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RESEARCH ARTICLE

Rethinking *Antillothrix*: The Mandible and Its Implications

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A mandible of the Hispaniolan primate *Antillothrix bernensis*, virtually complete and providing the only definitive evidence of the species' lower dentition, has been discovered in a submerged Dominican Republic cave. The new specimen enables a more certain assessment of the species' phylogenetic position than previously possible. It belongs to the same individual as the nearly complete young adult cranium and postrcranial elements found earlier at the same site. Of the extinct Caribbean platyrrhines, the jaw compares well with partial mandibles representing *Xenothrix mcgregori*, from Jamaica. Among living platyrrhines, it closely resembles *Callicebus* and *Aotus*, as documented in a biometric analysis employing three-dimensional geometric morphometrics of *Callicebus*, *Aotus*, *Pithecia*, *Chiropotes*, *Cacajao*, *Cebus*, and *Saimiri*. The jaw falls within the morphological variability of *Callicebus* and *Aotus* in this three-dimensional analysis, is otherwise most similar to *Pithecia*, and is distinct from cebines. Lower molars resemble the Haitian primate, *Insulacebus*, a genus known by a full dentition and gnathic fragments with a pattern of derived features also present in *Xenothrix*. Considering the available craniodental and postcranial evidence, we conclude that *Antillothrix* is not properly classified as cebid but rather is best grouped with Pitheciidae, an idea long central to discussions of the phylogenetic affinities of the Greater Antillean primates. Since *Antillothrix* and *Insulacebus* are more primitive anatomically than the highly modified *Xenothrix*, it is tempting to surmise that the origins of the latter involved a vicariance or dispersal event via Hispaniola isolating it on Jamaica. Am. J. Primatol. 75:825–836, 2013. © 2013 Wiley Periodicals, Inc.

Key words: *Antillothrix*; *Xenothrix*; *Insulacebus*; Caribbean primates; platyrrhines; biogeography

INTRODUCTION

In 2009, field work by the Museo del Hombre Dominicano, Universidad Autónoma de Santo Domingo and Brooklyn College recovered a largely intact cranium and associated postcranial elements (MHD 01) of the Hispaniolan platyrrhine primate, *Antillothrix bernensis*, from an underwater cave located in La Altagracia Province of the Dominican Republic [Rosenberger et al., 2011]. Subsequent work at the same locality in 2010 produced more of the same individual, including the first mandible and lower dentition that can be reliably assigned to *A. bernensis*. Since the initial discovery and publication of the cranium, a second primate cranium from a nearby site was also described [Kay et al., 2011], and a new genus and species from Haiti, *Insulacebus toussaintiana*, was published [Cooke et al., 2011]. These new discoveries have prompted a rethinking of our interpretation of the phylogenetic position of *Antillothrix* and its consequences for the origins and biogeography of the West Indian primates. They also underscore the importance of the fossil record as a unique source of morphological information crucial to

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reconstructing phylogeny and tracing morphological evolution.

The cranium of *Antillothrix* was the first specimen discovered in the submerged karst limestone cave, Cueva de La Jeringa, which is situated on an emergent Plio-Pleistocene reef complex that dominates the geology of the eastern region of the Dominican Republic. It was a serendipitous find, seen resting atop a small boulder field. Additional searching at the time revealed other monkey remains lodged among nearby rocks, several long bones, ribs, and a few vertebrae, all part of the same individual. In 2010, the team returned to the discovery site, removing more of the breakdown of pebbles and boulders to open up a larger field for closer inspection. This yielded a new batch of material, including specimens of rodents and bats. The primate remains included the lower jaw, discussed here, as well as a humerus, partial scapula, an isolated right P^3, and a left femoral head epiphysis, which fits with material found previously.

METHODS

No living animals were used in this study, and all extant species were represented by skeletal specimens. Thus, the protocol did not require either review or approval by any Institutional Animal Care and Use Committee or adherence to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

The Sample

The mandible (Figs. 1–2, Table I) was discovered in Cueva de La Jeringa, situated in the Parque Nacional del Este of the Dominican Republic. The fossil collection was made under the auspices of the Museo del Hombre Dominicano, where all materials are curated, and with the full permission of Secretaría de Estado de Cultura, Secretaría de Estado de Áreas Protegidas y Biodiversidad, and authorized by Ministerio de Medio Ambiente y Recursos Naturales (Project title: Paleontología de Cuevas Sumergidas en República Dominica). The specimen has been assigned to the same individual (MHD 01) first found in June 2009.

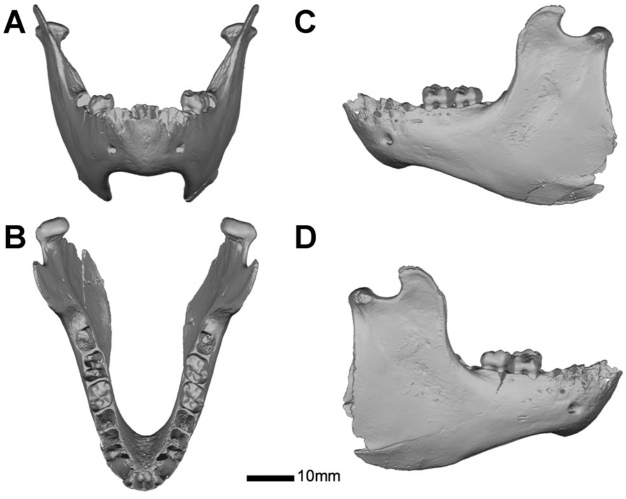

Fig. 1. MicroCT images of newly discovered *Antillothrix bernensis* mandible. (A), anterior; (B), superior; (C), left lateral; (D), right lateral.

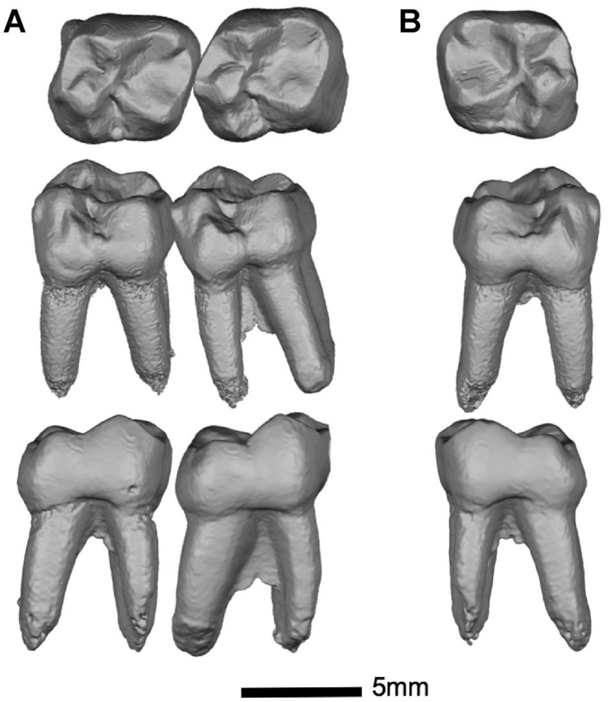

Fig. 2. MicroCT images of *Antillothrix bernensis* molars in occlusal (top row), buccal (middle row), and lingual (bottom row) views. A: Left M_1 and M_2 (mesial is to the left in top and middle rows and to the right at bottom). B: Right M_1 (mesial to right in top and middle rows, to the left at bottom).

The newly recovered mandible was compared with a sample of seven extant New World monkey genera represented by 10 species and 146 individuals (Table II), using three-dimensional geometric morphometric techniques. Two species each were chosen from *Cebus*, *Aotus*, *Callicebus*, *Chiropotes*, and *Cacajao* in order to capture intrageneric variation in these forms. The sample was drawn from the collections of the American Museum of Natural History (AMNH). The largest (atelid) and smallest (callitrichine) platyrrhines were excluded from the analysis because current phylogenetic hypotheses do not suggest that they are germane. Their absence also means the operative comparative set is restricted to a single, fairly coherent, medium body size class of 900–4,000 g [Ford, 1994] within the platyrrhine radiation. *Cebus* and *Saimiri* were specifically included in the analysis because molecular evidence consistently aligns these cebines with *Aotus* [see review in Osterholz et al., 2009].

TABLE I. A: Measurements (mm) of Mesiodistal (MD) Length and Buccolingual (BL) Breadth of $M_{1,2}$ of *Antillothrix bernensis*, *Xenothrix mcgregori*, and *Insulacebus toussaintiana* and B: Measurements of isolated specimens of first or second molars of *Paralouatta varonai*

		Left M_1		Right M_1		Left M_2		Right M_2	
Species	Specimen	MD	BL	MD	BL	MD	BL	MD	BL
(A)									
Antillothrix bernensis	MHD 01[a]	5.06	4.89	5.48	4.83	5.48	5.96		
Xenothrix mcgregori	AMNH 148198[b]	6.07	5.04			5.94	4.43		
Insulacebus toussaintiana	UF 114714[c]	5.5	5.06	5.5	Damaged			5.02	5.24

		Left $M_{1,2}$[e]		Right $M_{1,2}$	
Species	Specimen	MD	BL	MD	BL
(B)					
Paralouatta varonai	V139[d]	6.45	5.43		
	V123	7.04	5.47		
	V138			7.06	5.78
	V144	7.04	5.76		
	Cueva Alta molar	7.53	5.47		

[a] Museo del Hombre Dominicano.
[b] American Museum of Natural History.
[c] Florida Museum of Natural History.
[d] Museo Nacional de Historia Natural, La Habana, Cuba.
[e] M_1 and M_2 are indistinguishable based on size and morphology.

To clarify nomenclature, we follow Rosenberger [2011] (see Rosenberger et al. [2009]), noting there are unresolved questions about the higher-level cladistics of the radiation [e.g., Schneider and Rosenberger, 1996], which means that taxonomic terms may be used differently by various authors. We interpret the platyrrhine radiation to comprise three major groups, Cebidae, Pitheciidae, and Atelidae. The latter is not especially pertinent here. Among the non-controversial taxa, the cebids in our extant sample, *Saimiri* and *Cebus*, both belong to Subfamily Cebinae. The pitheciids include *Callicebus*, *Pithecia*, *Chiropotes*, and *Cacajao*. The latter three are placed in Subfamily Pitheciinae, Tribe Pitheciini; *Callicebus* is placed in Subfamily Homunculinae. The position of *Aotus* within this scheme remains a matter of debate, with morphological evidence [e.g., Tejedor and Rosenberger, 2008; see also Rosenberger and Tejedor, in press] suggesting pitheciid (possibly homunculine) affinities (here supported by A.L.R.) and the genetic research arguing for a cebid relationship (here supported by S.B.C.). Among the extinct Caribbean taxa mentioned, *Xenothrix* and *Insulacebus* are classified as pitheciids [see Cooke et al., 2011], whereas *Paralouatta* is an atelid [Cooke, 2011; Rosenberger, 2002]. Other mainland extinct pitheciids mentioned below include *Cebupithecia sarmientoi*, *Soriacebus ameghinorum*, *Homunculus patagonicus*, *Lagonimico conclucatus*, *Nuciruptor rubricae*, and in some analyses [see Rosenberger et al., 2009], *Aotus dindensis*.

TABLE II. Extant Comparative Sample of Platyrrhines Studied at the American Museum of Natural History and Included in this Study

Taxon	Male	Female	N
Aotus	**15**	**14**	**29**
Aotus azarae	10	10	20
Aotus vociferans	4	2	6
Aotus nigriceps	1	2	3
Callicebus	**17**	**12**	**30**
Callicebus torquatus	12	8	20
Callicebus cupreus	5	5	10
Pithecia	**10**	**10**	**20**
Pithecia monachus	10	10	20
Chiropotes	**9**	**10**	**19**
Chiropotes albinasus	4	3	7
Chiropotes satanas	4	7	11
Chiropotes sp.	1		1
Cacajao	**10**	**7**	**17**
Cacajao melanocephalus	2	3	5
Cacajao calvus	8	4	12
Cebus	**11**	**10**	**21**
Cebus apella	5	5	10
Cebus albifrons	6	5	11
Saimiri	**5**	**5**	**10**
Saimiri boliviensis	5	5	10

Data Collection and Analyses

Forty-eight x, y, z coordinate landmark points were selected to characterize mandibular shape (Fig. 3

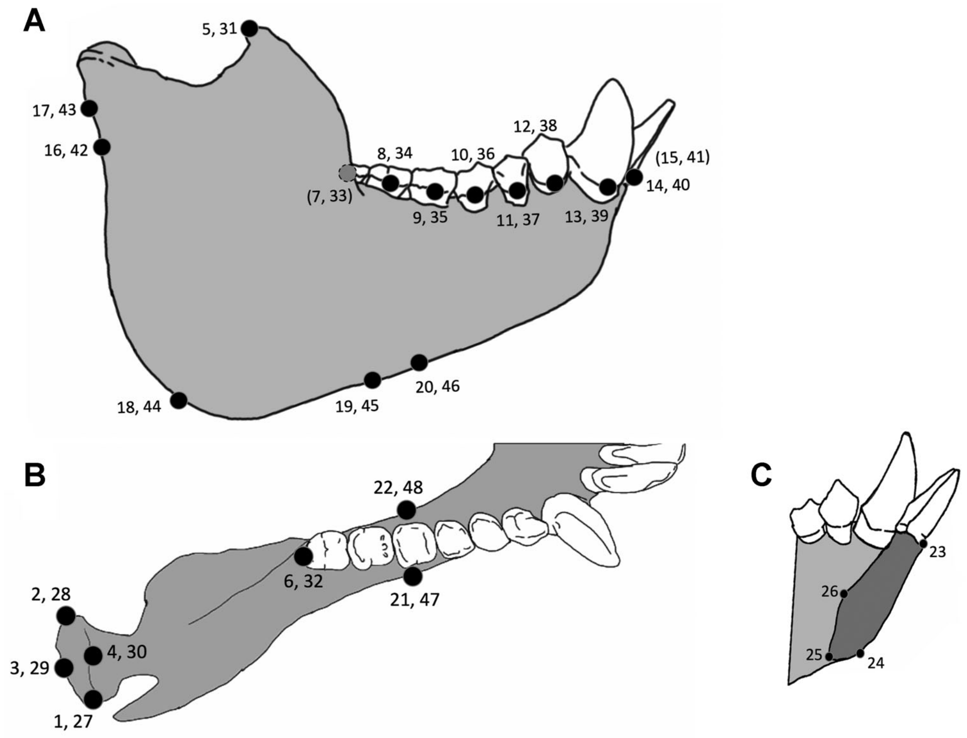

Fig. 3. Diagrammatic representation of bilateral (A and B), and midline (C) landmarks used for the three-dimensional geometric morphometric study. Landmarks located at the cemento-enamel junction on the living forms were taken at the corresponding alveoli of the fossil mandible where no teeth were present. See Table III for more details.

and Table III). Mandibles were first fixed in place with plasticine clay. Points were collected with a MicroScribe 3D Digitizer, using the fine dental tip. As these fall on opposite sides of the mandible, a transparent plastic compass was used as a left-to-right spanning guide for digitizing points 16, 17, 19, 20, 42, 43, 45, and 46. Protocols differed slightly for the *Antillothrix* mandible. Substitute dental landmarks were taken at the alveoli where teeth were missing, except in the case of the landmarks at the canines (13 and 39), which were then excluded. Since the fossil alveoli exhibit no significant bone resorption, for the level of resolution required by this analysis, we believe these repeatable measuring points serve as a close approximation of the equivalent landmarks taken at the cemento-enamel junction of the complete mandibular specimens.

The metrical data were analyzed using Morphologika 2.5 (O'Higgans and Jones, 2006). Landmark points were first aligned using generalized Procrustes analysis (GPA), which minimizes the least squared distance between sets of landmark points through scaling, rotation, transposition, and translation [Gower, 1975; Rohlf and Slice, 1990]. Principal components analysis (PCA), conducted in PAST [Hammer et al., 2001], was then used to analyze the GPA-aligned landmark points. Procrustes distances between species means were derived using generalized Procrustes analysis; these are shown in Table IV.

RESULTS

Like many of the other individual elements of the skeleton, the mandible is undistorted and exceptionally preserved (Fig. 1). There are no other platyrrhine fossil jaws where the morphology of both corpus and ramus is as comprehensive. On the right side, for example, the lateral face and profile of the corpus presents perfectly from front to rear, with nothing more than minor damage to a few alveoli. Posteriorly, the full ramus including the coronoid process and mandibular condyle is complete and undamaged. The postero-inferior border of the corpus is marred only by small breaks at the mandibular angle. Three cheek teeth, a right M_1, left M_1 and M_2, are well preserved and unworn.

Statistical Analysis

In a principal components analysis of landmark data (Fig. 4), the first two components show morphological overlap among *Antillothrix*, *Callicebus*, and *Aotus*. In these taxa the mandibular corpus deepens posteriorly; the gonial region is greatly inflated; the mandibular ramus is tall and antero-

TABLE III. Landmarks Used in Three-Dimensional Geometric Morphometric Analysis of Mandibles (See Also Fig. 3)

Descriptions	Right	Center	Left
Lateral edge of condyle	1		27
Medial edge of condyle	2		28
Posterior edge of condyle	3		29
Anterior edge of condyle	4		30
Apex of coronoid process	5		31
Distal side of M_3 at CEJ[a]	6		32
Buccal side of M_3 at CEJ	7		33
Buccal side of M_2 at CEJ	8		34
Buccal side of M_1 at CEJ	9		35
Buccal side of P_4 at CEJ	10		36
Buccal side of P_3 at CEJ	11		37
Buccal side of P_2 at CEJ	12		38
Buccal side of C_1 at CEJ	13*[b]		39*
Labial side of I_2 at CEJ	14		40
Labial side of I_1 at CEJ	15		41
Point at end of line drawn through the CEJs of P_4–M_2 terminating at posterior edge of ramus	16		42
Point at end of line drawn through the CEJs of M_1–M_3 terminating at posterior edge of ramus	17*		43*
Approximate apex of gonial angle	18		44*
Point at inferior edge of corpus, drawn perpendicular to a line drawn between P_4 and M_2, below M_2	19		45
Point at inferior edge of corpus, drawn perpendicular to a line drawn between P_4 and M_2, below M_1	20		46
Most lateral point of corpus inferior of M_1	21		47
Most medial point of corpus inferior of M_1	22		48
Inter-incisor alveolus		23	
Anterior apex of curvature at the mandibular symphysis between points 23 and 25		24	
Most inferior point of the mandibular symphysis		25	
Posterior apex of curvature at the mandibular symphysis between points 23 and 25		26	

[a] Landmarks placed on the CEJ of extant taxa were placed on the edge of the alveolus where teeth were absent from the *Antillothrix bernensis* mandible unless extensive damage to this area was present.

[b] Asterisks (*) mark the landmarks omitted due to prohibitive damage on the *Antillothrix* jaw.

posteriorly short; the coronoid process is hooked; and the tooth rows have a parabolic or semi-parabolic contour in superior view. This configuration is distinct from the pitheciins, *Pithecia*, *Chiropotes*, and *Cacajao*, and also from the cebines, *Cebus*, and *Saimiri*. Most of the variation of all the individuals is captured by the first three axes of the PCA, which account for 31.3%, 27.8%, and 8.5% of the variance, respectively. Subsequent components account for 3% of the variance or less. Ln centroid size shows no significant correlation with the first three principal components. In addition to a PCA including the complete sample, another analysis using mean shapes was conducted to reduce the influence of sampling bias. In this model, the first three components for species means account for 42.9%, 32.6%, and 9.3% of the variance (see Figs. 5–6).

Shape changes in PC space are shown using wireframes representing maximum and minimum values along the axes (Figs. 4–6). Wireframes were created using Morphologika 2.5 [O'Higgans and Jones, 2006]. The first component in the analyses of both individuals and species means is best explained as the shape of the dental arcade, the depth of the corpus, and the relative thickness of the mandibular symphysis. The second component is most easily explained as the depth and posterior inflation of the gonial region of the mandible. The third component illustrates the relative breadth of the condyles such that *Antillothrix* appears to exhibit a narrow bicondylar breadth for the overall size of the mandible.

Minimum spanning trees (MST) (Figs. 5–6) link the *Antillothrix* jaw with the mean shape of *Callicebus torquatus*. An MST takes into account all the components from the PCA and links the individuals or sample taxa that are most similar overall. While the trees illustrate the single closest similarity, the tabulated Procrustes distances show that *Antillothrix* is essentially equidistant from both mean shapes of *C. torquatus* (proc. dist. = 0.090) and *Aotus azarae* (0.091), with the next most similar

TABLE IV. Procrustes Distances Based on Mean Shape Between Selected Platyrrhine Taxa

	Aotus azarae	*Aotus* sp.	*Callicebus torquatus*	*Callicebus cupreus*	*Chiropotes satanas*	*Chiropotes albinasus*	*Cacajao calvus*	*Cacajao melanocephalus*	*Pithecia monachus*	*Cebus apella*	*Cebus albifrons*	*Saimiri boliviensis*	*Antillothrix bernensis*
Aotus azarae		0.0406	0.0782	0.0725	0.1412	0.1367	0.1298	0.1222	0.0915	0.1007	0.1107	0.1182	0.0909
Aotus sp.	0.0406		0.1018	0.0815	0.1381	0.1377	0.1265	0.1178	0.1012	0.0977	0.0959	0.1020	0.1028
Callicebus torquatus	0.0782	0.1018		0.0738	0.1470	0.1352	0.1402	0.1368	0.0882	0.1276	0.1505	0.1567	0.0901
Callicebus cupreus	0.0725	0.0815	0.0738		0.1262	0.1238	0.1312	0.1230	0.0851	0.1326	0.1458	0.1501	0.1035
Chiropotes satanas	0.1412	0.1381	0.1470	0.1262		0.0400	0.0621	0.0499	0.0785	0.1258	0.1361	0.1633	0.1489
Chiropotes albinasus	0.1367	0.1377	0.1352	0.1238	0.0400		0.0510	0.0521	0.0674	0.1188	0.1332	0.1610	0.1447
Cacajao calvus	0.1298	0.1265	0.1402	0.1312	0.0621	0.0510		0.0370	0.0714	0.1077	0.1134	0.1405	0.1366
Cacajao melanocephalus	0.1222	0.1178	0.1368	0.1230	0.0499	0.0521	0.0370		0.0695	0.1015	0.1067	0.1302	0.1335
Pithecia monachus	0.0915	0.1012	0.0882	0.0851	0.0785	0.0674	0.0714	0.0695		0.0915	0.1143	0.1385	0.0977
Cebus apella	0.1007	0.0977	0.1276	0.1326	0.1258	0.1188	0.1077	0.1015	0.0915		0.0522	0.0864	0.1103
Cebus albifrons	0.1107	0.0959	0.1505	0.1458	0.1361	0.1332	0.1134	0.1067	0.1143	0.0522		0.0598	0.1260
Saimiri boliviensis	0.1182	0.1020	0.1567	0.1501	0.1633	0.1610	0.1405	0.1302	0.1385	0.0864	0.0598		0.1335
Antillothrix bernensis	0.0909	0.1028	0.0901	0.1035	0.1489	0.1447	0.1366	0.1335	0.0977	0.1103	0.1260	0.1335	

species being *Pithecia monachus* (0.098, Table IV). This metric suggests that the overall similarity among *Antillothrix*, *C. torquatus*, and *A. azarae* mean values is analogous to the resemblances shared by *P. monachus* and *Callicebus cupreus* (0.085), or between *P. monachus* and *Cebus apella* (0.091). Still, it is the first two components that make up the majority of the variation in the model (59.074%), and using those components *Antillothrix* falls within the *Aotus*–*Callicebus* space (Fig. 4).

Character Analysis

Regarding discrete morphology, in addition to extant platyrrhines there are several mainland fossils apt for comparison. The early Middle Miocene *H. patagonicus* from Argentina closely resembles modern *Aotus* in mandibular shape [Tejedor and Rosenberger, 2008], as does the middle Miocene *A. dindensis* from La Venta, Colombia [Setoguchi and Rosenberger, 1987]. *S. ameghinorum* from Argentina also exhibits an enormously deep posterior mandible, as illustrated in Fleagle and Tejedor [2002], while those of *N. rubricae* and particularly *L. conlculatus*, both from La Venta, show evidence of this shape, too [e.g., Hartwig and Meldrum, 2002]. In the Greater Antilles, *Xenothrix* also has a posteriorly deep mandible with an inflated gonial region resembling *Callicebus* in its lateral profile [e.g., MacPhee and Horovitz, 2004; Rosenberger, 1977].

The ancestral condition for mandibular shape in platyrrhines and anthropoids probably resembles the pattern widespread among haplorhines and prevalent among Eocene–Oligocene anthropoids in the Fayum, Egypt [e.g., Seiffert et al., 2010], that is, a shallow corpus [e.g., Rosenberger, 1981] of relatively even depth from front to back, without an inflated mandibular angle. This is the pattern common among cebids. Pitheciids and atelids uniformly exhibit the alternative state, a posteriorly deepening profile. One of the most modified versions of the atelid–pitheciid pattern occurs universally in genus *Callicebus*, with its enormously expanded gonial angle, but the *Callicebus* configuration also overlaps with *Aotus*, as we document metrically above. While it can be argued that this results from parallel evolution between *Aotus*, *Callicebus*, and several other pitheciids, one would also have to invoke parallelism to explain other jointly shared features of the mandible and dentition, such as ramus shape, arcade shape, conformation of the anterior dentition and very low-crowned, non-dimorphic lower canines [see Rosenberger and Tejedor, in press], a position supported by the genetic evidence. Alternatively, one could argue that this pattern of mandibular shape is primitive for platyrrhines, but neither *Branisella boliviana* [Rosenberger, 1981; Takai et al., 2000], currently the oldest known platyrrhine preserving a mandible, nor any Old World anthropoids have

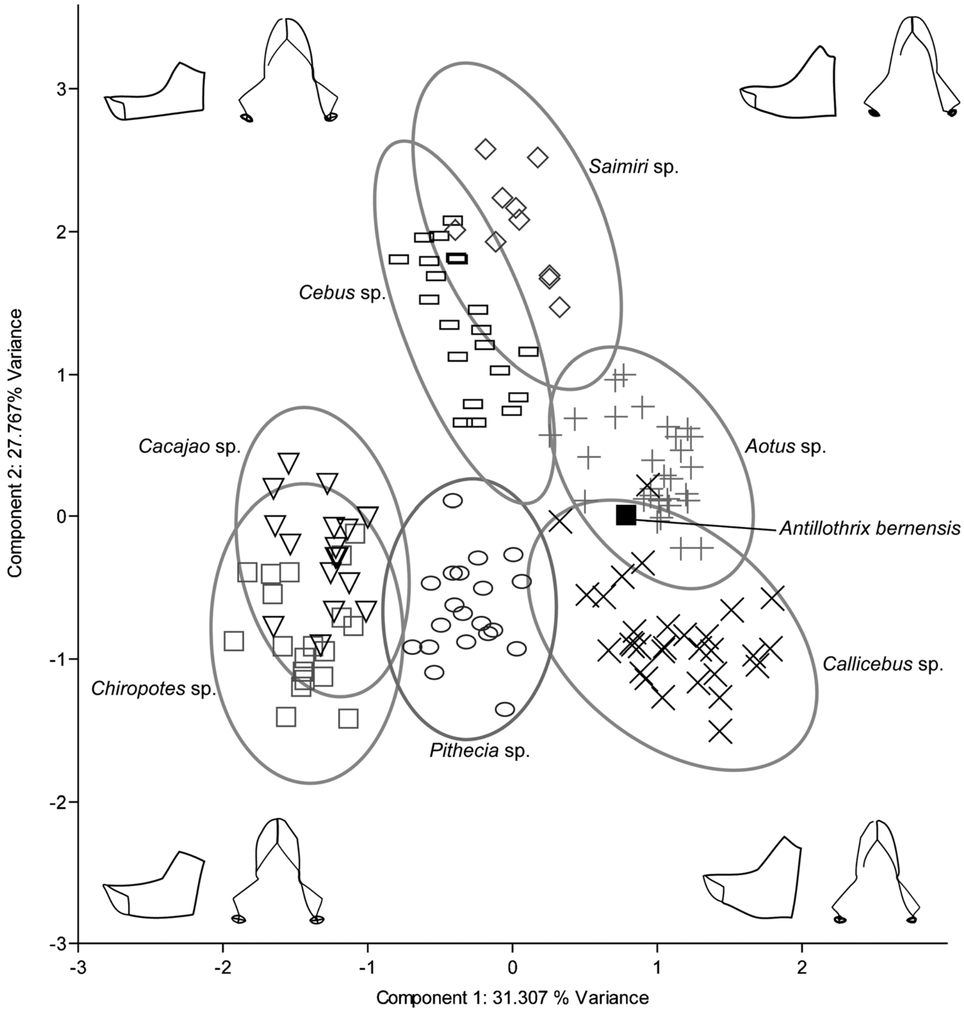

Fig. 4. Plot of a principal components analysis of Procrustes aligned landmarks (see Fig. 3 and Table III) with 95% confidence ellipses. First and second principal components account for 59.1% of the variance.

similar morphology. They present a condition similar to that observed in the cebids. This means that based on the morphological evidence, the most parsimonious hypothesis is that the pitheciid–atelid condition is an integrated, derived pattern among platyrrhines. The functional morphology behind this anatomy is inadequately known, but one can surmise it involves modifications of the masseter muscle as a feeding adaptation, perhaps relating to gape, specifically use of the incisors to harvest and crop fruits that are large relative to the size of the skull.

Character analysis of dental arcade shape results in a similar taxonomic distribution of two contrasting states (ignoring the autapomophic *Callithrix*/*Cebuella* V-shaped situation; [see Tejedor and Rosenberger, 2008]) when one compares modern cebids, pitheciids, atelids, and Fayum anthropoids. However, here the interpretation is more complex. *Aotus* and *Callicebus* have been described as having parabolic arcades and the others in our morphometric sample have decidedly U-shaped arcades. The parabolic state is associated with highly reduced canines in *Callicebus* and *Aotus*, orthognathic premaxillae and absence of upper and lower diastemata. Cebine and pitheciin anterior jaws are squared off in the symphyseal region by different configurations of their anterior teeth. The determining features of pitheciins involve the massive, everted lower canines, a transversely compact row of narrow, tall incisors, enlarged diastemata above and below, and everted premaxillae. The U-shaped arcade of cebines is associated with transverse, broad, low-crowned incisors, sexually dimorphic, vertical canines, modest diastemata, and upper premolars that are buccolingually wide. Since the inferred ancestral platyrrhine pattern, common in Oligocene Old World anthropoids and apparently retained in *Branisella*, appears to be a posteriorly diverging tooth row [see Takai et al., 2000; Tejedor and Rosenberger, 2008], this means the parabolic and U-shaped arrangements

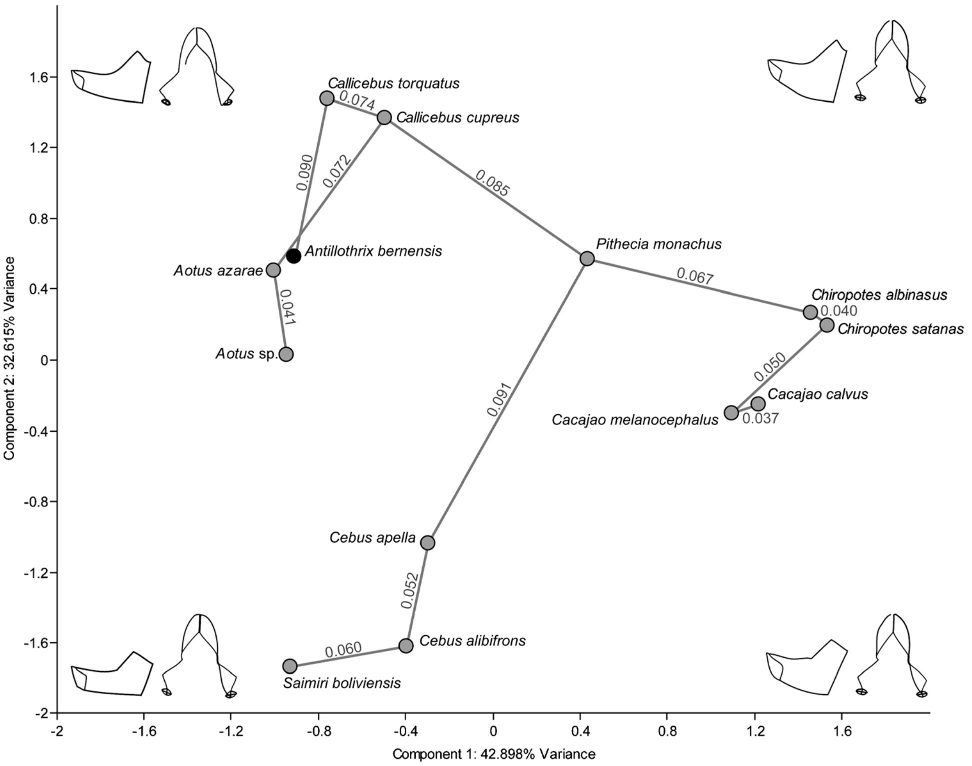

Fig. 5. Plot of a principal components analysis of species means with minimum spanning tree linking the mean shape. PC 1 and PC 2 account for 75.5% of the variance in this model. Inset wireframes illustrate the components driving PC 1, which are arcade shape and corpus height, and PC 2, which is driven by depth and posterior inflation of the gonial region. Procrustes distances for similar shapes are figured with their respective branches. These data illustrate that multidimensional similarity is highest between *Antillothrix bernensis* and *Callicebus torquatus*. See Table IV for a list of Procrustes distances.

each are derived, with the latter evolving convergently in pitheciins and cebines. As quantified here using 3DGM techniques, the mandibular shape of *Antillothrix* falls within the parameters of the *Aotus–Callicebus* pattern, a parabolic or semi-parabolic arcade.

The new lower molars of *Antillothrix* are similar to but distinct from those of *Insulacebus* (Fig. 2). Both genera are quite different superficially from the two-molared *Xenothrix*, although the Haitian monkey shares with *Xenothrix* several important traits of possible phylogenetic significance [Cooke et al., 2011]. *Antillothrix* differs in the following ways: crowns are overall more cristodont with the lingual cusps placed more at the perimeters of the occlusal table; $M_{1,2}$ protoconids and metaconids are not divided by a distinct cleft and are less closely spaced apart; cristid obliquas are more distinct, raised and relatively longer; and, buccal flare below protoconids is less developed, so mesial crown width is less conspicuous on M_2 and the ectoflexid is less marked on M_1.

The dimensions of the lower molars are shown in Table I. Based on regressions of M_1 area against body mass for anthropoids and all primates [Conroy, 1987], the inferred body size of *Antillothrix* is 4.2–5.6 kg. An additional regression restricted to female platyrrhines [Kay et al., 2008] yields a body weight of 4.9 kg. These estimates should be considered provisional, however, given that this taxon appears to have relatively large teeth compared to other cranial dimensions [Rosenberger et al., 2011]. Based on our calculation of mandible centroid size (Fig. 7), the *Antillothrix* jaw is comparable to the median centroid sizes of *Pithecia* and *Chiropotes*, whose weights range roughly <2 kg to >3.1 kg [Ford, 1994; Ford and Davis, 1992].

DISCUSSION

The new mandibular evidence presented here induces us to alter our prior interpretation of the phylogenetic position of *Antillothrix* based largely on the cranium and its teeth [Rosenberger et al., 2011]. That assessment stated the difficulties of isolating derived craniodental features shared with any of the major modern clades, callitrichines, cebines, pitheciids, and atelids. We were, however, persuaded in their absence, coupled with similarities shared by *Antillothrix* upper molars and Patagonian early Middle Miocene fossils such as *Killikaike blakei* [Tejedor et al., 2006], that *Antillothrix* was probably

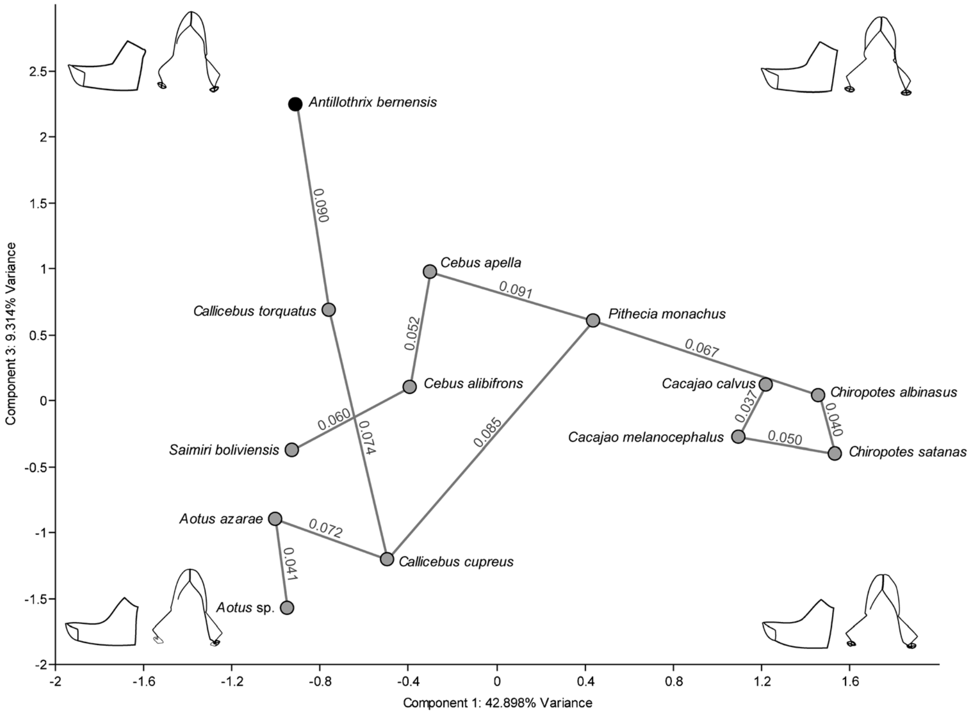

Fig. 6. Plot of a principal components analysis of species means with minimum spanning tree linking the mean shapes that are most similar overall. PC 1 and PC 3 account for 52.2% of the variance in this model. Inset wireframes illustrate the components driving PC 1, which are arcade shape and corpus height, and PC 3, which is driven by the relative breadth of the mandibular condyles and breadth of the mandible. Procrustes distances for similar shapes are figured with their respective branches. These data illustrate that multidimensional similarity is highest between *Antillothrix bernensis* and *Callicebus torquatus*. See Table IV for a list of Procrustes distances.

a cebid. This view of *Antillothrix* was current prior to the mid-1990s [see MacPhee and Horovitz, 2002], when new material of *Xenothrix* from Jamaica and *Paralouatta* from Cuba allowed more substantive examinations of the interrelationships of all Antillean fossil primates. Since atelids and pitheciids are characterized confidently by a derived mandibular morphology lacking in cebids, and often by derived molar occlusal patterns, cebids, perhaps unfortunately, have also been something of a taxonomic default into which difficult fossils lacking such cladistically diagnostic features have been allocated (e.g., *B. boliviana*, *Szalatavus attricuspis*, *Chilecebus carrascoensis*).

The new mandible of *Antillothrix*—morphometrically indistinguishable from *Callicebus* and *Aotus* along PC 1 and PC 2—and with its deepening lateral profile, expanded mandibular angle and tall, anteroposteriorly short ramus, presents strong evidence that the fossil is a pitheciid. This idea is in keeping with the analyses of MacPhee and colleagues [Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004; MacPhee et al., 1995], who affined *Antillothrix* to a monophyletic group associated with *Callicebus*. Newer, better information, including evidence of a continuity in dental morphology shared with *Insulacebus* and then *Xenothrix*, in a morphocline-like way, adds further credibility to this hypothesis [Cooke et al., 2011].

Additional corroboration may eventually come from the postcranium. While the evidence is highly incomplete and tenuous at best, it bears mentioning for the reasons given below. The known limb bones of *Antillothrix*, particularly the ulna and a femur, are unusual [Rosenberger et al., 2011]. The ulna is short relative to femur length and the femoral shaft is very robust relative to its length, that is the limbs are relatively squat and stout. This atypical blueprint matches no modern platyrrhines but could resemble *Xenothrix* [MacPhee and Fleagle, 1991; MacPhee and Meldrum, 2006], which appears to display a heavy-limbed pattern that is even more exaggerated. MacPhee and Fleagle [1991] hypothesized that *Xenothrix* was a slow moving arboreal quadruped and/or climber, a position that continued to receive support with recovery of additional postcranial evidence [MacPhee and Meldrum, 2006]. It is worth noting that it was only with caution that these authors allocated several elements (femur, partial pelvis, partial tibiae) to *Xenothrix* from the type-site of Long Mile Cave, given the highly unusual robusticity of the bones and their lack of diagnostic platyrrhine features. This means our comparisons must be tempered with the same caveats. Nevertheless, it adds to the impression that in both general and specific ways, where the body parts of *Antillothrix*, *Insulacebus*, and *Xenothrix* are known, they

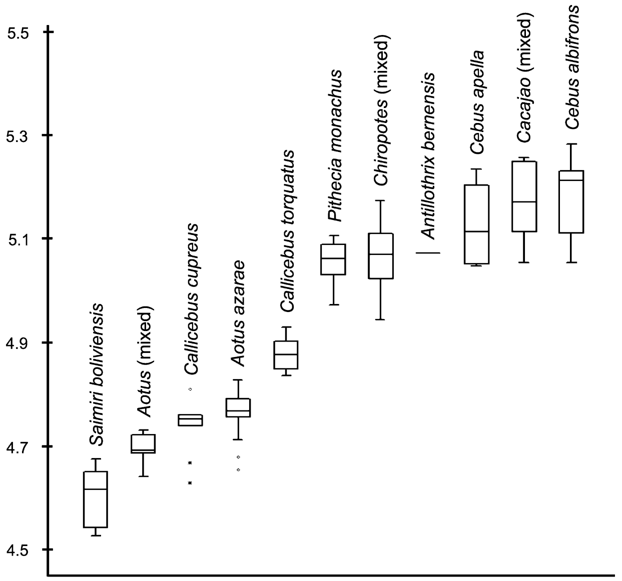

Fig. 7. Ln centroid size of mandibles based on landmarks used in the three-dimensional geometric morphometric study. The *Antillothrix* mandible most closely approximates the median ln centroid sizes of *Pithecia* and *Chiropotes*.

appear to constitute a series of overlapping morphologies that are derived among platyrrhines and are either uniquely shared among them or exhibited elsewhere only among pitheciids, most notably *Callicebus* [see Cooke et al., 2011; Rosenberger et al., 2011].

Drawing on Cooke and colleagues [2011], the new information can be summarized and broadly contextualized as follows: (1) the mandibular profile and ramus proportions of *Antillothrix* are *Callicebus*- and *Aotus*-like, with the corpus also resembling *Xenothrix*; (2) the dental arcade shape of *Antillothrix* is configured like *Callicebus*, *Aotus*, and *Xenothrix*; (3) the lower molar crowns of *Insulacebus* resemble *Xenothrix* and *Antillothrix* in overall pattern, but to a lesser extent in the details; (4) the relatively short and robust femur of *Antillothrix* potentially resembles the hyper robust femur attributed to *Xenothrix*; (5) more broadly, the narrow, elongate lower molars of *Xenothrix*, with notched trigonids, resemble *Soriacebus*; and (6) the configuration of the lower canine crown of *Insulacebus* closely matches the stout, pointed, three-sided tooth, as well as the unique cingulum structure, found in living and fossil pitheciins, including *Cebupithecia*, *Soriacebus*, *Nuciruptor*, and *Lagonimico*.

This body of evidence strongly suggests these three Greater Antillean genera are closely related, which is in keeping with other current phylogenetic hypotheses. For example, Cooke and colleagues [2011] argued that *Insulacebus* was probably a sister-genus to *Xenothrix*, while also presenting derived features shared with *Aotus*. Rosenberger [1977] had long held that *Xenothrix* was closely related to *Callicebus*, and later [Rosenberger, 2002] proposed that it was possibly more closely related to *Aotus*; either way, among the living platyrrhines he maintains that *Aotus* and *Callicebus* are potentially a sister-group [e.g., Rosenberger and Tejedor, in press]. And, MacPhee and colleagues [Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004; MacPhee et al., 1995] have also advocated all the Greater Antillean primates are monophyletically related to *Callicebus*.

Notwithstanding the strong phylogenetic signal from the mandible, the cranium is another matter. In our original description and trait tabulation [Rosenberger et al., 2011] we emphasized that *Antillothrix* not only lacks clear cut similarities in body mass that might associate it cladistically with the derivedly small callitrichines or large atelines, but that the cranium also lacked various hallmark synapomorphies of the other pertinent clades (cebines, pitheciines, and *Callicebus–Aotus*). We remarked on the absence of such apomorphies as the narrow interorbital pillar of *Cebus*, *Saimiri*, and *Killikaike*; the absence of a pitheciin facial structure, wherein the maxilla is highly modified to accommodate massive, everted maxillary canines; or, a bullar morphology comparable to the unique anatomy of *Callicebus* and *Aotus*. We also mentioned several possible autapomorphies, features that might be parallelism to the traits of pitheciines, and likely primitive platyrrhine features such as the high, angular nuchal plane. Our conclusion was that the cranium was phenetically most like modern *Cebus*, or an enlarged version of *Saimiri*. This notion was reinforced by the upper molar occlusal morphology shared with the early middle Miocene *Killikaike*, from Argentina [Tejedor et al., 2006].

The evidence presented here, which weighs heavily the mandibular morphology, sheds more light on the matter. It enables us to recast our analysis and thus arrive at a new perspective on *Antillothrix* and the evolution of the pitheciid skull. The bilaterally preserved, large-caliber canine alveoli in the fossil's cranium, which we saw as a possible (male) cebid-like trait, we now interpret as a resemblance to pitheciines, consistent with their enlarged, stout canines and strong canine roots. The presence of a modestly narrow interorbital pillar is a retentive platyrrhine trait that is carried over among most pitheciids, rather than a derived state of the transformation series foreshadowing the extremely narrow interorbitum of cebines. The relatively domed frontal, restricted to cebines among the cebids and normally seen in pitheciines only in *Chiropotes* and *Cacajao* but generally not in *Pithecia*, may be a labile feature of the frontal trigon, variably expressed among platyrrhines depending on the conformation of the craniofacial junction and relative brain size; *Chiropotes* and *Cacajao* have now been shown to have relatively enlarged brains [Hartwig et al., 2011], perhaps as a correlate. If correct, this reassessment indicates *Antillothrix* retains a variety of cranial and dental features primitive for pitheciids and crown platyrrhines.

An additional primate specimen recovered from the Dominican Republic is an intact cranium [Kay et al., 2011] from the nearby Padre Nuestro cave. The specimen is incompletely described, but it has bearing here. Although it was allocated to *Antillothrix*, it exhibits a different morphology from the cranium described from La Jeringa [Rosenberger et al., 2011]. For example, the Padre Nuestro specimen has a more vertical nuchal region, marked temporal lines, a wide zygomatic root, and a more globular neurocranium overall. Based on a modern reference framework, the Padre Nuestro cranium has an *Alouatta* aspect to it, as noted by Kay and colleagues [2011], but comparable features are lacking in the La Jeringa specimen.

Finally, we address briefly the biogeographical implications of the foregoing, a matter of persistent debate. Alternative models pertaining to primates support either one, two, or several dispersive emigrations into the Greater Antilles from the South American mainland. The first idea [Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2004; MacPhee et al., 1995] rests on the proposition that all the monkeys are descendants of a single ancestral population. But if more than one lineage is present, a singular event, while possible, cannot be presumed [Cooke et al., 2011; Rosenberger et al., 2011]. Though we formerly thought *Antillothrix* was evidence that a non-pitheciid and non-atelid clade entered the Caribbean, our revised interpretation of this fossil cannot be considered as evidence of a third lineage. On the other hand, it strengthens the notion of inter-island exchange between Hispaniola and Jamaica [see Cooke et al., 2011].

In conclusion, the following main points summarize what we have gleaned from the new remains discovered in Hispaniola:

1. The mandible of the fossil platyrrhine *Antillothrix* is evidence that this primate is a pitheciid, not a cebid.
2. *Antillothrix* and the other Hispaniolan genus, *Insulacebus*, may be monophyletically related to *Xenothrix*, from Jamaica.
3. While at least two platyrrhine clades are present in the Caribbean (pitheciids and alouattins, i.e., *Paralouatta* in Cuba and possibly the Dominican Padre Nuestro cranium), it is unknown how many dispersal events this represents, but phylogenetic links between the primates on Hispaniola and Jamaica, and between Hispaniola and Cuba, indicate inter-island exchange.
4. Various Caribbean platyrrhines preserve archaic cranial and dental traits, some resembling early Middle Miocene platyrrhines of Argentina, indicating a remote origin for the group before the Amazonian ecosystem evolved its present configuration.
5. Not surprisingly, mosaic evolution of platyrrhine crania complicates character analyses that particularly emphasize the living forms, but an expanding fossil record can contribute significantly to minimizing inferential errors concerning the homology and polarity of traits.

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REFERENCES

Conroy GC. 1987. Problems of body-weight estimation in fossil primates. Int J Primatol 8:115–137.

Cooke SB. 2011. Paleodiet of extinct platyrrhines with emphasis on the Caribbean forms: three-dimensional geometric morphometrics of mandibular second molars. Anat Rec 294:2073–2091.

Cooke SB, Rosenberger AL, Turvey S. 2011. An extinct monkey from Haiti and the origins of the Greater Antillean primates. Proc Natl Acad Sci 108:2699–2704.

Fleagle JG, Tejedor MF. 2002. Early platyrrhines of South America. In: Hartwig WC, editor. The primate fossil record. Cambridge: Cambridge University Press. p 161–173.

Ford SM. 1994. Evolution of sexual dimorphism in body weight in platyrrhines. Am J Primatol 34:221–244.

Ford SM, Davis LC. 1992. Systematics and body size: implications for feeding adaptations in New World Monkeys. Am J Phys Anthropol 88:415–468.

Gower JC. 1975. Generalized procrustes analysis. Psychometrika 40:33–55.

Hammer Ø, Harper DAT, Ryan PD. 2001. *PAST*: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9.

Hartwig WC, Meldrum DJ. 2002. Miocene platyrrhines of the northern Neotropics. In: Hartwig WC, editor. The primate fossil record. Cambridge: Cambridge University Press. p 175–188.

Hartwig WC, Rosenberger AL, Norconk MA, Young Owl M. 2011. Relative brain size, gut size, and evolution in New World Monkeys. Anat Rec 294:2207–2221.

Horovitz I, MacPhee RDE. 1999. The Quaternary Cuban platyrrhine *Paralouatta varonai* and the origin of the Antillean monkeys. J Hum Evol 36:33–68.

Kay RF, Fleagle JG, Mitchell TRT, et al. 2008. The anatomy of *Dolichocebus gaimanensis*, a stem platyrrhine monkey from Argentina. J Hum Evol 54:323–382.

Kay RF, Hunt KD, Beeker CD, et al. 2011. Preliminary notes on a newly discovered skull of the extinct monkey *Antillothrix* from Hispaniola and the origin of the Greater Antillean monkeys. J Hum Evol 60:124–128.

MacPhee RDE, Fleagle JG. 1991. Postcranial remains of *Xenothrix mcgregori* (Primates, Xenotrichidae) and other Late Quaternary mammals from Long Mile Cave, Jamaica. Bull Am Museum Nat Hist 206:287–320.

MacPhee RDE, Horovitz I. 2002. Extinct Quaternary platyrrhines of the Greater Antilles and Brazil. In: Hartwig WC, editor. The primate fossil record. Cambridge: Cambridge University Press. p 189–200.

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 Museum Novitates 3434: 1–51.

MacPhee RDE, Meldrum J. 2006. Postcranial remains of extinct monkeys of the Greater Antilles, with evidence for semiterrestriality in *Paralouatta*. Am Museum Novitates 3516:1–65.

MacPhee RDE, Horovitz I, Arredondo O, Jiménez Vásquez O. 1995. A new genus for the extinct Hispaniolan monkey *Saimiri bernensis* (Rimoli, 1977), with notes on its systematic position. Am Museum Novitates 3134:1–21.

Osterholz M, Walter L, Ross C. 2009. Retropositional events consolidate the branching order among New World monkey genera. Mol Phylogenet Evol 50:507–513.

Rohlf FJ, Slice DE. 1990. Methods for comparision of sets of landmarks. Syst Zool 29:40–59.

Rosenberger AL. 1977. *Xenothrix* and ceboid phylogeny. J Hum Evol 6:461–481.

Rosenberger AL. 1981. A mandible of *Branisella boliviana* (Platyrrhini, Primates) from the Oligocene of South America. Int J Primatol 2:1–7.

Rosenberger AL. 2002. Platyrrhine paleontology and systematics: the paradigm shifts. In: Hartwig WC, editor. The primate fossil record. Cambridge: Cambridge University Press. p 151–160.

Rosenberger AL. 2011. Evolutionary morphology, platyrrhine evolution, and sysematics. Anat Rec 294:1955–1974.

Rosenberger AL, Tejedor MF. in press. The misbegotten: long lineages, long branches and the interrelationships of Aotus, Callicebus and the saki-uakaris. In: Barnett A, Veiga L, Ferrari S, Norconk M, editors. Evolutionary biology and conservation of Titis, Sakis and Uacaris. Cambridge: Cambridge University Press.

Rosenberger AL, Cooke SB, Rímoli R, Ni X, Cardoso L. 2011. First skull of *Antillothrix bernensis*, an extinct relict monkey from the Dominican Republic. Proc R Soc B: Biol Sci 278: 67–74.

Rosenberger AL, Tejedor MF, Cooke SB, Halenar LB, Pekkar S. 2009. Platyrrhine ecophylogenetics, past and present. In: Garber P, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB, editors. South American primates: comparative perspectives in the study of behavior, ecology and conservation. New York: Springer. p 69–113.

Schneider H, Rosenberger AL. 1996. Molecules, morphology and platyrrhine systematics. In: Norconk MA, Rosenberger AL, Garber PA, editors. Adaptive radiations of neotropical primates. New York: Plenum Press. p 3–19.

Seiffert ER, Simons EL, Fleagle JG, Godinot M. 2010. Paleogene anthropoids. In: Werdelin L, Sanders WJ, editors. Cenozoic mammals of Africa. Berkeley: University of California Press. p 369–391.

Setoguchi T, Rosenberger AL. 1987. A fossil owl monkey from La Venta, Colombia. Nature 326:692–694.

Takai M, Anaya F, Shigehara N, Setoguchi T. 2000. New fossil materials of the earliest New World monkey, *Branisella boliviana*, and the problem of platyrrhine origins. Am J Phys Anthropol 111:263–281.

Tejedor MF, Rosenberger AL. 2008. A Neotype for *Homunculus patagonicus* Ameghino, 1891, and a New Interpretation of the Taxon. PaleoAnthropology 2008:68–82.

Tejedor MF, Tauber AA, Rosenberger AL, Swisher CC III, Palacios ME. 2006. New primate genus from the Miocene of Argentina. Proc Natl Acad Sci 103:5437–5441.