



News and Views

Preliminary notes on a newly discovered skull of the extinct monkey *Antillothrix* from Hispaniola and the origin of the Greater Antillean monkeys

Richard F. Kay^{a,*}, Kevin D. Hunt^b, Charles D. Beeker^{b,c}, Geoffrey W. Conrad^{b,d}, Claudia C. Johnson^e, Jessica Keller^c

^a Department of Evolutionary Anthropology, Duke University, Durham, North Carolina 27708, USA

^b Department of Anthropology, Indiana University, Bloomington, Indiana 47405-7100, USA

^c Office of Underwater Science, School of Health, Physical Education and Recreation, Indiana University, Bloomington, Indiana 47405, USA

^d William Hammond Mathers Museum, Indiana University, Bloomington, Indiana 47408-3812, USA

^e Department of Geological Sciences, Indiana University, Bloomington, Indiana 47405-1405, USA

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Introduction

In July 2009, a team from Indiana University discovered a spectacularly preserved cranium of an extinct platyrrhine primate of middle Holocene age in the Padre Nuestro underwater cavern complex, southeastern Dominican Republic, Hispaniola (Fig. 1).

The skull (specimen number PNE-PNP-PN-09-01, PN-09-01¹ for short; Fig. 2) is referred to *Antillothrix bernensis*, and until recently was known only from a few jaw fragments and teeth. Here, we place the discovery on record, briefly describe the pertinent information about the cavern and its associations, and offer some comments on its phylogenetic affiliations and adaptations. PN-09-01 was recovered from the Padre Nuestro cavern, part of an interconnected cave complex accessible through several openings of which Padre Nuestro is one (Conrad et al., 2001; Beeker et al., 2002). The cavern entrance is <10 m above sea level. Explored parts are filled with fresh water, but travertine formations are

present that only form in dry conditions. The fossil material was found <50 m from the cavern entrance at water depths of 5–10 m. Also recovered were fragments of carbonized wood, flaked stone tools, and thousands of bones of extinct sloths, caviomorph rodents, soricomorphs, fish, birds, reptiles, and terrestrial and nearshore marine gastropods. Several lines of evidence suggest that this material is no younger than mid-Holocene.

First, a working hypothesis is that the cave drowned 6,500 years BP when worldwide sea levels rose to within 3 m of current levels, having risen 22 m in the preceding 1500 years (Fleming et al., 1998). Curtis et al. (2001) suggest that as the Holocene progressed, water levels in such caves responded to global sea level changes, rather than merely to local hydrologic changes.

Second, pre-ceramic “Casimiroid” lithics also occur deep in the cave, but ceramics occur only at the very front in <1 m of water. The earliest reported radiometrically dated human occupation of Hispaniola of the “Casimiroid” type is 5780–6180 yrs BP (Veloza Maggiolo and Vega, 1982; Moore, 1991; Wilson et al., 1998; MacPhee et al., 2007; Wilson, 2007).

Third, while PN-09-01 is undated, remains of the extinct sloths referable to *Acratocnus* and *Parocnus* (McDonald, personal communication; Keller, 2009) were found in close association. The only dated occurrence of these taxa in Hispaniola is a date for *Parocnus* at Trouing Gallery that is greater than 14,200 years BP (Steadman et al., 2005).

Lastly, the type specimen of *Antillothrix bernensis* (CENDIA-1¹) (Rímoli, 1977) was dated at 3,850 ± 135 BP. This date should be considered a minimum age because the dated plant material came from a stratigraphic level 10–20 cm above the primate and other vertebrate remains and is not associated with human activities (Rímoli, 1977).

The Skull

PN-09-01 (Fig. 2) is the best preserved primate cranium and only the third skull of any primate found in the Greater Antilles. A skull of *Paralouatta* (see below) from Cuba is more fragmentary. The fossil record of primates from the island of Hispaniola is particularly poor.

* Corresponding author.

E-mail address: richard.kay@duke.edu (R.F. Kay).

¹ Abbreviations: PNE-PNP: Parque Nacional Del Este-Padre Nuestro Park. CENDIA: Centro Dominicano de investigaciones Antropológicas, UASD; MHD: Museo del Hombre Dominicano.



Figure 1. Entrance to the Padre Nuestro cave, a part of the Padre Nuestro cave complex in southeastern Dominican Republic.

The only extinct species formally described is *Antillothrix bernensis*, based on the type maxilla preserving P^3 – M^1 , root sockets for C^1 and P^2 , and a referred fragmentary mandible with M_2 (Rímoli, 1977; MacPhee and Woods, 1982; MacPhee et al., 1995). Another specimen consisting of a skull reassembled from fragments, associated with postcranial bones of a young adult *Antillothrix*, was reported after submission of this manuscript (Rosenberger et al., 2010).

The type maxilla of *Antillothrix bernensis* is directly comparable with PN-09-1, making allocation to that species secure. The tooth crown dimensions and proportions of P^4 – M^2 of the type and referred specimen are within 10% of one another. P^4 of CENDIA-1 is 12% buccolingually broader than PN-09-1. Similar within species variability is encountered in ten specimens of *Cebus capucinus*. Judging from the root sockets of the C – P^3 , the proportions of the anterior teeth are likewise similar: the canine socket is as large as that of the M^1 ; alveoli of a single-rooted P^2 and two-rooted P^3 follow a graded size increase with respect to P^4 . In both specimens, P^4 has two cusps and a poorly developed lingual cingulum. In both specimens, M^1 is larger than M^2 . M^1 and M^2 have four principal cusps. A distolingually positioned hypocone is supported by a strong lingual cingulum that wraps lingually around the protocone and is separated from the trigone by a pronounced sulcus. All teeth have weak buccal cingula. Accessory cusps also are weak (M^1 paraconule) and/or absent (M^1 – M^2 metaconule). The length and sharpness of the cusps and crests is moderate, comparable with those of extant *Pithecia* or *Cebus*.

Phylogenetic and biogeographic hypotheses

Three genera of extinct platyrrhines are known in the Greater Antilles—one each from Cuba, Jamaica, and Hispaniola.

Paralouatta, from the late Quaternary of Cuba, is known from the skull of an old individual, unassociated postcranial bones, and isolated teeth (Rivero and Arredondo, 1991; Horovitz and MacPhee, 1999; MacPhee and Meldrum, 2006). A talus from the late early Miocene of Cuba (MacPhee et al., 2003) is referred to *Paralouatta marianae* (MacPhee, 2009). Some regard *Paralouatta* to be closely related to the living howler monkey, *Alouatta* (Rivero and Arredondo, 1991; Rosenberger, 2002). Others hold that resemblances between *Alouatta* and *Paralouatta* are homoplastic and that the latter forms a clade with *Xenothrix* and *Antillothrix* (see below) (Horovitz, 1999; Horovitz and MacPhee, 1999).

Holocene-aged *Xenothrix* from Jamaica is documented from several mandibles, a palate, and limb bones (Williams and Koopman, 1952; Rosenberger, 1977, 2002; MacPhee and Fleagle, 1991; MacPhee and Horovitz, 2004; MacPhee and Meldrum, 2006). Rosenberger (1977) and Rosenberger et al. (1990) identified a combination of dental and mandibular features that support an affiliation with the living pitheciid, *Callicebus*. Ford and Morgan (1986) thought that *Xenothrix*, by virtue of its reduced molar formula, might be a large callitrichine. Based upon the larger sample, Horovitz and colleagues (Horovitz, 1999; MacPhee and Horovitz, 2004; MacPhee and Meldrum, 2006) agree with Rosenberger (1977) that *Xenothrix* is related to *Callicebus*. They demonstrate that *Xenothrix* does not have large orbits, as Rosenberger (2002) claimed, and therefore shows no special similarity to *Aotus*.

The Hispaniolan monkey *Antillothrix* was, until 2010, the most poorly known Greater Antillean monkey. The first specimen was described as a new species of *Saimiri* by Rímoli (1977). MacPhee and Woods (1982) agreed that CENDIA-1 is cebine, but elevated it to a new genus, *Antillothrix*. Some researchers continue to regard *Antillothrix* as a cebine (*Saimiri* plus *Cebus*) (Rosenberger, 2002; Rosenberger et al., 2010), while others combine *Antillothrix*, *Paralouatta* and *Xenothrix* into a clade that they consider to be a sister-taxon to *Callicebus* (MacPhee et al., 1995; Horovitz, 1999; MacPhee and Horovitz, 2004) (Fig. 3).

PN-09-01 evinces a number of features at odds with all current phylogenetic views. *Antillothrix* lacks a host of shared-derived cranial features that characterize crown cebines (*Cebus* and *Saimiri*). As noted by Rosenberger (1979), cebines have unusually narrow interorbital regions, dorsoventrally narrow zygomatic arches, shallow glenoid fossae, and weak postglenoid processes. The cebine brain is disproportionately large for a platyrrhine (Isler et al., 2008) and the neocortex is expanded over the olfactory bulbs. The outer table of the frontal conforms to the profile of the neocortex (Kay and Fleagle, 2010). Posterior expansion of the brain has repositioned the foramen magnum beneath the braincase, yielding a quite horizontal nuchal plane. Also, perhaps as a consequence of brain enlargement (Ross and Ravosa, 1993), the cebine angle of basicranial flexion is relatively acute, producing a pronounced klinorhynch.

PN-09-01 has none of the above mentioned crown cebine features. Its interorbital region is broad and glabella is broadly separated from a relatively small frontal cortex by a thick layer of spongy bone (a frontal sinus is not present). The zygomatic arch is dorsoventrally deep, and a very strong postglenoid process borders the glenoid fossa posteriorly. The nuchal plane is oriented quite vertically, and the angle of basicranial flexion is distinctly air-orhynch. Some of the features of the new skull (the robusticity of the zygomatic arch and the degree of cranial flexure) are unknown hitherto—the area is broken away in the recently described specimen MHD-01¹ (Rosenberger et al., 2010). PN-09-01 and MHD-01 apparently differ in several features. Rosenberger et al. (2010)

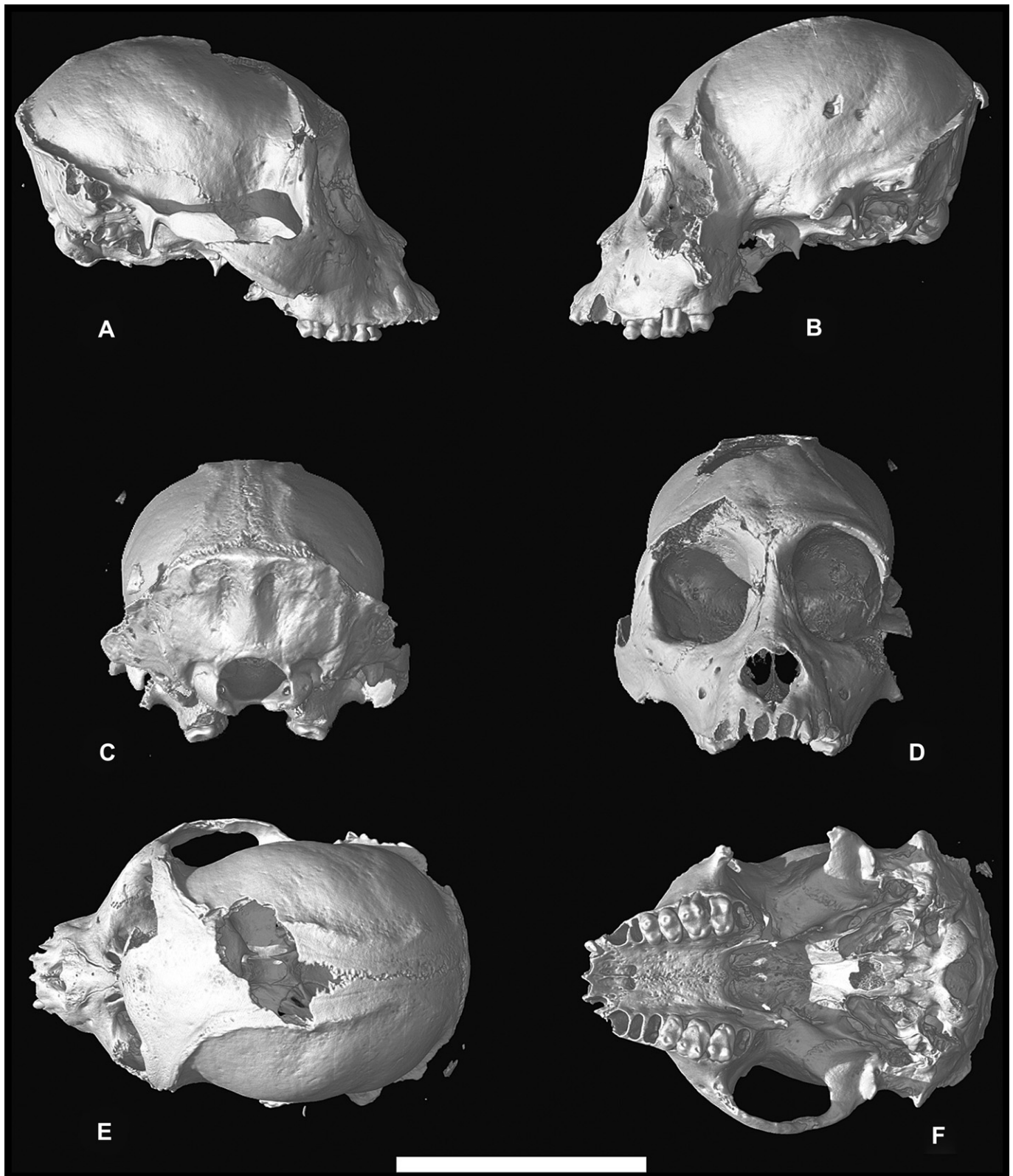


Figure 2. CT reconstruction of the skull of *Antillothrix* cf. *A. bernensis*, Field number PN-09-01 (Museo del Hombre Dominicano). A. right lateral, B. left lateral, C. posterior, D. frontal, E. dorsal, F. ventral. Scale bar equals 5 cm.

report a narrow interorbital breadth and a small postglenoid process in MHD-01. These features may be accounted for by age differences. PN-09-01 is a mature specimen, whereas MDH-01 is a late juvenile or very young adult, as indicated by epiphyses

missing from the femur. Taken as a whole, the newly recognized anatomy does not support cebine affinities for *Antillothrix*.

Furthermore, *Antillothrix* does not exhibit any convincing features indicative of a relationship with *Callicebus*, as suggested by

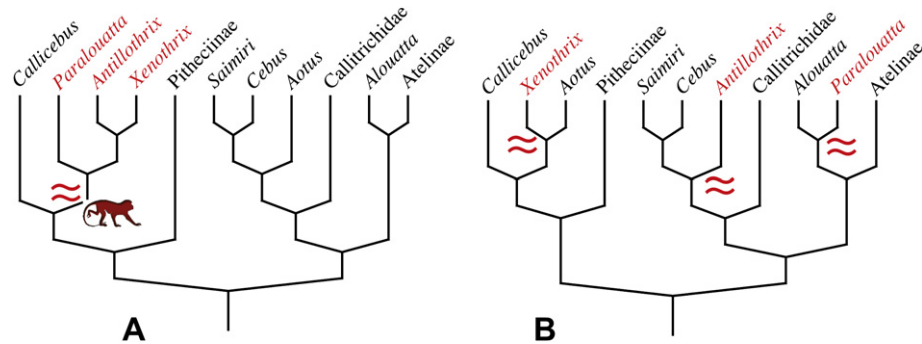


Figure 3. Simplified scenarios of platyrrhine origins in the Greater Antilles. A. Hispaniolan primates *Antillothrix*, *Paralouatta*, and *Xenothrix* form a clade sister to *Callicebus* (Pitheciidae) that arrived in the Antilles either by vicariance (monkey symbol) or less likely by rafting (wavy lines) (Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004). B. Hispaniolan primates *Antillothrix*, *Paralouatta*, and *Xenothrix* are variously related respectively to cebines (*Saimiri* and *Cebus*), *Alouatta*, and *Callicebus* (or *Aotus*), and each arrived by rafting (wavy lines) (Rosenberger, 1977; Rosenberger et al., 1990; Rosenberger, 2002; Rosenberger et al., 2010).

Horovitz and MacPhee (1999). Among the derived features of *Callicebus* are the robust, ventrally deflected zygomatic arch, the presence of paired prominences in the middle ear where two coils of the cochlea bulge into the middle ear, and the presence of a small canine relative to premolar size (Horovitz and MacPhee, 1999). The robust zygomatic arch of *Antillothrix* is not ventrally displaced as in *Callicebus*, and only one cochlear coil bulges into the middle ear cavity.

Finally, several aspects of the anatomy of *Antillothrix* argue against the hypothesis that *Antillothrix*, *Xenothrix* and *Paralouatta* form a monophyletic clade related to the Pitheciidae, as Horovitz and MacPhee have suggested (MacPhee et al., 1995; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004). In *Xenothrix* and *Paralouatta*, the nasal cavity is broadly expanded so that it overlaps the roots of M¹ in coronal cross-section (Figure 10 in Horovitz and MacPhee, 1999). Horovitz and MacPhee (1999) suggested that a broad nasal cavity is a shared derived feature among Antillean monkeys. However, PN-09-01 evinces the typical platyrrhine narrow nasal fossa (CT scan, not illustrated).

Perhaps the most surprising feature of PN-09-01 is the arrangement of the bones at pterion. In extant platyrrhines, the parietal broadly contacts the zygomatic, excluding the frontal from contact with the sphenoid, whereas living and fossil catarrhines have a frontal-sphenoid contact. *Antillothrix* has the catarrhine condition. Stem platyrrhines from the early Miocene (*Tremacebus* and *Homunculus*) also have this ‘catarrhine’ arrangement of bones (Tauber, 1991; Kay et al., 2008), suggesting that this is the primitive condition for crown anthropoids and that perhaps *Antillothrix* has a deep evolutionary history independent of mainland species.

Although far more information needs to be accumulated to support it, the absence of evident synapomorphies between *Antillothrix* and any of the living families of platyrrhines or their extinct relatives, in combination with the presence of several important symplesiomorphies not found in crown platyrrhines, hints that *Antillothrix* is a stem platyrrhine unrelated to any of the living families of South American monkeys.

Adaptations

Antillothrix was a medium-sized platyrrhine (2–5 kg) (MacPhee and Meldrum, 2006). Rosenberger et al. (2010) describe a femur and ulna of the same animal, and suggest that this species was a heavily built arborealist that may have engaged in arboreal climbing. However, an undescribed distal humerus from Trou Wôch Sa Wo, Haiti, associated with teeth referable to *A. bernensis*, resembles that of typical platyrrhine arboreal quadrupeds (personal observation, MacPhee et al., 2007; MacPhee, 2009).

PN-09-01 evinces a steeply angled nuchal plane and air-rhynch, yielding a cranial gestalt similar to *Alouatta* spp. To the extent that cranial morphology is related to postcranial morphology, and in turn positional behavior, a *prima facie* expectation might be that *Antillothrix* shares some positional adaptations with howler monkeys. Although further research on the link between head posture and cranial morphology is needed, we find some support for this *prima facie* hypothesis. Among platyrrhines, *Alouatta* spp. have both the steepest nuchal planes (Hershkovitz, 1977) and a unique positional repertoire. The positional behavior of atelids, including both *Alouatta* and *Ateles*, includes a high frequency of tail suspension and tail + hindlimb suspension, postures in which the head is inferior to the body and the vertebral column is suspended beneath the tail (Schön-Ybarra and Schön, 1987). However, while tail/hindlimb suspension (without forelimb involvement) among *Alouatta* is high, averaging 15.4% of all posture in four studies (range: 3.8–30.7%), suspensory behavior involving a forelimb is rare, averaging only 0.6% (range: 0–2%) (Mendel, 1976; Schön-Ybarra, 1984; Schön-Ybarra and Schön, 1987; Bezanson, 2009) compared with 8.9% in *Ateles* (Youlatos, 2002; Cant et al., 2003). In forelimb-assisted suspensory modes, the spine is positioned more vertically and the head is superior to most of the body, thus requiring a more typical primate flexed neck/shallow nuchal plane posture and morphology. Thus, the presence of an *Alouatta*-like nuchal angle leads us to expect that *Antillothrix* would have postcranial adaptations consistent with hindlimb suspension, tail suspension, or both, but that it is unlikely to have possessed *Ateles*-like adaptations for forelimb suspension.

The orbits of the new skull are not enlarged, indicating that *Antillothrix* was diurnal. The low-crowned teeth with attenuated shearing edges suggest a diet of fruit, nuts, or hard-shelled invertebrates. CT images show the molar enamel cap in *Antillothrix* to be very thin, inconsistent with a hard-object feeding regimen and suggesting that the diet was more likely soft fruit.

Biogeographical implications

Definitive phylogenetic placement of *Antillothrix* awaits a revised phylogenetic analysis combining *Paralouatta*, *Xenothrix*, PN-09-01, and MHD-01 (Rosenberger et al., 2010). Such an analysis may provide insight into the manner and timing of the arrival of mammals into the Greater Antilles. Competing models emphasize vicariance and rafting to explain how mammals reached the Antilles. Iturralde-Vinent and MacPhee (1999) postulate vicariance to explain presence of primates, sloths and rodents in the Greater Antilles. From 34 to 32 Myr, the Greater Antilles and northwestern South America were connected along an emergent Aves Ridge. This

connection could have served as a bridge for the nonvolant mammals into the Antilles. Subsequent tectonic events separated Cuba, Jamaica, Hispaniola, and Puerto Rico with attendant vicariant biotic events.

In an alternative scenario, vertebrates entered the Antilles on rafted vegetation, and dispersal among islands was due to a combination of rafting and vicariance (Hedges, 1996, 2006). This view is supported by molecular evidence that salt water intolerant fish, lizards, snakes and amphibians entered the islands across a broad spectrum of time, some more recently and some earlier than the 34 to 32 Ma interval (Hedges, 1996, 2006). A better understanding of the phylogenetic position of *Antillothrix* and the question of whether Antillean primates form a single clade should contribute significant evidence to this debate.

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