

First skull of *Antillothrix bernensis*, an extinct relict monkey from the Dominican Republic

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The nearly pristine remains of *Antillothrix bernensis*, a capuchin-sized (*Cebus*) extinct platyrrhine from the Dominican Republic, have been found submerged in an underwater cave. This represents the first specimen of an extinct Caribbean primate with diagnostic craniodental and skeletal parts in association, only the second example of a skull from the region, and one of the most complete specimens of a fossil platyrrhine cranium yet discovered. Cranially, it closely resembles living cebines but is more conservative. Dentally, it is less bunodont and more primitive than *Cebus*, with crowns resembling *Saimiri* (squirrel monkeys) and one of the oldest definitive cebines, the late Early Miocene *Killikaike blakei* from Argentina. The tricuspid second molar also resembles the enigmatic marmosets and tamarins, whose origins continue to present a major gap in knowledge of primate evolution. While the femur is oddly short and stout, the ulna, though more robust, compares well with *Cebus*. As a member of the cebid clade, *Antillothrix* demonstrates that insular Caribbean monkeys are not monophyletically related and may not be the product of a single colonizing event. *Antillothrix bernensis* is an intriguing mosaic whose primitive characters are consistent with an early origin, possibly antedating the assembly of the modern primate fauna in greater Amazonia during the La Venta horizon. While most Greater Antillean primate specimens are quite young geologically, this vanished radiation, known from Cuba (*Paralouatta*) and Jamaica (*Xenothrix*) as well as Hispaniola, appears to be composed of long-lived lineages like several other mainland clades.

Keywords: fossil primates; platyrrhines; Caribbean; Dominican Republic; *Antillothrix*; island relicts

1. INTRODUCTION

Ricklefs & Birmingham [1] called the Greater Antilles a ‘laboratory of biogeography and evolution’. Interest in this region in the early 21st century (e.g. [2,3]) mirrors the attention given to it by biologists of earlier periods no less influential than A. R. Wallace and G. G. Simpson. Wallace [4] deemed it ‘one of the most interesting of zoological subregions’. Simpson [5,6] used its mammals in developing his sweepstakes deployment mechanism to counter speculative land bridge routes linking insular locations, and establishing quantitative methods for describing regional faunal similarities—both are cornerstones of modern biogeography. Interest blossomed further with the development of new ecological models, cladistic analysis,

continental drift, vicariance thinking and molecular phylogenetics (e.g. [7–11]). The Greater Antilles is also important as a laboratory for investigating recent extinctions [12].

The islands once harboured a largely endemic, depauperate mammalian fauna composed of insectivores, rodents, sloths, bats and primates. With the insectivores presumably coming from North America early in the Tertiary [13] and the bats being the exceptional travellers they are, it is the rodents, sloths and primates that potentially offer the most concerning historical biotic connections between the Greater Antilles and the mainland. The specimen described here, apparently a primitive relict of the South American mainland mammal fauna, provides important new information about the primates pertaining to phylogenetic derivation, temporal blueprint, ecological adaptation and patterns of mosaic evolution. It raises considerable doubt that the Caribbean monkeys could have originated from a single

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common ancestral species, as one major school of thought advocates [14].

2. THE ANTILLEAN PRIMATE FAUNA

The presence of native monkeys in the Caribbean islands seemed such an anomaly when the scrappy materials of the earliest candidates were discovered between 1888 and 1928 [15], it took another quarter century before the first good specimen was even recognized as a legitimate New World primate [16]. Since then, three genera have emerged in the Greater Antilles revealing a diverse radiation. Their morphological differences from one another and from the living mainland forms have fuelled debate concerning the phylogenetic and biogeographic models that might explain the group's origins. Discovery of the first platyrrhine cranium and its associated skeletal remains of *Antillothrix bernensis*, a fossil from the Dominican Republic, sheds light on these matters as well as the history and pattern of platyrrhine evolution on the mainland. This new material adds evidence supporting the notion that Antillean primates descended from archaic elements of the South American fauna, perhaps differentiating before the Amazonian neotropical community, dominant today, was assembled in the middle Miocene [17]. It adds new data pertinent to platyrrhine and anthropoid evolution generally, for the New World fossil record, apart from two stunning monkey skeletons from Brazil, is mostly composed of isolated jaws and teeth, and skulls that are edentulous, heavily tooth-abraded or crushed—a scant collection by comparison with the better-sampled Old World higher primates (e.g. [18]). The new find is one of only three fossil platyrrhine crania, out of more than two dozen genera, that preserve intact the vital morphology of cheek teeth, orbits, braincase and ear region.

Saimiri bernensis [19], since referred to *Antillothrix* [14], was the second authentic, extinct platyrrhine discovered in the Caribbean (electronic supplementary material, figure S1). It demonstrated unequivocally that indigenous primates once occupied the Greater Antilles and that the previously discovered *Xenothrix mcgregori* [16] was not a biogeographic oddity confined to Jamaica but part of a regional stock of insular monkeys derived from mainland South and/or Central America, probably without human intervention. The taxonomic scope of this splinter radiation has yet to be determined, but discovery of two additional species from Cuba, *Paralouatta varonai* [20] and *P. marianae* [21], the latter possibly dating to about 17.5–18.5 Myr before present, suggests the fauna has a long history, even though most of the known remains are only several thousands of years old, or fewer.

The phylogenetic relationships of each of the three Caribbean platyrrhines have been difficult to determine [15,16,19,22–30]. For *Antillothrix*, alternative interpretations range from an affinity with squirrel monkeys [19], with pitheciines [24], or exclusively with the other Caribbean platyrrhines in a new clade linked monophyletically with the modern titi monkey (*Callicebus*) of South America [14,30] (electronic supplementary material, figure S2). The divergence in views stems, in part, from the nature of the material discovered thus far. The original *Antillothrix* specimen is a partial maxilla

with three cheek teeth, including two molars exhibiting an unusual morphology. The two other specimens come from different, widely separated sites (electronic supplementary material, figure S1). Both of these latter assignments are questionable, however, as the material lacks conventional diagnostic information. One is a partial lower jaw with a single damaged molar from western Haiti [25], now apparently lost; the other a partial tibia from Samaná Bay, Dominican Republic [26,31].

3. GEOLOGICAL CONTEXT

The landscape of Padre Nuestro State Park where the specimen reported here was discovered includes a karst formation of raised Quaternary corals [32] marked by caves both wet and dry. The discovery site, La Jeringa Cave, is a submerged natural limestone tunnel system that once served as a freshwater aquifer. It was mapped by divers in 2009. Vertebrate remains, including the primate, were collected by Walter Pickel and Curt Bowen in October 2009, under the auspices of the Museo del Hombre Dominicano, Secretaría de Estado de Medio Ambiente y Recursos Naturales de la República Dominicana (SEMARENA), and Brooklyn College. The location is about 25 km from the *Antillothrix* type site of Cueva de Berna, near Boca de Yuma (electronic supplementary material, figure S1). The new primate, discovered 28 July 2009, was an isolated find located in the Monkey Room, a distinct chamber of the system that opens beneath a structural fracture in the limestone ceiling. The excellent condition of the specimen, little damaged and with multiple anatomical regions represented, and the confined distribution of the material suggests minimal post-decomposition transport of the carcass's parts, which ultimately were strewn in a natural rubble pile forming the cave floor. Other mammals collected at La Jeringa Cave, including sloths and rodents, were concentrated near its mouth, in small fields about 75 m and three to four tunnel-turns away from the Monkey Room. They are an unrelated taphonomic assemblage. While the primate specimen has proved undatable thus far, a C¹⁴ date from the Cueva de Berna excavation produced an associated age of 3850 ± 150 [19] for the type of *A. bernensis*.

4. DESCRIPTION AND COMPARISON

The specimen (figures 1–3; electronic supplementary material, figure S3 and tables S1 and S2) is of an unworn young adult, with well-formed M³ alveoli. It consists of the greater part of a cranium (lacking mandible) with pristine premolar and molar teeth *in situ*, a femur and ulna with epiphyses missing, one vertebra and five whole ribs. Sex is uncertain because the anterior snout, including the premaxillae and canines, is missing. However, the posterior surfaces of both canine alveoli are preserved. Their size and shape is suggestive of a large-canined male. The cheek teeth of the La Jeringa find closely match the type specimen (figure 2). Their size differences are negligible (electronic supplementary material, table S2). They differ morphologically only in that the new specimen has slightly puffer cusps and the P⁴ is approximately 20 to 25 per cent wider when considering breadth : length ratio.



Figure 1. The *Antillothrix bernensis* skull (MHD-01) shown in several views: (a) right, (b) left, (c) superior, (d) anterior and (e) inferior. Measurements in millimetres (unless otherwise noted) include: maximum length of the incomplete skull lacking the premaxillae [78.75], cranial capacity [58 cm³], interorbital breadth [6.62], biorbital breadth [44.38], orbital height [20.50], orbital width [18.51], post-orbital constriction [37.48], bimolar width [25.50] and nasion–basion [46.56]. Scale bar, 1 cm. See electronic supplementary material, tables S1 and S3.

The La Jeringa specimen also differs from the type in the number of roots found on P³ and P⁴. The type has two roots on each of these teeth while the new specimen has three. *Antillothrix* teeth generally resemble *Cebus* and *Saimiri* in proportions and cusp patterns, although the crowns of squirrel monkeys are more cristodont while those of Capuchins are more bunodont. In this narrow frame of reference, *Antillothrix* postcanines would be categorized as being morphologically intermediate, though more similar to *Saimiri* overall, in part because the *Cebus* hypocone is large and connected to the trigon in its own distinctive way.

Cranial measurements suggest this individual approaches the size of a small capuchin monkey (electronic supplementary material, table S1 and figure S3). Sex-pooled, wild-shot adult weights for four species of *Cebus* range from 2110 to 3212 g [33,34]. Estimates of body mass in fossil platyrrhines based on cranial spans and maxillary postcanine tooth measures are not highly reliable [35]. A more robust estimate can potentially be obtained using lower molars [36,37], although the one isolated primate mandible and tooth attributed to *A. bernensis* by MacPhee et al. [14] is problematic. Using this M₁ yields an average weight of 4.7 kg, as derived from five regression equations relating dental measures to adult body mass in platyrrhines and/or anthropoids [36,38,39]. This suggests that the species would have been about 50 per cent larger than the heaviest reported samples of wild-shot adult capuchins, *Cebus capucinus* [33,34]. However, several standard cranial dimensions, other than interorbital breadth, average about 10 per cent smaller than adults of *C. apella*, a species with mean weights between 2110 [34] and

2645 g [33]. Assignment of the Haitian lower jaw to *A. bernensis* thus remains questionable, and a more precise body weight projection for the species still needs to be determined.

The La Jeringa cranium was reconstructed from more than 20 fairly large pieces, none of which were warped. Many were bones that separated at barely knit sutures. They fitted together very well at the joints; other pieces presented fresh breaks for which the matching edges were also easily attached. The final assembly, however, includes a few misalignments of the cranial modules as we rebuilt them. All of the major paired bones of the cranium are present on at least one side and the unpaired basicranial bones are also unbroken. This allowed a fairly accurate reconstruction of braincase size and shape, which yields an estimated endocranial capacity of 58 cm³. In the face, the premaxillae and the nasals are missing, but a lacrimal is intact on the left side. Parts of the petrosal bullae suffered superficial damage, but much of the internal and external anatomy is preserved on at least one side.

All major modern platyrrhine clades are easily distinguishable by the skull (electronic supplementary material, table S3). The cranium of *Antillothrix*, which is roughly midway in size between *Cebus* and *Saimiri* (electronic supplementary material, table S1), compares well with cebines (*Cebus*, *Saimiri* plus fossils) in appearance and generally resembles *Cebus* (electronic supplementary material, figure S3). In pattern and detail, cebine crania are recognized as being highly derived among platyrrhines, built around such non-primitive features as a short face, close-set eyes and a large, smoothly vaulted braincase housing a relatively large brain. There are no craniodental features suggesting

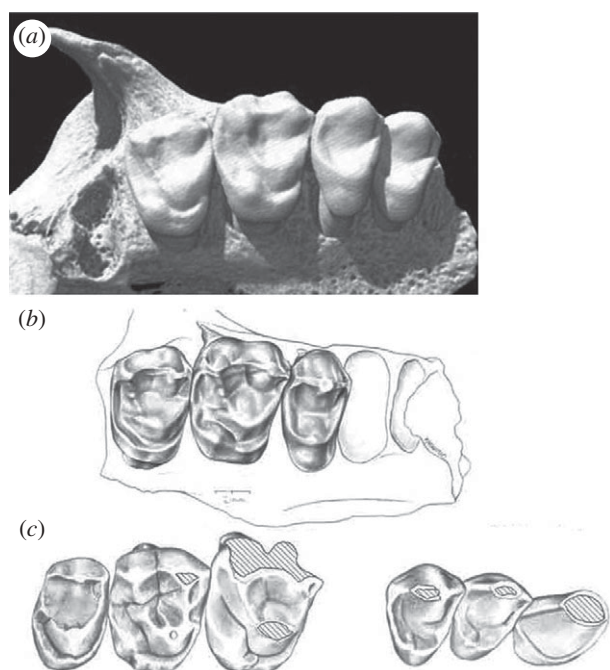


Figure 2. Comparison of (a) the new dentition of *Antillothrix bernensis* with (b) the type specimen (P^3 - M^2) and (c) the early Middle Miocene cebine from Patagonia, *Killikaike blakei* (C - P^3 , M^1 - M^3). Measurements of the new specimen are (mesio-distal length, bucco-lingual breadth; in mm) as follows: P^3 [3.6, 6.1], P^4 [3.6, 6.6], M^1 [5.3, 7.1] and M^2 [4.8, 6.8]. (a) is from a micro-computed tomography scan and is canted slightly buccally. Note the proportionately large and broad premolars (and alveoli) of *Antillothrix*, compared with the more triangular, proportionately smaller anterior premolars of *Killikaike*; the heteromorphy of M^1 and M^2 ; and the strong resemblance of M^1 with the $M^{1,2}$ of *Killikaike*. See electronic supplementary material, table S2.

that the fossil has an affinity with any other platyrrhine clade. One likely primitive platyrrhine feature [22] not seen in *Cebus* or *Saimiri* but evident in *Antillothrix* is a steeply angled nuchal plane, which is also found in two early Middle Miocene forms, *Dolichocebus* and *Tremacebus* [40]. The shape of its posterior braincase, therefore, contrasts markedly with the low, rounded, less inclined and posteriorly prolonged occiputs of *Cebus* and *Saimiri*. With respect to the interorbital region, a very narrow fronto-nasal pillar is characteristic of *Cebus*, *Saimiri* and *Killikaike*, and occurs convergently in some pitheciines. The state of *Antillothrix* (electronic supplementary material, figure S4), which is somewhat wider relatively, may be authentically more primitive than the other cebines, or it may represent a (relatively minor) reversal of state.

Like these cebines, $P^{3,4}$ of *Antillothrix* are bucco-lingually wide, with wide shallow internal basins (figure 2). Each tooth has a large flaring protocone sidewall that lacks the distinct shelf-like cingulum seen in *Saimiri* and some *Cebus*. On P^4 , this region is angled mesially, giving the tooth a slightly bent or kidney-bean-shaped appearance in crown outline, which contributes to a large interproximal embrasure between P^4 and M^1 . This feature differentiates *Antillothrix* from modern cebines, where the $P^{3,4}$ crowns tend to be simple transverse ellipses in occlusal view and P^4 is packed closely



Figure 3. Comparison of the femur (a, anterior view; b, posterior view) and ulna (c, lateral; d, medial) of *Antillothrix bernensis* (top) and a male *Cebus apella* with unfused epiphyses (bottom). Scale bar, 1 cm. See electronic supplementary material, figures S5 and S6.

against the mesial aspect of M^1 . M^1 is bucco-lingually wide with distinct trigon cusps connected by strong crests outlining a shallow trigon basin. As in the type specimen of *Antillothrix*, the postprotocrista divides near the base of the metacone and gives off a small crest running into the talon. This 'distal crest', described by MacPhee *et al.* [14] as a diagnostic feature of the species, appears on $M^{1,2}$. Lingually, M^1 has a prominent distal cingulum with a distinct, low hypocone, which is slightly more bulbous on the type than the new specimen. In both cases the hypocone is offset on the cingulum rather than merged with the protocone, does not form a shelf-like extension of the talon basin and lacks a prehypocrista crest tying the cusp to the back of the trigon. The lingual cingulum continues around the tooth distally to outline a small to moderately sized talon region. Mesially, it becomes flush with the front sidewall of the tooth midway between protocone and paracone.

M^2 is similar to M^1 in the morphology of the trigon, but it lacks a distinct hypocone; instead, it has only a small rise along the cingulum disto-lingual to the protocone (figure 2). Such $M^{1,2}$ heteromorphy is unique among New World monkeys. Living non-callitrichine platyrrhines universally exhibit the hypocone on both $M^{1,2}$ and show no variation in this feature despite difference in hypocone morphology. Among moderns, only callitrichines fully lack an M^2 hypocone and they also lack one on M^1 , except for *Callimico*, where the M^1 hypocone is very small if it is at all definable as distinct from the cingulum.

5. DISCUSSION

The addition of a P^3 crown to the hypodigm adds evidence supporting the initial interpretations of *Antillothrix* as a cebid¹ [19,25]. Homomorphically wide P^3 s and P^4 s (and P^2 s) with well-formed internal basins and strongly developed lingual regions are typical of *Saimiri* and *Cebus* among living platyrrhines. The *Antillothrix* $P^{3,4}$ are similarly configured, and P^2 probably had a wide crown as well, judging by its very broad alveolus (figure 2). Such a pattern is also found in *Chilecebus*, from the late Early Miocene [41], but in *Killikaike* the $P^{2,3}$ crowns are relatively narrow, not enlarged lingually, and have a triangular crown occlusal outline. The P^4 of the late Early Miocene cebine *Dolichocebus* [40] is also broad with a cusp-filled, large basin. As there is good cranial and molar evidence showing *Killikaike* is a cebine [42], and its molars conform to expectations of the plesiomorphic cebid pattern, we take its simple, narrow premolars to be ancestral among cebines. *Chilecebus* is insufficiently known morphologically. Its affinities may lie with cebines [43] or elsewhere. But it appears to have unusually wide $P^{3,4}$ s combined with relatively large molar crowns. The whole series has distinctly enlarged distolingual features, including molars with large lingual cingula and unusually expanded but low molar hypocones. This suggests that resemblances of *Chilecebus* to modern cebines and *Antillothrix* in premolar shape may be convergent.

The *Saimiri*-like occlusal morphology of the *Antillothrix* M^1 also resembles *Killikaike* (figure 2) and is not grossly dissimilar from one of the oldest platyrrhines, the late Oligocene *Branisella*, although the latter has relatively broader molar crowns, probably a primitive platyrrhine feature. They all share a common architecture: at least moderately cristodont, transversely organized molars with moderately developed hypocones, well-formed, continuous trigon crests and an extensive lingual cingulum. *Cebus* differs in having an enlarged, elevated hypocone, blunter cusps, de-emphasized crests, absent lingual cingulum and enamel that is probably thicker overall.

The marked heteromorphy of $M^{1,2}$ (figure 2) in *Antillothrix* is a feature without parallel among extant and extinct platyrrhines. This pattern may eventually turn out to be broadly relevant to callitrichines, whose phyletic origins and anatomical transformation remain one of the more interesting problems in primate evolution. It is widely accepted that callitrichines and cebines are monophyletically related (e.g. [24,44]), and the presently favoured working hypothesis is that they are a highly modified dwarfed radiation with a novel

dentition (e.g. [45]). Their molars appear to have been reduced from a four-cusped to a three-cusped occlusal pattern. For *Antillothrix*, the equilateral arrangement of trigon cusps and modest, lingually positioned M^1 hypocone, which occurs in combination with little more than a cingulum on M^2 , could be interpreted as a synapomorphic pattern presaging crown simplification in callitrichines. Further study may clarify whether other evidence would support this hypothesis as opposed to the more conservative, preliminary position we adopt here that *Antillothrix* is a cebid without demonstrable close ties to either cebines or callitrichines. On the basis of the femoral anatomy of a primate specimen without certain taxonomic allocation, Ford [26] earlier suggested that ‘giant’ callitrichines were present on Hispaniola.

The morphological evidence is too limited to assess the adaptations of *Antillothrix* in detail, but the novelty of this find compels us to present some initial observations. Analogies with *Cebus* are important in this regard, as there are numerous mutual resemblances in ecologically and biomechanically significant features: rough comparability in body mass and cranial capacity; gracility of braincase features such as the temporal lines; flat glenoid fossa; short postglenoid process; shortness of face; development of maxillary sinuses; and prominence of the premolar series (electronic supplementary material, figure S3). We hasten to add that the smaller-bodied *Saimiri* overlaps in this anatomical suite as well, but it also exhibits a radically modified cranial architecture and craniofacial proportions. The absence of bunodonty, enlarged hypocones, a platform-like series of close-packed molar and premolar crowns, and thick enamel indicates little or no evolutionary commitment to the challenging, hard-chewed diet found in the most modified species of *Cebus*, *C. apella*, which involves specialized crushing-and-grinding masticatory features [34,46,47]. More like *Saimiri*, *Antillothrix* tends towards a cristodont molar crown design. This points to a diet dominated by more succulent fruits, fewer hard seeds and less pith or other fibrous material—certainly not leaves—combined with insects and other forms of prey. This is a feeding profile more like the ‘unspecialized’ members of *Cebus* (see [48]) but perhaps not as animal-based as the highly predaceous *Saimiri* (i.e. a primitive version of the distinctly omnivorous *Cebus* plan). This model is in keeping with the hypothesis that cebids were probably frugivore–insectivores at their base [34,49].

The postcranials are intriguingly novel. The ulna is comparable in length to that of various species of *Cebus*, which may indicate it is long with respect to body size, but the femur is stout and relatively short (electronic supplementary material, figures S5 and S6). This suggests a behavioural contrast not only with *Cebus* but also with the other middle-sized platyrrhines of approximately 1–3.5 kg body mass (see [50]). The latter tend to have long, slender legs, and they engage mostly in quadrupedalism and leaping. A short, stout femur, albeit less robust, has also been found in *Xenothrix*, from Jamaica [29]. It was interpreted as evidence of a slow form of quadrupedal locomotion. The Cuban *Paralouatta* is also distinctive postcranially in exhibiting features suggesting semi-terrestriality [39]. If this pattern holds, it would appear that Caribbean platyrrhines employed postural and locomotor

modalities unlike those prevalent among the modern New World monkeys, perhaps signifying markedly contrasting ecological circumstances. For *Antillothrix*, a short, robust femur combined with a relatively long forearm may be indicative of arboreal clinging and climbing on relatively large non-horizontal supports. Forelimb elongation may also be associated with extractive foraging for prey in New World monkeys (see [22]).

6. CONCLUSIONS

The morphology of *Antillothrix* points to an affinity with cebids, albeit, as indicated, appearing to be somewhat more primitive than modern cebines in some respects and callitrichines in others. There are no evident derived characters shared with any of the other major clades or individual extant genera outside Cebidae. Given its skull size and inferred body size bracket, *Antillothrix* does not meet the derived mass thresholds of the largest (atelines) or smallest (callitrichines) platyrrhines (electronic supplementary material, table S3). The dental and facial morphology is fundamentally unlike the saki-uakari pitheciines (*Pithecia*, *Chiropotes*, *Cacajao*). The bulla and temporomandibular morphology lacks the derived features exhibited by *Aotus* and *Callicebus* [51]. Nor are there any compelling phenotypic or apomorphic similarities suggesting a phyletic connection with the other Caribbean genera themselves—*Xenothrix* and *Paralouatta*. Concerning fossils on the mainland, *Antillothrix* resembles the 14.6-Myr-old cebine *Killikaike blakei* from Patagonia [42] in M¹ morphology in particular, and there is resemblance to the older *Dolichocebus* as well. Another very large-bodied cebine from western Brazil, *Acrecebus fraileyi*, approximately 8 Myr old [52], is more closely related to *Cebus* and contrastive anatomically, having attained the large hypocone, crown bunodonty and quadrate cusp-and-crest arrangement associated with modern capuchins.

As a securely recognizable cebid from the Caribbean, *Antillothrix* lends support to one of the two origination models for the Greater Antillean primates. It means more than a single platyrrhine clade is represented in the extinct indigenous fauna. MacPhee and co-workers (e.g. [15]) proposed that all these primates radiated from a sole ancestral species linked cladistically with the mainland pitheciine atelid *Callicebus*. Rosenberger [24] argued instead that at least two clades were present, one embodied by *Paralouatta*, related to howler monkeys, and another by *Xenothrix*, possibly related to *Aotus*—or to *Callicebus*, according to his earlier view [23]. While the specifics of these two phylogenetic hypotheses may be debated, evidence of a cebid element in the fauna is fundamentally inconsistent with the essentials of the monophylum notion as proposed by MacPhee & Horovitz [15], including its implied single colonizing event. The more parsimonious working hypothesis, barring a still untestable multiple dispersal scenario, is that the Antillean primates are a stranded community comprised of as many as three major platyrrhine clades that became isolated in the Caribbean: atelines, pitheciines and cebids [17]. But reconstructions of the Caribbean basin during the Miocene indicate that inter-island faunal connections would have been rare and intermittent. The older Tertiary subaerial peninsular extension that might

have been a feeder platform into the Greater Antilles from the coast of Venezuela was largely defunct by the Oligocene–Miocene boundary [53]. Given this phylogenetic structure, the Antillean primates may conform to the over-dispersed model of Cardillo *et al.* [2], wherein the assemblage is composed of forms not randomly drawn from the source stock, but they are less closely related than expected.

Additional information is necessary to determine the timing and patterning of events involved in the origins and differentiation of the primate fauna. However, at least two genera present indirect evidence in accordance with the idea that relocation to the proto-Greater Antilles was an ancient occurrence. Both *Paralouatta* and *Antillothrix* are curiously primitive in aspects of their morphology relative to their nearest living relatives. In the case of *Antillothrix*, resemblances to fossils penetrate deeply in time to the Patagonian early Middle Miocene. Similarly, the upper molars of *Paralouatta* are clearly more primitive than those of the Middle Miocene La Ventan *Stirtonia*, a genus stunningly similar to living *Alouatta*.

This suggests the Caribbean assemblage may be composed of relicts derived from the mainland platyrrhine radiation before the La Venta horizon, which is near the time when the modern geophysical and biotic configuration of the Amazonian basin was emerging [54]. An early origin for *Antillothrix* involving cebines or callitrichines, or a more basal lineage, is accommodated by both palaeontological and molecular evidence. For example, Schneider *et al.* [44] estimate the beginnings of cebids at 23 Myr, cebines at 22 Myr and callitrichines at 16 Myr before present, well before the lowlands began to modernize. This brackets the maximum likely age of Cuba's *Paralouatta marianae* as 17.5–18.5 Myr old [21]. The retained primitiveness and long lineage histories of *Paralouatta* and *Antillothrix* further imply that the Caribbean monkeys may have been prone to long periods of morphological stasis, like an impressive number of their mainland counterparts (e.g. [55]), thus shedding a unique insular light on this phenomenon and a little-known phase of pre-Amazonian platyrrhine evolution.

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ENDNOTE

¹The family-level classification of platyrrhines is in flux. We use the concept Cebidae to include living and fossil genera within the cebine (*Cebus*, *Saimiri* plus fossils) and callitrichine (*Callithrix*,

Cebuella, *Saguinus*, *Leontopithecus*, *Callimico* plus fossils) clades. Here we do not include *Aotus* (owl monkeys) among cebids, although this view is advocated by S.C.

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