distal crown breadths, one of the distinctive features of *X. mcgregori* (34).

The third molar of *I. toussaintiana* 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, a similarity shared with *Aotus dindensis* (IGM-KU 98001) (35).

The preserved portion of the mandibular symphysis (Fig. 3) 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 *X. mcgregori* (32). The mandible of the Cuban *P. 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 naturally raises questions about the possibility of island effects. Table 2 provides estimates of body weight for the fossils derived from predictive equations based on lower molar area and compares them to other pertinent fossils. An impressively large number of the Caribbean platyrrhines—*I. toussaintiana*, *X. mcgregori*, *P. varonai*, and a jaw from the Haitian site Trou Woch Sa Wo, of poor condition and uncertain assignment—are quite large compared with mainland forms, falling either well outside or at the very top of the body weight range of living counterparts such as *Aotus* or *Callicebus* (Table S1). *A. bernensis*, with limbs as large as a *Cebus* and a skull larger than a *Saimiri*, appears to have been larger than all living pitheciines and cebids except *Cebus* (5). The Caribbean primates are also larger than all fossil primates from La Venta except for the alouattin, *Stirtontia* (Table 2).
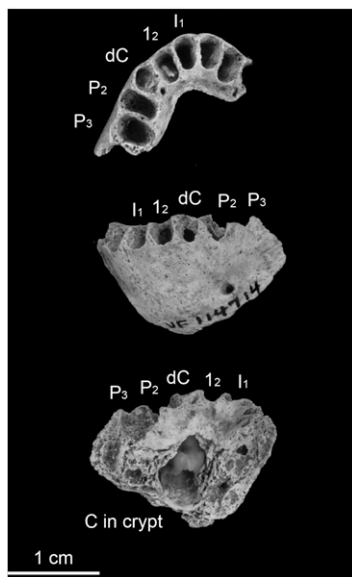
Fig. 3. Mandible of *I. toussaintiana*, with adult canine shown in the crypt, in superior (*Top*), lateral (*Middle*), and medial (*Bottom*) views.

The possibility of island gigantism occurring among the Greater Antillean primates has been proposed before (36). Although Ford (36) 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 among these island bound primates has been a real pattern and a departure from the mainland norm. As a group with a modal weight of approximately 4k to 5k, 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 3.5k, the size of *Cebus* and *Pithecia*, and 5k, the size of the smallest *Alouatta*.

### Evolutionary Relationships of *Insulacebus* and the Greater Antillean Primates
The phylogenetic affinities of the Greater Antillean primate radiation remain a matter of some controversy with two hypotheses purporting to explain their relationships. The single-lineage

model (1, 4, 32, 37) 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. Although this is an intriguing possibility given the biogeographic isolation of the islands, additional evidence would be required to accept this hypothesis, (32, 37).

Proponents of the multilineage hypothesis argue several clades are present, each aligned with different mainland lineages. This could mean either colonization by a community derived from mainland South America or episodic dispersal, possibly over an extended period. Rivero and Arredondo (6) initially proposed a *Paralouatta–Alouatta* connection based on the close resemblance of the two forms in their highly unusual cranial morphology. This hypothesis and its reasoning was endorsed by Rosenberger and colleagues (31, 38). Rímoli (3), MacPhee and Woods (11), and Ford (36) have suggested cebine affinities for *A. bernensis* based on limited dental evidence. The recovery of a complete skull of *A. bernensis* (5) provided additional evidence in support of this interpretation; however, newly discovered material now under study is causing the authors to question this interpretation.

Another non-alouattin lineage appears to be represented by the enigmatic *X. mcgregori* from Jamaica. The type specimen (Fig. S1), a lower jaw with two molars, was not formally allocated to any particular platyrrhine group when first published by Williams and Koopman in 1952 (2); the occlusal morphology, the shape of the jaws, and two-molar dental formula differed radically from all New World monkeys, living and extinct. In 1970, Hershkovitz named a new platyrrhine family, Xenotrichidae, for the species (39). Soon thereafter, in an early cladistic analysis, Rosenberger (34) linked *X. mcgregori* with modern Titi Monkeys (*Callicebus*). Description of primate postcranial remains from Anthony's original collection revived the notion that family-level separation of *X. mcgregori* was warranted (9). In the late 1990s, new facial specimens were recovered (32), leading Rosenberger (31) to alter his earlier assessment, stressing possible morphological evidence of an enlarged orbit and relatively broad upper central incisors that indicated a closer affinity with *Aotus* than *Callicebus*. This position was not supported by MacPhee and Horovitz (32), 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. With the current evidence, however, the question of orbital morphology remains unresolved.

I. toussaintiana likely shares a phylogenetic relationship with *X. mcgregori*, providing some support to MacPhee and colleagues' inter-Antillean platyrrhine clade, although we currently remain
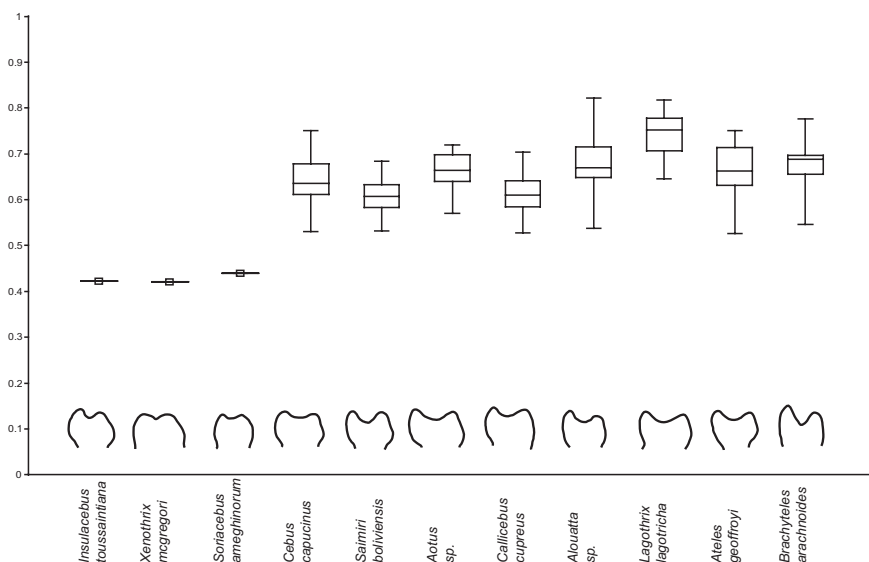
Fig. 4. Cusp approximation ratio is the linear distance between the protoconid and metaconid divided by the maximum buccolingual breadth of the trigonid. A cross-section through the protoconid and metaconid of each right M_2 is shown below each box plot; these are schematic and not to the same scale. These data were collected and cross sections created from laser scan-generated models. The extinct sample includes *I. toussaintiana* (UF 114714), *X. mcgregori* (AMNHM 148198), and *S. ameghinorum* (MACN SC-2, 33). The mixed-sex extant sample includes *C. capucinus* ($n = 25$), *S. boliviensis* ($n = 30$), *Aotus* sp. ($n = 29$), *C. cupreus* ($n = 29$), *A. seniculus* ($n = 28$), *L. lagotricha* ($n = 23$), *A. geoffroyi* ($n = 30$), and *B. arachnoides* ($n = 21$).

dubious about the position of the two *Paralouatta* species in this framework. Both *I. toussaintiana* and *X. mcgregori* share an unusual occlusal pattern on the low-relief M_{1-2} in which trigonid and talonid cusp are closely approximated, and both have unusual, extensively flared buccal crown sidewalls, especially exaggerated in the trigonid moiety. No modern platyrrhine shows this pattern. Only the early middle Miocene fossil *S. ameghinorum* from Patagonia (40–43) resembles these Caribbean forms in having such closely approximated cusps, but it also exhibits quite a different, unusually narrow crown morphology. Another phenetic resemblance of *I. toussaintiana* and *X. mcgregori* that bears mentioning for completeness, although still of uncertain cladistic significance, is the tendency toward polycuspate final lower molar crowns, M_3 or M_2 as the case may be. Finally, these species share a smoothly parabolic mandibular symphysis.

I. toussaintiana and *X. mcgregori* may likely share a relationship with the modern genus *Aotus*, although this phylogenetic connection is far from secure. The unusual incisor proportions and morphology, simplified anterior premolars, and multicusped M_3 are suggestive of an *Insulacebus–Aotus* connection. Characteristics that unite *X. mcgregori* 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 colleagues' *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 pitheciines (4, 32, 37).

Origins, Differentiation, and Biogeography

Although the exact date of primate entry into South America is unknown, the first fossil evidence, from Salla, Bolivia, is dated to the late Oligocene (43, 44), and by the early middle Miocene, at least 10 species of New World monkeys were present in Patagonia. In general, the Patagonian primates were primitive, with the molar teeth resembling morphotype reconstructions for Platyrrhini (34, 45). Regardless of their hypothesized phylogenetic affinities, 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* (46, 47). Although the phylogenetic affinities of this fossil have been debated (48–50), the species, known only by a skull, does appear to show at least some orbit enlargement (51, 52), a derived hallmark of the nocturnal and crepuscular habits of the Owl Monkey lineage. Cebines may be represented by *Killikaike blakei* (53) and the *Saimiri*-like *Dolichocebus gaimanensis*, which possess derived cranial characteristics of the subfamily, including a narrow interorbital region and a domed frontal (see ref. 18 for an alternate view). The thin procumbent incisors of *S. ameghinorum* in combination with a somewhat laterally projecting canine are suggestive of pitheciine affinities (40, 41). These fossils demonstrate that crown platyrrhine lineages, albeit still primitive in form, had already differentiated by early middle Miocene times.

Although 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 tatacoensis* and *S. victoriae*, the *Saimiri*-like *Neosaimiri fieldsi*, and the earliest member of an extant genus, *A. dindensis*, that a nearly modern radiation had appeared in South America by this juncture. The dentally primitive *I. toussaintiana* was likely derived from a fauna that was evolving on the mainland before the La Venta horizon and stems from a pre-middle-Miocene colonization from the mainland (4, 37, 54).

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 vicariance and dispersal. Faunal continuity at the generic level among

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 (16, 55). Into the Neogene, these islands formed a close-packed emergent geotectonic array that experienced progressive disruption and fragmentation (1, 56). Jamaica, however, remained largely distinct and partially submerged during much of this period, and it lacks characteristic Greater Antillean mammal groups such as megalonychid sloths, insectivores, and echmiyid rodents. There was, however, a possible Tertiary land connection between the Jamaican Blue Mountains Block and the southern peninsula of Hispaniola (1), providing an intriguing line of geological congruence with the apparent affinity shown here between *X. mcgregori* and *I. toussaintiana*. This phylogenetic connection was anticipated by Ford (36), who suggested that a yet-undescribed primate femur from western Haiti was nearly indistinguishable from a Jamaican primate femur.

Within Hispaniola, *I. toussaintiana* has been found only on the Tiburon Peninsula, whereas convincing specimens of *A. 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. Hispaniola consists of formerly independent northern and southern paleo-islands, which remained separated by a prominent depression that was periodically or permanently inundated into the Late Quaternary (1, 57, 58). The southern paleo-island, 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 (57). All three of these regions are biogeographically distinct and are characterized by substantial levels of endemism in birds, reptiles, amphibians, invertebrates, and plants (59–64). Among the mammals, Woods (15) described a genus and species of extinct capromyid rodent, *R. lemkei*, which was apparently restricted to the Massif de la Hotte, and Ottenwalder (65) classified Hispaniolan solenodons (*Solenodon paradoxus*) from the north and south paleo-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. Although 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 nonendemic 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 *I. toussaintiana* now brings Hispaniola's endemic land mammal fauna to 25 species, of which only two still survive today, the insectivore *S. paradoxus* and the rodent *Plagiodontia aedium* (10, 66). Although further study is needed to clarify the island's patterns of evolution and diversity, the description of a new primate species and its potential affinity with the Jamaican *X. mcgregori* provides a new line of evidence in understanding the evolution of the primitive Caribbean primates and the mammalian fauna more generally.

1. Iturralde-Vinent MA, MacPhee RDE (1999) Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bull Am Mus Nat Hist* 238:1–95.
2. Williams EE, Koopman KF (1952) West Indian Fossil Monkeys. *Am Mus Nov* 1546:1–16.
3. Rímoli R (1977) A new species of monkey (Cebidae: Saimirinae: *Saimiri*) from Hispaniola (original title in Spanish). *Cuadernos CENDIA Univ Autónoma Santa Domingo* 242:5–14.
4. MacPhee RDE, Horovitz I, Arredondo O, Vasquez OJ (1995) A new genus for the extinct Hispaniolan monkey Saimiri bernensis Rímoli, 1977, with notes on its systematic position. *Am Mus Nov* 3134:1–21.
5. Rosenberger AL, Cooke SB, Rímoli R, Ni X, Cardosa L (2011) First skull of Antillothrix bernensis, an extinct relict monkey from the Dominican Republic. *Proc Biol Sci* 278:67–74.
6. Rivero M, Arredondo O (1991) *Paralouatta varonai*, a new Quaternary platyrrhine from Cuba. *J Hum Evol* 21:1–11.
7. MacPhee RDE, Iturralde-Vinent MA, Gaffney ES (2003) Domo de Zaza, an early Miocene vertebrate locality in south-central Cuba, with notes on the tectonic evolution of Puerto Rico and the Mona Passage. *Am Mus Nov* 3394:1–42.
8. MacPhee RDE (1984) Quaternary mammal localities and Heptaxodontid rodents of Jamaica. *Am Mus Nov* 2803:1–34.
9. MacPhee RDE, Fleagle JG (1991) Postcranial remains of *Xenothrix mcgregori* (Primates, Xenotrichidae) and other Late Quaternary mammals from Long Mile Cave, Jamaica. *Bull Am Mus Nat Hist* 206:287–321.
10. MacPhee RDE, Flemming C (1999) Requiem æternam: The last five hundred years of mammalian species extinctions. *Extinctions in Near Time: Causes, Contexts, and Consequences*, ed MacPhee RDE (Kluwer/Plenum, New York), pp 333–371.
11. MacPhee RDE, Woods C (1982) A new fossil cebine from Hispaniola. *Am J Phys Anthropol* 58:419–436.
12. Opazo JC, Wildman DE, Prychitko T, Johnson RM, Goodman M (2006) Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). *Mol Phylogenet Evol* 40:274–280.
13. Baena A, et al. (2007) Primate TNF promoters reveal markers of phylogeny and evolution of innate immunity. *PLoS ONE* 2:e621.
14. Rosenberger AL, Tejedor MF The misbegotten: Long lineages, long branches and the interrelationships of Aotus, *Callicebus* and the saki-uakaris. *Evolutionary Biology and Conservation of Titis Sakis and Uakaris*, eds de Oliveira SG, Veiga LM, Ferrari S, Norconk M, Barnett A (Cambridge Univ Press, Cambridge, UK) , in press.
15. Woods CA (1989) A new capromyid rodent from Haiti: The origin, evolution, and extinction of West Indian rodents, and their bearing on the origin of New World hystricognaths. *Nat Hist Mus Los Angeles County Sci Ser* 33:59–90.
16. MacPhee RDE, White JL, Woods CA (2000) New megalonychid sloths (Phyllophaga, Xenarthra) from the Quaternary of Hispaniola. *Am Mus Nov* 3303:1–32.
17. Conroy GC (1987) Problems of body weight estimation in fossil primates. *Int J Primatol* 8:115–137.
18. Kay RF, et al. (2008) The anatomy of *Dolichocebus gaimanensis*, a stem platyrrhine monkey from Argentina. *J Hum Evol* 54:323–382.
19. MacPhee RDE, Meldrum J (2006) Postcranial remains of the extinct monkeys of the Greater Antilles, with evidence for semiterrestriality in Paralouatta. *Am Mus Nov* 3516:1–65.
20. Takai M (1994) New specimens of *Neosaimiri fieldsi* from La Venta, Colombia: A middle Miocene ancestor of the living squirrel monkeys. *J Hum Evol* 27:329–360.
21. Setoguchi T, Rosenberger AL (1987) A fossil owl monkey from La Venta, Colombia. *Nature* 326:692–694.
22. Luchterhand K, Kay RF, Madden RH (1986) Mohanamico hershkovitzi, gen. et sp. nov., a middle Miocene primate from South America. *Compt Rend Acad Sci Paris* 303:1753–1758.
23. Setoguchi T, Rosenberger AL (1985) Miocene marmosets: First fossil evidence. *Int J Primatol* 6:615–625.
24. Kay RF, Meldrum DJ (1997) A new small platyrrhine and the phyletic position of Callitrichinae. *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta Colombia*, eds Kay RF, Madden RH, Cifelli RL, Flynn JJ (Smithsonian Institution Press, Washington, DC), pp 435–458.
25. Takai M, Anaya F, Suzuki H, Shigehara N, Setoguchi T (2001) A new platyrrhine from the Middle Miocene of La Venta, Colombia, and the phyletic position of Callicebinae. *Anthropol Sci* 109:289–307.
26. Meldrum DJ, Kay RF (1997) *Nuciruptor rubricae*, a new Pitheciin seed predator from the Miocene of Colombia. *Am J Phys Anthropol* 102:407–427.
27. Fleagle JG (1999) *Primate Adaptation and Evolution* (Academic Press, San Diego).
28. Ford SM, Davis LC (1992) Systematics and body size: Implications for feeding adaptations in New World monkeys. *Am J Phys Anthropol* 88:415–468.
29. Kay RF (1994) "Giant" Tamarin from the Miocene of Colombia. *Am J Phys Anthropol* 95:333–353.
30. Rosenberger RL (1992) Evolution of feeding niches in New World monkeys. *Am J Phys Anthropol* 88:525–562.
31. Rosenberger AL (2002) Platyrrhine paleontology and systematics: The paradigm shifts. *The Primate Fossil Record*, ed Hartwig W (Cambridge Univ Press, Cambridge, UK), pp 151–159.
32. MacPhee RDE, Horovitz I (2004) New craniodental remains of the Quaternary Jamaican monkey Xenothrix mcgregori (Xenotrichini, Callicebinae, Pitheciidae), with a reconsideration of the Aotus hypothesis. *Am Mus Nov* 3434:1–55.
33. Anapol F, Lee S (1994) Morphological adaptation to diet in Platyrrhine primates. *Am J Phys Anthropol* 94:239–261.
34. Rosenberger AL (1977) *Xenothrix* and ceboid phylogeny. *J Hum Evol* 6:461–481.
35. Takai M, Nishimura T, Shigehara N, Setoguchi T (2009) Meaning of the canine sexual dimorphism in fossil owl monkey, *Aotus dindensis* from the Middle Miocene of La Venta, Colombia. *Comparative Dental Morphology: Selected Papers of the 14th International Symposium on Dental Morphology, August 27-30, 2008, Greifswalk, Germany (Frontiers of Oral Biology)*, eds Koppe T, Meyer G, Alt KW, Brook A, Dean MC (Karger, Basel), pp 55–59.
36. Ford SM (1990) Platyrrhine evolution in the West Indies. *J Hum Evol* 19:237–254.
37. Horovitz I, MacPhee RDE (1999) The quaternary Cuban platyrrhine *Paralouatta varoni* and the origin of the Antillean monkeys. *J Hum Evol* 36:33–68.
38. Rosenberger AL, Tejedor M, Cooke SB, Pekar S (2009) Platyrrhine ecophylogenetics in space and time. *South American Primates: Comparative Perspectives in the study of behavior, Ecology and Conservation*, eds Garber P, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (Springer, New York), pp 69–116.
39. Hershkovitz P (1970) Notes on Tertiary platyrrhine monkeys and description of a new genus from the late Miocene of Colombia. *Folia Primatol (Basel)* 12:1–37.
40. Fleagle JG, Powers DW, Conroy GC, Watters JP (1987) New fossil platyrrhines from Santa Cruz province, Argentina. *Folia Primatol (Basel)* 48:65–77.
41. Fleagle JG (1990) New fossil platyrrhines from the Pinturas formation, southern Argentina. *J Hum Evol* 19:61–83.
42. Rosenberger AL, Setoguchi T, Shigehara N (1990) The fossil record of callitrichine primates. *J Hum Evol* 19:209–236.
43. Fleagle JG, Tejedor MF (2002) Early platyrrhines of southern South America. *The Primate Fossil Record*, ed Hartwig W (Cambridge Univ Press, Cambridge, UK), pp 161–173.
44. Takai M, Anaya F, Shigehara N, Setoguchi T (2000) New fossil material of the earliest New World monkey, *Branisella boliviana* and the problems of Platyrrhine origins. *Am J Phys Anthropol* 111:263–281.
45. Kay RF (1980) Dental evolutionary trends of relevance to the origin and dispersion of the platyrrhine monkeys. *New World Monkeys and Continental Drift*, eds Ciochon RL, Chiarelli AB (Plenum Press, New York), pp 153–187.
46. Rosenberger AL (1979) Ph.D. Thesis (City University of New York, New York).
47. Szalay F, Delson E (1979) *Evolutionary History of the Primates* (Academic Press, New York).
48. Hodgson JA, et al. (2009) Successive radiations, not stasis, in the South American primate fauna. *Proc Natl Acad Sci USA* 106:5534–5539.
49. Rosenberger AL (2010) Platyrrhines, PAUP, parallelism, and the Long Lineage Hypothesis: A reply to Kay *et al.* (2008). *J Hum Evol* 59:214–217.
50. Kay RF, Fleagle JG (2010) Stem taxa, homoplasy, long lineages, and the phylogenetic position of *Dolichocebus*. *J Hum Evol* 59:218–222.
51. Fleagle JG, Rosenberger AL (1983) Cranial morphology of the earliest anthropoids. *Morphologie, Evolutive, Morphogenese du Crane et Anthropogenese*, ed Sakka M (Centre National de la Recherche Scientifique, Paris), pp 141–153.
52. Kay RF, Campbell VM, Rossie JB, Colbert MW, Rowe TB (2004) Olfactory fossa of *Tremacebus harringtoni* (Platyrrhini, early Miocene, Sacanana, Argentina): Implications for activity pattern. *Ann Rec Part A* 281A:1157–1172.
53. Tejedor MF, Tauber AA, Rosenberger AL, Swisher CC, III, Palacios ME (2006) New primate genus from the Miocene of Argentina. *Proc Natl Acad Sci USA* 103:5437–5441.
54. Rosenbeger AL (1978) New species of Hispaniolan monkey. *Annuario Cientifico Universidad Central del Este, Republica Dominicana* (Universidad Central del Este, San Pedro De Macoris, Dominican Republic), pp 249–251.
55. Roca AL, et al. (2004) Mesozoic origin for West Indian insectivores. *Nature* 429:649–651.
56. MacPhee RDE, Iturralde-Vinent MA (1995) Earliest monkey from Greater Antilles. *J Hum Evol* 28:197–200.
57. Maurrasse F, Pierre-Louis R, Rigaud J-G (1982) Cenozoic facies distribution in the southern peninsula of Haiti and the Barahona Peninsula, Dominican Republic, and its relations concerning tectonic evolution of the La Selle-Baoruco block. *Caribb Geol Coll Contr* 9:1–24.
58. Mann P, Draper G, Lewis JF (1991) An overview of the geologic and tectonic evolution of Hispaniola. *Geologic and Tectonic Development of the North America–Caribbean Plate Boundary in Hispaniola (Geological Society of America Special Publication 262)*, eds Mann P, Draper G, Lewis JF (Geological Society of America, Boulder, CO), pp 1–51.
59. Mertens R (1939) Herpetological results from a journey to Hispnaiola, West Indies (original title in German). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 449:1–84.
60. Williams EE (1961) Notes on Hispaniolan herpetology. 3. The evolution and re-lationships of the *Anolis semilineatus* group. *Mus Comp Zool Breviora* 136:1–8.
61. Schwartz A (1980) The herpetogeography of Hispaniola, West Indies. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 61:86–127.
62. Dod DD (1984) Massif de la Hotte, peculiar island: New orchid illuminates its history (original title in Spanish). *Moscosoa* 3:91–99.
63. Ricketts TH, et al. (2005) Pinpointing and preventing imminent extinctions. *Proc Natl Acad Sci USA* 51:18497–18501.
64. Townsend AK, Rimmer CC, Latta SC, Lovette IJ (2007) Ancient differentiation in the single-island avian radiation of endemic Hispaniolan chat-tanagers (Aves: *Calyptophilus*). *Mol Ecol* 16:3634–3642.
65. Ottenwalder JA (2001) Systematics and biogeography of the West Indian genus Solenodon. *Biogeography of the West Indies: Patterns and Perspectives*, eds Woods CA, Sergile FE (CRC Press, Boca Raton, FL), pp 253–259.
66. Turvey ST (2009) *Holocene Extinctions* (Oxford Univ Press, Oxford, UK).