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## A New Genus for the Extinct Hispaniolan Monkey *Saimiri bernensis* Rímoli, 1977, with Notes on Its Systematic Position

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### ABSTRACT

The extinct Hispaniolan primate heretofore known as *Saimiri bernensis* is distinct in numerous ways from true squirrel monkeys and all other known Recent mainland platyrrhines. We therefore remove it to a new genus, *Antillothrix*. Parsimony analysis of 32 craniodental characters indicates that the closest known relative of *Antillothrix* is the newly described (and likewise extinct) Cuban platyrrhine *Paralouatta varonai* (supported by 5 unambiguously placed synapo-

morphies of maxillary fourth premolar and maxillary and mandibular first molars). The sister group of *Antillothrix* and *Paralouatta* is *Callicebus* (supported by 3 unambiguously placed synapomorphies of mandibular and maxillary canines). This clade is sister to a grouping consisting of extant atelids and *Stirtonia* (sister-group arrangement supported by 1 unambiguously placed synapomorphy, large zygomaticofacial foramen relative to buccolingual breadth of maxillary first molar).

### RESUMEN

El primate extinto de La Española, hasta ahora conocido como *Saimiri bernensis*, es diferente en numerosos aspectos de los verdaderos monos ar-

dilla. Además difiere de todos los demás platirrininos vivientes conocidos y es por ello que creamos un nuevo género, *Antillothrix*, para esta especie.

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Un análisis cladístico basado sobre 32 caracteres del cráneo y dientes, indica que el taxón más cercanamente emparentado con *Antillothrix* es *Paralouatta varonai*, una especie cubana extinta recientemente descrita. Esta relación está apoyada por 5 sinapomorfias no ambiguas del cuarto premolar superior y los primeros molares superiores e inferiores. Tres caracteres no ambiguos de los

caninos superiores e inferiores apuntan a *Callicebus* como grupo hermano de *Antillothrix* y *Paralouatta*. A su vez, el grupo hermano de este clado son los atélidos y *Stirtonia*, relación apoyada por una sinapomorfia no ambigua: un foramen cigomaticofacial grande relativo al tamaño bucolin-gual del primer molar superior.

## INTRODUCTION

Systematic understanding of the relationships of the extinct Quaternary monkeys of the Greater Antilles has long been hampered by a severe shortage of informative fossils (Ford, 1990). However, some progress has been made in recent years, thanks to new discoveries as well as new assessments of existing evidence (Ford and Morgan, 1986, 1988; Ford, 1990; Rivero de la Calle and Arredondo, 1991; MacPhee and Fleagle, 1991; MacPhee and Iturralde-Vinent, 1994, 1995a, 1995b; MacPhee and Rivero de la Calle, in press). One recently gained insight, reported here, is that two Antillean monkeys—*Saimiri bernensis* (Rimoli, 1977) from Hispaniola, and *Paralouatta varonai* (Rivero de la Calle and Arredondo, 1991) from Cuba—appear to be more closely related to each other than they are to any mainland taxon (MacPhee et al., 1994). This may seem to be an uncontroversial conclusion, given the proximity of the islands on which they once lived. However, in the past these species were believed to be deeply nested within different platyrrhine clades<sup>5</sup> (cebines in the case of *S. bernensis*, atelines in that of *P. varonai*), which perforce requires that they originated from separate colonizing ancestors.

Another matter that requires reassessment is the assumption that the monkeys of the Greater Antilles only recently evolved from their mainland progenitors, and that therefore anthropoids could not have had a long history in those islands (see discussion by MacPhee and Fleagle, 1991). Discovery of an

Early Miocene platyrrhine astragalus at Domo de Zaza in Cuba (MacPhee and Iturralde-Vinent, 1994a, 1994b, 1995) demonstrates that New World monkeys already had a presence in the Greater Antilles by the end of the Paleogene or earliest Neogene. Indeed, nothing now known about the history of anthropoids in the New World excludes the possibility that the Antillean colonization was essentially coeval with the original invasion of South America by the ancestral platyrrhine—however that feat was achieved (cf. MacFadden, 1990). It is becoming increasingly clear that although the Antillean primate fauna is restricted and peculiar in some respects, it can no longer be ignored in working out the historical biogeography and ultimate origins of Platyrrhini.

The purpose of this paper is to explore the relationships of *Saimiri bernensis* and *Paralouatta varonai* to each other and to other platyrrhines. Through a parsimony analysis of an array of craniodental characters, we conclude that these taxa are cladistic sisters. Nevertheless, the higher-level relationships of the Cuban-Hispaniolan monkey clade as revealed by this analysis should be considered on test, partly because the evidence is fragmentary, but also because these monkeys exhibit a distinctive combination of characters which is hard to relate to morphological patterns in Recent mainland groups. What evidence there is tends to support the argument that these island endemics are probably related more closely to *Callicebus* than to any other South American monkey analyzed. By contrast, character evidence for a close connection with either *Saimiri* (and/or *Cebus*) or *Alouatta* (and other atelids) is much less substantial.

In view of these facts and for economy of reference in later sections of this paper, it is convenient at this point to provide *bernensis*

<sup>5</sup> There is little agreement among platyrrhine systematists regarding the content, name, and rank of platyrrhine suprageneric assemblages. For the purposes of this paper we adopt Fleagle's (1988, his fig. 1.2) arrangement of genera by subfamilies without, however, endorsing his preferred scheme of their interrelationship.

with a new genus-level name and to amend its diagnosis. This is necessary in any case because *bernensis* is not cladistically a squirrel monkey, as has long been recognized by students of platyrrhine evolution, and its continued inclusion within *Saimiri* renders this genus polyphyletic. To facilitate comparisons with its sister taxon, we also provide the first illustrations of unworn or little-worn teeth of *Paralouatta varonai* collected during recent AMNH/MNHNH expeditions.

#### ACKNOWLEDGMENTS

We thank members of Grupo "Pedro A. Borrás" of the Sociedad Espeleológica de Cuba, particularly Efrén Jaimez Salgado and Diwaldo Gutiérrez Calvache, for their continuing help in recovering *Paralouatta* fossils from the "monkey caves" of Pinar del Río. For other assistance, including access to specimens and casts, we thank Manuel A. Iturralde-Vinent and Gilberto Silva Taboada of the Museo Nacional de Historia Natural (La Habana), M. Rivero de la Calle of the Universidad de La Habana, and John G. Fleagle of the State University of New York at Stony Brook. Richard Kay (Duke University), A. L. Rosenberger (National Zoological Park, Smithsonian Institution), Walter Hartwig (State University of New York at Stony Brook), and Tim Cole (Johns Hopkins University) read various manuscript versions of this paper; we are grateful to each of them for their comments. Finally, we are especially grateful to the following persons for their assistance (as indicated): Lorraine Meeker and Chester Tarka (figs. 1, 2, and 4; mounting/labeling), Veronica MacPhee (editing), and Clare Flemming (specimen preparation, editing, and fig. 5). This research was supported by NSF BSR 900002 (to RDEM), and is contribution 918 of the Department of Ecology and Evolution, State University of New York at Stony Brook.

#### ABBREVIATIONS

##### Institutional

AMNHM	American Museum of Natural History, Department of Mammalogy
AMNHVP	American Museum of Natural History, Department of Vertebrate Paleontology

CENDIA	Centro Dominicano de Investigaciones Antropológicas
CGM	Cairo Geological Museum
DUPC	Duke University Primate Center
MACN-SC	Museo Argentino de Ciencias Naturales—Santa Cruz Collection
MNHNH	Museo Nacional de Historia Natural, La Habana
UCMP	University of California (Berkeley), Museum of Paleontology
UF	Florida Museum of Natural History, Gainesville
USNMM	United States National Museum of Natural History, Division of Mammals
YPM	Yale Peabody Museum

##### Anatomical

(To avoid confusion, "maxillary" or "mandibular," as appropriate, is placed in front of all single-letter abbreviations for teeth. Tooth loci are enumerated in the conventional manner.)

I	incisor
C (in roman)	canine
M	molar
P	premolar

##### Other

C (in bold)	character (followed by character number/state)
<sup>14</sup> C yr bp	radiocarbon years before present (i.e., 1950)
CI	consistency index
CS	character state (appendix 1 only)
MPT	most parsimonious tree
RC	rescaled consistency index
rev.	image photographically reversed to facilitate specimen comparison
TL	tree length

#### SYSTEMATIC PALEONTOLOGY

##### *ANTILLOTHRIX*, new genus

**TYPE SPECIES:** *Saimiri bernensis* Rímoli, 1977, type and only known species, = *Antillothrix bernensis* (Rímoli, 1977), new combination.

**ETYMOLOGY:** *Antillo-*, combining form developed from neoLatin "Antillia" (classically, landmass at edge of Western Ocean; Nordenskiöld, 1889) + Greek *thrix*, "hair" (frequently used in platyrrhine scientific names).

**DIAGNOSIS AND DESCRIPTION:** As for the single included species, below.

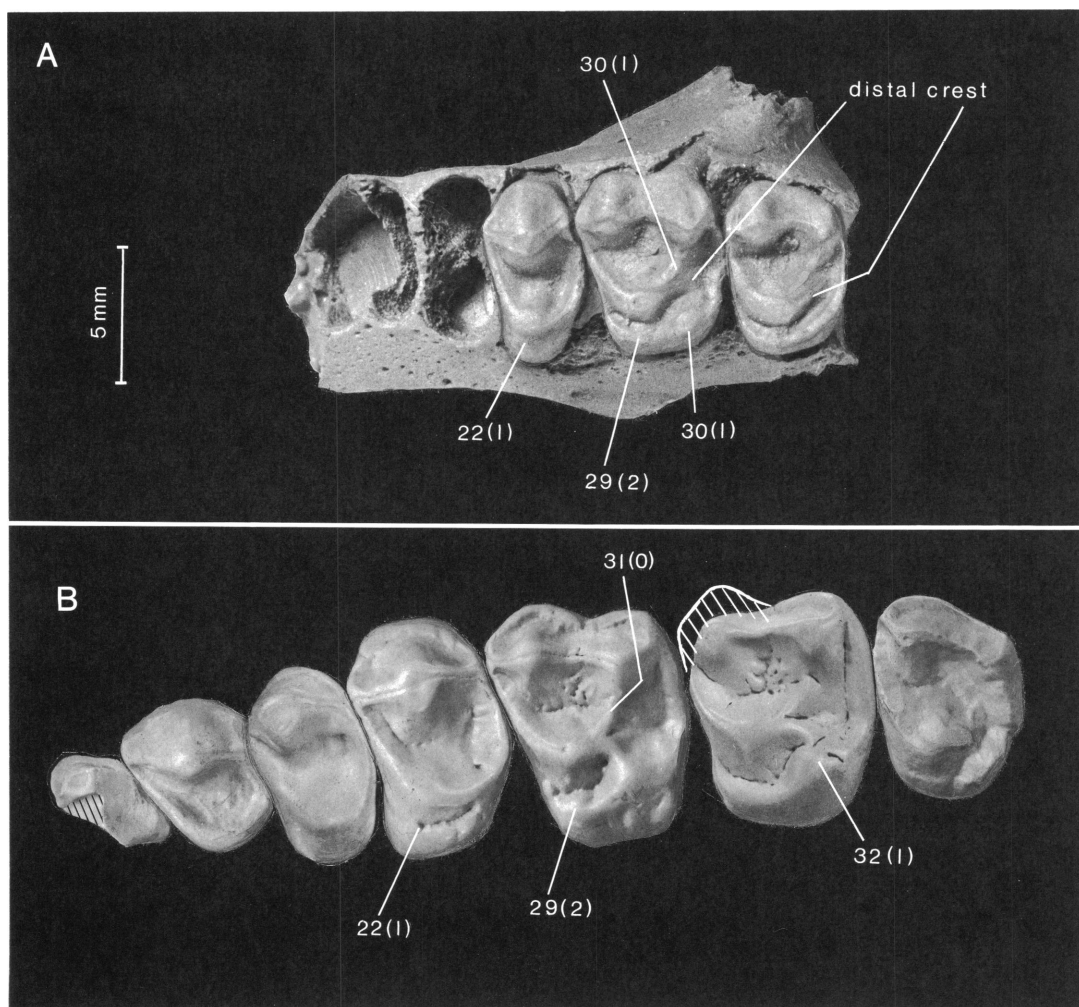


Fig. 1. **A**, *Antillothrix bernensis* CENDIA 1 (cast of holotype, rev.), partial right maxilla retaining P4–M2, in occlusal aspect; **B**, *Paralouatta varonai*, isolated maxillary teeth (C–M3) in occlusal aspect arranged to form composite upper dentition (but not corrected for individual differences in size and wear). From left to right, accession numbers are MNHNH V 159, 115, 177, 116, 125, 121 (rev.), and 122. The mesiobuccal margin of the M2 is broken; shaded area is reconstructed (cf. canine also). Numbers refer to specific character states defined in appendix 1. In A, C 30 is in two parts because reference is being made to states of two features (in this case, postprotocrista present, prehypocrista absent).

*Antillothrix bernensis* (Rímoli, 1977)

**HOLOTYPE:** Right maxilla fragment (CENDIA 1), preserving P4, M1–2, and part or all of the alveoli of the two anterior premolars and canine (fig. 1A). Referred material is noted below.

**TYPE LOCALITY:** Holotype collected at a depth of 1.8–1.9 cm in calcareous sediments

in the entrance of Cueva de Berna, near Boca de Yuma (prov. La Altigracia, Dominican Republic), on 16 August 1975 by M. Veloz Maggiolo, F. Luna Calderón, and R. O. Rímoli (fide Rímoli, 1977). Boca de Yuma is situated at approximately 18°23'N, 68°35'W, near the southeastern extremity of Hispaniola.

**AGE:** Quaternary, surviving into Recent.

TABLE 1  
Comparison Between *Antillothrix bernensis* and Other Selected Taxa, Using Known Character States Employed in PAUP Analysis<sup>a</sup>

<i>Antillothrix</i>	<i>Saimiri</i>	<i>Cebus</i>	<i>Alouatta</i>	<i>Callicebus</i>	<i>Paralouatta</i>
5.1	5.2	5.2	5.0	5.2	5.0
8.0	●	●	●	●	●
14.0	●	●	14.1	●	●
15.1	15.0	15.0	●	15.0	●
16.0	●	●	●	●	●
21.0	●	●	●	21.1	21.1
22.1	22.2	22.2	22.0	22.2	●
23.1	●	●	23.0	●	23.0
24.0	●	●	●/24.1	24.1	●
25.1	●	●	25.0	25.0	●
26.0	●	26.1	●	26.1	●
27.1	27.0	27.0	27.0	27.0	●
28.0	●/28.1	●	28.2	●	28.1
29.2	●	29.0	29.0/29.1	29.1	●
30.1	●	●	●	●	30.0
31.1	31.0	●	●	●	31.0
32.1	●	●	32.2	●	●
Differences from <i>Antillothrix</i>	5	6	9	9	6

<sup>a</sup> Listing includes only those features that can be identified on available specimens of *Antillothrix*, using the character list in appendix 1. In the columns under the named taxa, features are indicated only if different from *Antillothrix* (filled circles indicate identity). These differences are potential differentiae, for diagnostic purposes only. Their *phylogenetic* status is determined by their distribution on the MPT (fig. 3). Polymorphies are not included in total “differences from *Antillothrix*” if one of the polymorphic states occurs in the latter.

There are two pertinent <sup>14</sup>C dates: (1) 3850 ± 135 <sup>14</sup>C yr bp, for charcoal sample recovered 10 cm above layer yielding holotype at Cueva de Berna (Rímoli, 1977); and (2) 9550 ± 150 <sup>14</sup>C yr bp, for a bone sample collected near a referred mandibular fragment (UF 28038) from Trou Woch Sa Wo (or Caverne Sawo), Département du Sud, Haiti (MacPhee and Woods, 1982). Although <sup>12</sup>C/<sup>13</sup>C ratios have not been reported for these dates, given their recency it is unlikely that any adjustment for the effect of isotopic fractionation is required. Doubling the error expression (σ) of each determination yields age ranges that have a 95% statistical probability of including the correct age of the fossils, other factors being equal (Taylor, 1987). In this instance, ranges are 4120–3580 <sup>14</sup>C yr bp and 9250–9850 <sup>14</sup>C yr bp. Thus *Antillothrix* was still extant at least 2000 yr into the period of human occupation of Hispaniola (for discussion of arrival times of humans in Greater Antilles, see Burney et al. [1994] and references cited therein).

**OCCURRENCE:** Original distribution undefined; known only from remains collected at (1) Cueva de Berne (type locality), in eastern Dominican Republic; (2) Trou Woch Sa Wo (partial mandible, UF 28038, fig. 2A), situated at 18°09'N, 73°55'W in southwestern Haiti (see Woods, 1989); and (3) an unlocated site on “a key lying about half a mile east” of the mouth of the Río Naranjo Abajo (western end of Bahía de Samaná, D.R.), where Miller (1929: 3) recovered a distal tibia (USNMM 254682) later referred to this taxon by Rosenberger (1978; see also Herskovitz, 1988). Ford (1990) mentioned the existence of additional undescribed collections, of both teeth and postcranial elements, from localities in and around Trou Woch Sa Wo that are probably referable to this species.

**REMARKS:** In his species diagnosis, Rímoli (1977: 9) stated that, except in regard to size, there were only slight differences in molar and premolar morphology separating *Saimiri bernensis* from *S. sciureus*, the squirrel monkey of northwestern South America. He pro-

vided some measurements for both taxa, but made no detailed differential comparisons. Rosenberger (1978) and MacPhee and Woods (1982) provided morphological information on *bernensis* that tended to emphasize its distinctiveness from squirrel monkeys, but these authors made no formal systematic recommendations (other than to express their doubts that *bernensis* could be allocated to *Saimiri*). Here we take the necessary steps to create a new genus for *bernensis*. The following diagnosis utilizes the results of the phylogenetic analysis presented in the next section.

**EMENDED DIAGNOSIS:** Differential diagnosis will be limited to features that are readily interpretable from illustrations and text descriptions provided here. Article 13(a)(i) of the ICZN (3rd ed.) requires that every new scientific name be "accompanied by a description or definition that states in words characters that are purported to differentiate the taxon." A diagnosis is, of course, a combination of differentiae, some of which may turn out to be primitive and others derived in the context of a given tree or phylogenetic analysis. Accordingly, features used as differentiae have a function that is quite separate from their role as analytical devices for inferring phylogeny.

The outstanding diagnostic feature of *Antillothrix* is a crest on maxillary M1 and M2, not consistently present in any other platyrrhine, that we shall noncommittally describe as the distal crest (fig. 1A). The distal crest runs directly distally from the protocone, but is distinct from it. It cannot be considered part of the postprotocrista, because there is already a postprotocrista present in the expected position. It cannot be a prehypocrista, because it has no connection with the hypocone (indeed, it runs buccal to the hypocone and is separated from the latter by a deep gutter). On the other hand, the distal crest is remarkably reminiscent of the *Nannopithecus*-fold seen in a variety of omomyids and adapids, but is generally held to be absent in anthropoids (see discussion by Kay, 1980). Because the nature of the relationships of anthropoids, adapids, and omomyids is not under scrutiny here, we do not find it necessary to reach a conclusion regarding whether the distal crest of *Antillothrix* is homologous with

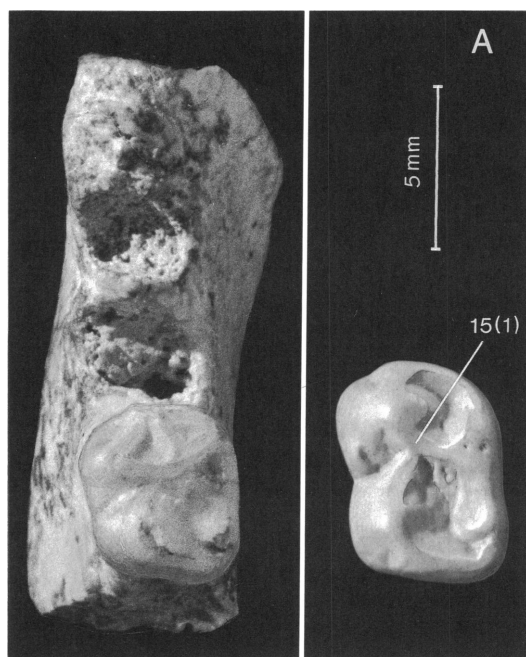


Fig. 2. A, *Antillothrix bernensis* UF 28038 (rev.), referred mandible fragment retaining M1, compared to MNHNH V 123, an isolated M1 or M2 of *Paralouatta varonai*; occlusal aspect. B, *Paralouatta varonai* MNHNH V 195, partial mandible retaining left P3–M3, right I2–C; occlusal and lateral aspects. Number refers to specific character state defined in appendix 1.

the *Nannopithecus*-fold of any early Tertiary primate. In the view of R. F. Kay (personal commun.), *Callicebus* and *Soriacebus* display a close morphological approach to *Antillothrix*, but specimens of these taxa available to us exhibit a typical prehypocrista connected to the hypocone (cf. fig. 4C), not a distal crest as we define it here. We recognize that the apparent absence of the distal crest in other anthropoids strongly implies that it is neomorphic in the Hispaniolan monkey.

Table 1 arrays 17 features of which *Antillothrix* can be directly scored against conditions in selected taxa of New World monkeys (see appendices 1 and 2). Taxa selected include all those purported, by this or other studies, to have a close relationship with *Antillothrix* or its relative *Paralouatta* (see next section). Of the features examined, *Antillothrix* differs from *Alouatta* and *Callicebus* in 9

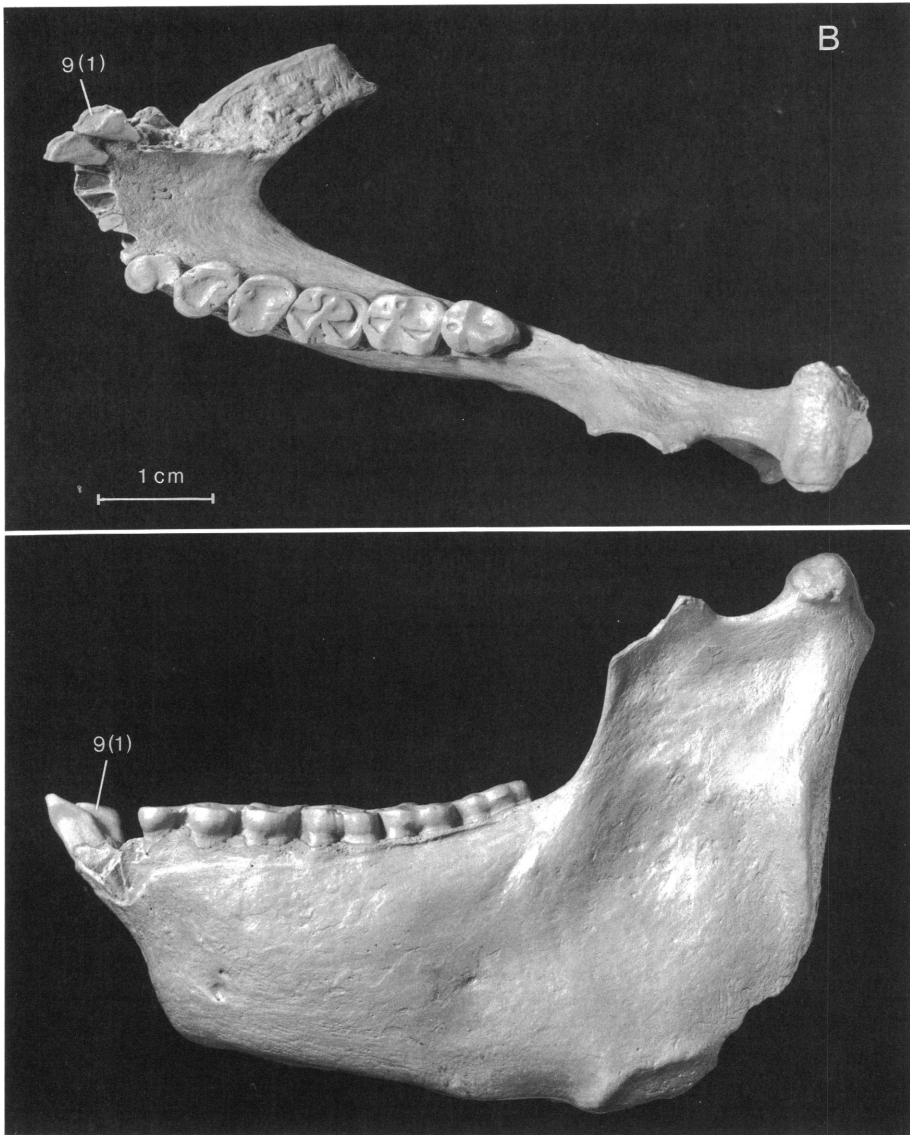


Fig. 2. Continued.

instances, *Cebus* and *Paralouatta* in 6, and *Saimiri* in 5. All of these constitute potential differentiae, but we draw particular attention to the ones described below.

*Antillothrix* differs (1) from *Saimiri* and *Paralouatta* in lacking a continuous distal wall of the trigon running from protocone to metacone on the maxillary M2 (C 31.1); (2) from *Saimiri*, *Cebus*, and *Callicebus* in displaying a relatively lingual intersection of the protolophid and oblique cristid on the mandib-

ular M1 (C 15.1); (3) from all listed taxa except *Paralouatta* in possessing a mesially projecting lobe of the lingual cingulum on the maxillary P4 (C 22.1) and an oblique alignment (relative to the midsagittal plane) of the maxillary M1 protocone and hypocone (C 27.1); and (4) from all listed taxa in the positioning of the infraorbital foramen above the interval between maxillary P3 and P4 (C 5.1).

From the standpoint of similarities (= phe-

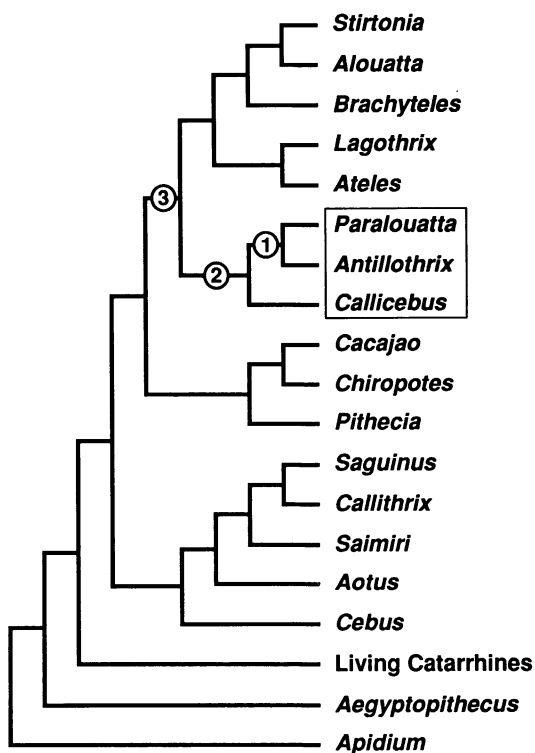


Fig. 3. Single MPT derived from parsimony analysis of 32-character matrix (TL = 105; CI = 0.59; RC = 0.38); box contains *Antillothrix* and its closest relatives as determined by this study. For analysis of characters positioned on numbered stems, see table 2 and text.

netic matches), inspection of table 1 shows that *Antillothrix* displays more resemblances to *Saimiri* than to any other taxon, a finding which appears to accord with Rímoli's (1977) original hypothesis of relationships for the Hispaniolan monkey. However, inspection also shows that the *exclusive* resemblances in the table are to *Paralouatta*, not to squirrel monkeys. Clearly, any effective examination of the relationships of *Antillothrix* will have to be based on a parsimony analysis of the character evidence, not on assertions arising from distributions of unanalyzed resemblances.

## PHYLOGENETIC ANALYSIS

### MATERIALS AND METHODS

In order to evaluate the phylogenetic position of *Antillothrix*, we arrayed 32 craniodental characters against their incidence in

19 taxa and analyzed the resulting matrix with the program Phylogenetic Analysis Using Parsimony (PAUP), version 3.1.1 (Swofford, 1993), using the branch-and-bound algorithm. In addition to *Antillothrix bernensis* and *Paralouatta varonai*, one or more species of 14 New World monkey genera (13 extant, 1 extinct) were selected for examination, some because they are allegedly related to Antillean monkeys, others because they help represent platyrrhine diversity. The hypodigm for *Paralouatta* now includes a number of unworn or slightly worn isolated teeth; these will be described and evaluated in a companion paper (MacPhee and Horovitz, in prep.). *Aegyptopithecus*, *Apidium*, and "living catarrhines" (represented by *Nasalis* and *Hylobates*) were selected as outgroups, for the purpose of rooting trees and fixing character polarities. In all runs, taxa were permitted to group without imposition of any monophyly constraints, and the full complement of taxa and characters was always used.

Our primary purpose in this analysis was to find an appropriate seating for *Antillothrix*, not to explore all relationships among known platyrrhine taxa. This required that we practise some economies. As desirable as it might be to include as many fossil taxa as possible, in order to keep the data matrix at a manageable size with most data cells filled, we had to make selections among the total array of known taxa. Because our primary interest is to evaluate the placement of certain West Indian taxa within the context of Quaternary platyrrhines, we decided to include as many Recent taxa as possible and omit most fossils. However, the Miocene alouattin *Stirtonia* was included in our analysis because Rivero de la Calle and Arredondo (1991) specifically drew attention to its apparent similarities to *Paralouatta*. Unlike the case with the limited published hypodigm of *Antillothrix*, the wealth of material now available for *Paralouatta* makes its comparison to a broad array of Tertiary platyrrhines worthwhile (MacPhee and Horovitz, in prep.).

The character list, character states, and supporting documentation are provided in appendix 1. Character codings are presented in the character/taxon matrix, which comprises appendix 2. Finally, a list of species and specimens used to score characters for each taxon appears in appendix 3.



The following considerations were involved in selecting characters and taxa for analysis.

(1) *Characters selected should capture as much information as possible from the target taxa.* Because of the incompleteness of the Antillean fossil material, it was considered important to emphasize characters for parsimony analysis that could be scored on at least one of the target taxa (although there are some exceptions). For this reason, features of the posterior cheek teeth are unavoidably emphasized in the character list.

*Paralouatta varonai* MNHNH V 194, the holotype skull, was not utilized for scoring dental character states in most instances because its teeth are so worn that virtually no features of the crowns can be discerned. As noted, a number of isolated teeth attributable to this taxon have been recovered in recent years (Jaimez Salgado et al., 1992) and were available for analysis.

(2) *Taxa selected for comparative analysis should constitute a reasonable cross-section of extant platyrrhines.* Choice of taxa was made with some bias toward including taxa previously named as possible relatives of *Antillothrix* and *Paralouatta* (species of the cebines *Cebus* and *Saimiri* and the atelines *Alouatta*, *Brachyteles*, *Ateles*, and *Lagothrix*). As noted earlier, in this paper the only non-Antillean fossil monkey we consider in detail is *Stirtonia*; a few comparative remarks on *Xenothrix* are included in the Discussion. *Ateles* (= *Montaneia*) *anthropomorphus*, the so-called "Cuban Spider Monkey," is omitted from consideration because it appears to be a post-Columbian introduction (MacPhee and Rivero de la Calle, in press).

## RESULTS

With *Apidium* specified as the outgroup, the branch-and-bound routine yielded a single MPT (fig. 3), 105 steps at length. Pertinent stems on the MPT are identified by numbers in figure 3: Stem 1, carrying *Antillothrix* + *Paralouatta* joins with one bearing *Callicebus*; this grouping (Stem 2) then unites with the common stem for atelines, thereby forming a clade (Stem 3) distinct from other platyrrhine clades.

To check on the stability of these results,

TABLE 2  
Unambiguously Placed Characters Supporting Stems 1-3 in Figure 3

Stem	Character	Transformation	Description
Stem 1 <sup>a</sup>	15.1	(0 → 1)	Oblique cristid on mandibular M1 intersects protolophid distolingual to protoconid apex (CI = 0.25)
	25.1	(0 → 1)	Maxillary P4 relatively wider buccolingually than maxillary M1 (CI = 0.25)
	26.0	(1 → 0)	Maxillary M1 postmetacrista oriented distobuccally (CI = 0.25)
	27.1	(0 → 1)	Maxillary M1 hypocone lingually displaced relative to paracone (CI = 0.50)
	29.2	(1 → 2)	Pericone present on lingual cingulum of maxillary M1 (CI = 0.56)
Stem 2 <sup>b</sup>	9.1	(0 → 1)	Mandibular C subequal to incisors (CI = 0.67)
	11.1	(0 → 1)	Mandibular C root highly compressed mesiodistally (CI = 0.33)
	20.0	(1 → 2)	Maxillary C root as prominent as I2 root on lower face (CI = 1.00)
Stem 3 <sup>c</sup>	1.1	(0 → 1)	Zygomaticofacial foramen large relative to maxillary M1 breadth (CI = 1.00)

<sup>a</sup> Also appearing on Stem 1 are C 4.1 (0 → 1), 17.2 (1 → 2), and 18.0 (1 → 0) in acctran only, and 22.1 (0 → 1) in deltran only.

<sup>b</sup> Also appearing on Stem 2 are C 21.1 (0 → 1) and 22.1 (0 → 1) in acctran only.

<sup>c</sup> Also appearing on Stem 3 is C 5.1 (0 → 1) in acctran only.

a second analysis was run, this time collecting all MPTs at +1 step (TL = 106). This run yielded 50 trees, which showed considerable variation in branching sequences and taxon placements. However, *Antillothrix* + *Paralouatta* formed a sister-group dyad in all 50 MPTs; in 47 (94%) of these, *Callicebus* formed the next outgroup.

Support for Stems 1-3 is briefly summarized in table 2, which displays collected

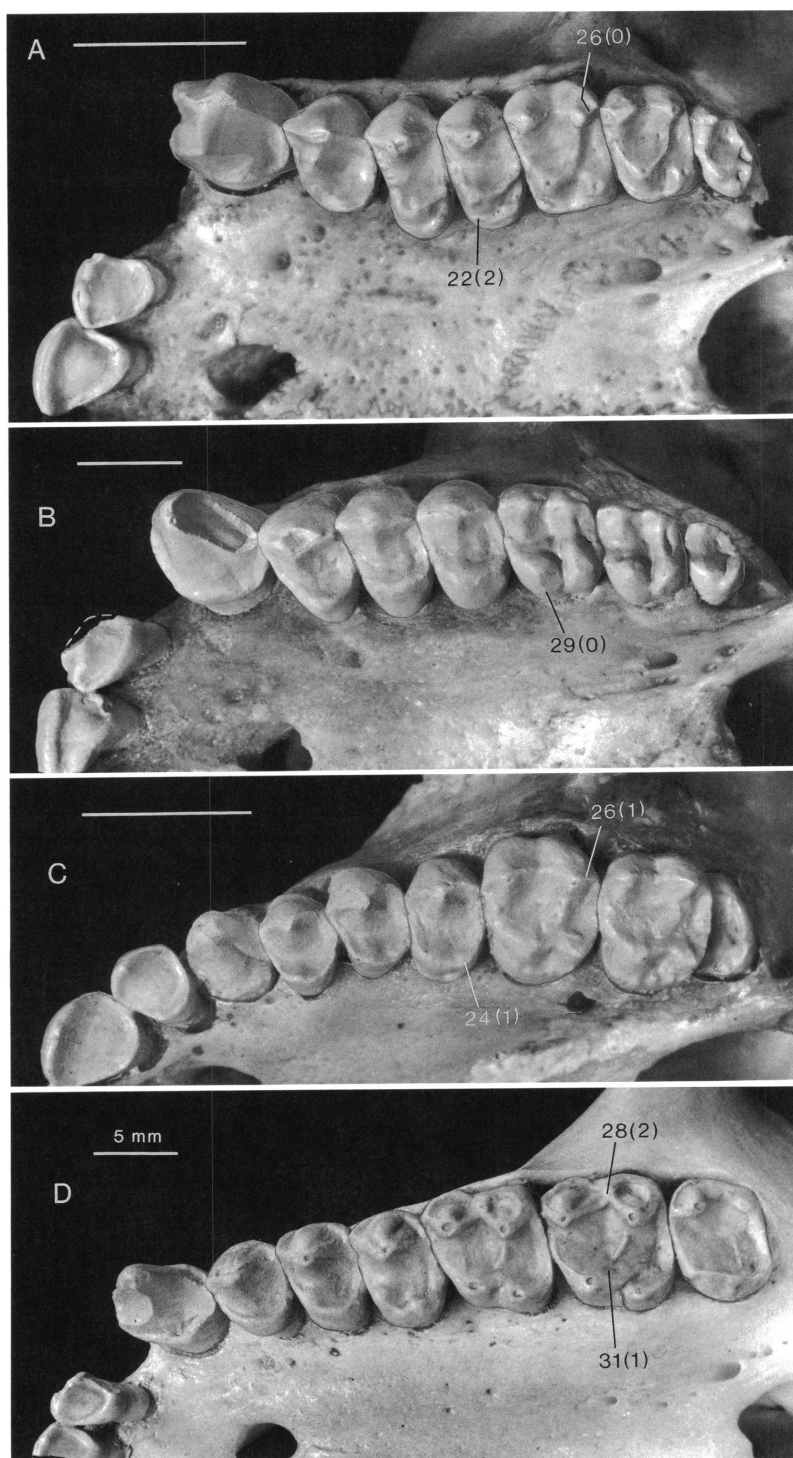


Fig. 4. Maxillary dentitions of representative platyrrhines, in occlusal aspect (scale bars = 5 mm): A, *Saimiri sciureus* AMNHM 73426 (male); B, *Cebus apella* AMNHM 133670 (female); C, *Callicebus cupreus* AMNHM 98388 (male); D, *Alouatta caraya* AMNHM 211512 (female). Numbers refer to specific character states defined in appendix 1. C 28.2 concerns M1, but feature (mesoloph) occurs on both M1 and M2.

character states and the direction of their transformation. Stem 1, bearing the *Antillothrix* + *Paralouatta* clade, is supported by C 15.1, 25.1, 26.0, 27.1, and 29.2. All of these are unambiguously placed (i.e., occur on this stem in any optimization) and are known to occur in both targets. Stem 2, bearing a grouping consisting of *Callicebus* + (*Antillothrix* + *Paralouatta*), is also supported by several characters. The unambiguously placed ones (C 9.1, 11.1, 20.0) provide direct empirical support for a relationship between *Callicebus* and *Paralouatta*, but the states of these characters in *Antillothrix* are not known at present. This is acknowledged to be problematic, since all three of the unambiguously placed characters describe canine morphology, and *Antillothrix* may well have had more primitive canines than *Paralouatta*. However, the grouping of the Antillean primates with *Callicebus* is the most parsimonious solution offered by the evidence at hand. Support for Stem 3, carrying the foregoing clade and atelids in a sister-group relationship, is limited to one unambiguously placed but uniquely transformed character, C 1.1.

Although an extended comparison of our general results to those of other recent investigations of platyrrhine systematics is beyond the scope of the present study, we note that the MPT has some features in common with results achieved with phylogenetic analysis of  $\epsilon$ -globin DNA sequences (Schneider et al., 1993) and combined morphological/molecular data sets (Horovitz and Meyer, in prep.). Both investigations show a first clade consisting of atelines, *Callicebus*, and pitheciines (with *Callicebus* grouping with pitheciines, not atelines), and a second clade containing callitrichids, *Saimiri*, *Aotus*, and *Cebus* (although with different ordering of sister taxa).

Finally, among other incidental results, the placement of *Brachyteles* next to alouattins rather than atelins echoes results reported by Kay et al. (1987), who also found that woolly spider monkeys failed to exclusively group with atelins when analysis was limited to craniodental traits.

Some of our reviewers stated that the use of *Apidium* as an outgroup was bound to deform our parsimony analysis because this taxon is significantly autapomorphic. Seeing no reason a priori to accept this conclusion

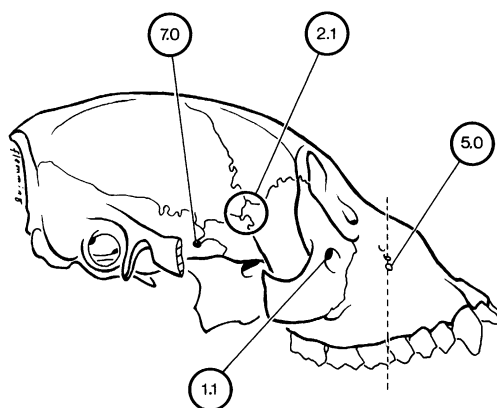


Fig. 5. Some character states defined in appendix 1 (for cranium of *Alouatta*).

(cf. discussion of “outgroup myths” by Nixon and Carpenter [1993]), we deleted *Apidium* from the taxon list and ran the matrix again, this time using *Aegyptopithecus* as the designated outgroup. Figure 6 reproduces the two MPTs from this run; they differ only in the position of the clade composed of *Paralouatta*, *Antillothrix*, and *Callicebus*. In both MPTs, the monophyly of Platyrrhini is preserved relative to the placement of “living catarrhines,” and most major groups found in the single MPT from the first run also occur (fig. 3). For our purposes, the important conclusion is that inclusion or exclusion of *Apidium* has only a small impact on taxon placement in the most parsimonious resolution(s) of the data matrix, and none at all on the resolution of the closest affinities of *Antillothrix*.

## DISCUSSION

Prevailing hypotheses concerning the identity of the closest sister groups of *Antillothrix* and *Paralouatta* are not corroborated by the results reported here. According to our investigation, their closest relatives are actually each other—a result that could hardly have been anticipated from their separate systematic histories. *Paralouatta* was originally described as conclusively ateline, and, within that grouping, as probably alouattin (Rivero de la Calle and Arredondo, 1991).

Until now, *Antillothrix* has been linked only with *Saimiri* and *Cebus* (e.g., see Rosenber-

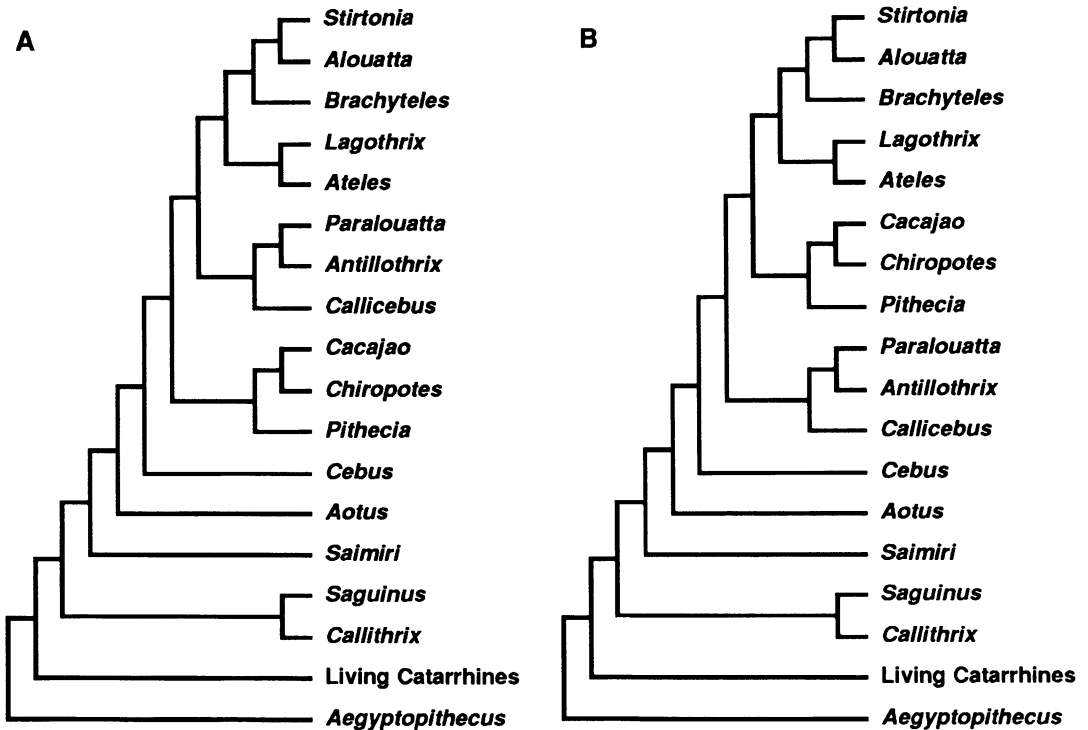


Fig. 6. Two MPTs (A, B) derived from parsimony analysis of 32-character matrix when *Apidium* is deleted and *Aegyptopithecus* is designated as outgroup (TL = 98). In general, results are similar to single MPT derived with *Apidium* included. The two MPTs in this run differ in the placement of the clade composed of *Antillothrix* and its allies.

ger, 1978; MacPhee and Woods, 1982). Similarities to both *Cebus* and *Saimiri* prompted MacPhee and Woods (1982) to conclude that "*Saimiri*" *bernensis* should be classified as a cebine, on the then-popular argument that capuchin and squirrel monkeys were each other's closest relative (e.g., Rosenberger, 1979; Fleagle, 1988). (Some recent studies of platyrrhine relationships [e.g., Kay, 1990; Horovitz and Meyer, in prep.] have questioned whether Cebinae is monophyletic.) Except for incidental references, MacPhee and Woods (1982) did not consider *Callicebus* at all. Among possible solutions for the placement of "*Saimiri*" *bernensis*, they noted (p. 427) that it could be

a distant collateral of the capuchin, perhaps a member of an otherwise unknown genus of cebines. The only other possibility is to assume that the Haitian monkey is the Antillean vicar of a noncebine lineage massively convergent upon *Cebus*.

Although MacPhee and Woods (1982) clearly preferred a cebine connection of some sort for the Hispaniolan monkey, they also noted that in several respects its morphology radically departed from that of both *Saimiri* and *Cebus* (e.g., size of buccal cingulum and distal projection of mandibular M1). With the discovery of *Paralouatta*, it has become clear that traits of *Antillothrix* that would have formerly been dismissed as specializations unique within Platyrrhini are actually important markers of a native Antillean radiation (table 2).

Although the mutual relationship of *Antillothrix* and *Paralouatta* has now been clarified, how their common stem connects with the rest of the platyrrhine tree is still open to refinement. Stem 3, supporting atelids, *Paralouatta*, *Antillothrix*, and *Callicebus*, bears only a single unambiguously placed transformation, large zygomaticofacial foramen (C 1.1). Although dental resemblances to titi

monkeys justify the sister-group arrangement on Stem 2, there are nevertheless some marked differences. For example, there is an outstanding difference between *Paralouatta* and *Callicebus* in the depth of the mandible, exaggerated by the presence in the former of a buttresslike mental eminence under the anteriormost teeth. (The situation in *Antillothrix* is not yet known.) However, in this regard, as in many others, *Paralouatta* is highly autapomorphic (MacPhee and Horovitz, in prep.).

More critically, the failure of *Paralouatta* to group first with *Alouatta* and other atelids may seem surprising in view of Rivero de la Calle and Arredondo's (1991) excellent study supporting their close affiliation. It must be noted that the hypodigm available to these authors was severely limited: the type skull of *Paralouatta varonai* is certainly one of the finest platyrrhine fossils in existence, but, as noted above, in vivo tooth wear was so extreme that virtually no details of cusp morphology can be discerned. Now that strong dental differences between *Paralouatta* and *Alouatta* have been brought to light, their general similarity in skull shape is probably better interpreted as a function of convergence. A similar conclusion has been reached independently by Cole (1995) on the basis of his preliminary study of discrete features of the cranium, MNHNH V 194. His evidence indicates that *Paralouatta* is not a close relative of *Alouatta* and may not even be an ateline, which meshes with our own view. (We note, however, that our MPT points to a relationship between *Paralouatta* and Ateleinae at a higher level.)

The molar morphology of *Antillothrix* and *Paralouatta* is quite unlike that of marmosets, as is the shape and detailed anatomy of the maxillary P4 (e.g., lobular mesial cingulum seen in the Antillean primates vs. characteristic "waist" seen in the premolars of all definite callitrichids). In our analysis, not only are they placed far apart on the most parsimonious cladogram, they even lack evidence of substantial convergence (e.g., C 15.1 on Stem 1 convergently occurs on terminal stem of *Saguinus*; C 11.1 on Stem 2 is convergent in *Callithrix*). Although we feel that these points effectively dispose of any dental argument that *Antillothrix* is most closely re-

lated to marmosets among platyrrhines, it is important to mention in this context Ford's (1986) argument that the tibial fragment from Bahia de Samaná (Dominican Republic) bears several derived characters otherwise restricted to marmosets and tamarins. If the published fossils here grouped as *Antillothrix bernensis* all relate to one species, then there is a clear conflict between the dental evidence and that small part of the postcranium known at present. In a more recent work, Ford (1990) steps back from her "giant callitrichid" hypothesis somewhat, noting that newly discovered postcranial and dental remains from Haiti may settle the issue concerning the number and nature of primate species from that island. In the interim, we prefer to adhere to the least complicated view, which is that because all known Hispaniolan monkey fossils come from animals of similar size, all probably relate to a single species.

To complete our survey of possible relatives of *Antillothrix bernensis*, brief reference needs to be made to *Xenothrix mcgregori* from Jamaica, the only other named Quaternary monkey from the Greater Antilles that is certain to be an endemic. Although a few postcranial elements have been tentatively ascribed to this species in recent years (MacPhee and Fleagle, 1991; MacPhee et al., 1994), knowledge of its dentition is exclusively based on the holotype jaw (AMNHM 148198, retaining M1 and M2 only). Rosenberger et al. (1990) concluded that, among known platyrrhines, *Xenothrix* is probably most closely related to *Callicebus* (which they regard as cladistically pitheciine). This is of obvious interest here because, according to our analysis, *Antillothrix* and *Paralouatta* also seem to be related in some meaningful way to titi monkeys (although not to pitheciines). Once again, the very limited material available for two of the three Antillean taxa obviates detailed comparisons. With respect to characters emphasized by Rosenberger et al. (1990), it can be said that *Xenothrix* and *Paralouatta* resemble each other in the (1) size and general organization of principal cusps on lower molars, (2) "post-talonid extension" on mandibular M1, and (3) small size of mandibular C. Confoundingly, *Antillothrix* appears to have had a large canine and little or no talonid extension, despite resemblances it

evinces to *Paralouatta* in other regards. *Xenothrix* dramatically differs from the Cuban and Hispaniolan monkeys in lacking M3 and protolophids on M1 and M2, both unique features within Platyrrhini. Although assessments might change should any additional craniodental remains of *Xenothrix* come to light, at present the evidence for joining this taxon to any specific clade within Platyrrhini is rather inconclusive. Biogeographically, the notion that the Cuban, Hispaniolan, and Jamaican monkeys might be part of a narrow monophyletic group is certainly attractive, because it permits the hypothesis that all of these endemics originated from a single Antillean initiator rather than several different ones (MacPhee and Iturralde-Vinent, 1995b).

### CONCLUSION

The number and interrelationships of Antillean monkeys continue to be in a state of flux. It is thus a victory of a small sort that a sister-taxon relationship has finally been confirmed between monkeys from adjoining

islands, despite the poverty of the fossil evidence. *Antillothrix* and *Paralouatta* appear to share a unique common ancestry with titi monkeys, a group that has been regarded, albeit inconclusively, as related to the Jamaican endemic *Xenothrix* (Rosenberger et al., 1990). At a higher level, a connection with Atelidae is thinly supported; by contrast, there is no support for the cebine hypothesis.

In platyrrhine studies there has been a longstanding prejudice against accepting substantial antiquity for island clades, the usual assumption being that the endemic Antillean monkeys were very recent derivatives of separate mainland groups and therefore of limited systematic interest. This thinking, while appropriately conservative in some ways, gives the false impression that Antillean monkeys differ little from their supposed continental relatives. The material reviewed in this paper establishes beyond any doubt that the endemic primates of the West Indies were highly distinctive. What their true role was in the evolutionary history of New World monkeys remains to be discovered.

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## APPENDIX 1

### CHARACTER LIST

Figures 1, 2, 4, and 5 illustrate many, but not all, of the features described in this appendix. Ordered characters are identified by an asterisk preceding character number.

#### 1. Zygomaticofacial foramen, size relative to maxillary M1 breadth: (0) small; (1) large

Buccolingual dimension of M1 was used as a measure of size, and a proportional factor was computed by dividing this measurement by zygomaticofacial foramen width (measured with an ocular reticule). In the case of multiple foramina, individual widths were taken and summed. A large gap in distribution of factors permitted the establishment of ranges for the two character states. In general, all atelids have large foramina in proportion to M1 breadth, as do *Paralouatta* and *Callicebus*. *Callithrix* and *Saguinus* had larger proportional factors than other taxa rated as CS 1(0), but their scores were nevertheless much lower than in the "large" group.

#### 2. Pterion, external contacts between bone territories: (0) frontal-alisphenoid; (1) zygomatic-parietal

Old World anthropoids are uniformly CS 2(0). Rarely, contacts are stellate, with all four bone territories making what amounts to "point" contacts. New World monkeys usually express CS 2(1). In individuals of *Brachyteles*, a tongue of the squamosal prevents what would otherwise be zygomatic-parietal contact. This character state is not separately distinguished here, so *Brachyteles* is scored as CS 2(1).

#### 3. Pterygoid fossa location: (0) isolated on pterygoid laminae; (1) fossa impinges on skull base

States define whether or not the pterygoid fossa is dorsally extensive (i.e., whether it is limited to a comparatively small pocketing in the lamina per se, or is so large that it impinges morphologically on the skull base).

#### 4. Relative orbit size (orbital height/foramen magnum width): (0) < 1.9; (1) > 2.1

Definition of states takes advantage of gap in distribution of ratios. Skull of *Aegyptopithecus* CGM 40237 is deformed in area of foramen magnum, but estimated measurements indicate that CS 4(0) applies.

#### \*5. Infraorbital foramen, vertical position relative to maxillary cheekteeth in Frankfurt plane: (0)

above interval between M1 and P4 (or caudal to this position); (1) above interval between P4 and P3; (2) above anteriormost premolar (or rostral to this position)

Vertical position of infraorbital foramen above cheekteeth was determined by dropping a perpendicular from foramen, with specimen positioned in Frankfurt plane (estimated for some fossils). Living catarrhine sample is polymorphic: in *Nasalis* (and most other taxa, including *Macaca*, *Cercopithecus*, and *Pan*), infraorbital foramen lined up over M1 or M2; in *Hylobates*, by contrast, its vertical position was rostral to anteriormost premolar. In cases of multiple infraorbital foramina, largest foramen was judged to be "the" infraorbital foramen.

#### 6. Canal in subarcuate fossa: (0) absent; (1) present

Subarcuate venous canal, draining from posterior wall of subarcuate fossa to sigmoid sinus, is present in all examined platyrrhines for which material is available, including all atelines (Horovitz, in press; contra Cartmill et al., 1981). Presence in *Brachyteles* could not be determined in available skulls. Scored as absent in specimens tentatively assigned to *Apidium* and *Aegyptopithecus* by Cartmill et al. (1981).

#### 7. Temporal emissary foramen, location of: (0) large and above plane of infratemporal margin of zygomatic process of squamosal; (1) small, absent, or differently positioned

Temporal emissary foramen is apparent to unaided eye in extant atelids and *Saimiri*. In these taxa, foramen is within the infratemporal fossa, dorsal to line of zygomatic process of squamosal, and usually in or near alispheno-squamosal suture. In other anthropoids examined, foramen is small or absent. In a few cases (e.g., some *Callicebus*, some *Aotus*), a tiny foramen is occasionally found well below the atelid position (and is therefore of uncertain homology).

#### 8. Molars, number: (0) three; (1) two

Maxillary M2 of *Antillothrix* CENDIA 1 bears a distal interproximal facet, proving that M3 was present.

#### 9. Mandibular C, size: (0) much larger than mandibular I<sub>s</sub>, extending well beyond incisor occlusal plane; (1) subequal to I<sub>s</sub>, extending little or not at all beyond incisor occlusal plane

Mandibular C size is judged by estimating (1) crown "volume" (length × width × height) and



(2) extent to which apex of crown rises above occlusal plane of Is. Using these criteria, only male and female *Callicebus* and some female *Aotus* exhibit CS 9(1). *Aotus* is scored as polymorphic. Gender of individual *Paralouatta* and *Apidium* specimens is unknown, but Cs are always subequal to Is in specimens in which this point can be evaluated.

In *Callithrix* (and *Cebuella*, not considered here), mandibular C and Is are all comparatively long. Comparing these teeth with the rest of the dentition, it is obvious that the incisors are autapomorphously enlarged while the canine has remained the same size that it is in other callitrichids, CS 9(0).

**10. Mandibular C, shape of lingual edge: (0) rounded; (1) sharp**

In pitheciines only, lingual edge of mandibular C is built out into a raised border, giving tooth a semipyramidal cross section (cf. Kay, 1990).

**11. Mandibular C, root shape: (0) rounded/suboval; (1) highly compressed mesiodistally**

Margins of mandibular C alveolus were measured in mesiodistal and buccolingual axes in all taxa in which this character could be studied. The distribution of ratios of these axes showed a gap between 1.33 and 1.42. Ratios less than 1.4 were considered to conform to the rounded/suboval pattern (actual range, 1.00 [*Cebus olivaceus*] to 1.33 [*Brachyteles arachnoides*]). Ratios more than 1.4 were considered to represent the highly compressed pattern (actual range, 1.42 [*Apidium*] to 1.59 [*Paralouatta*]). In *Stirtonia* UCMP 38989 the alveolar margin is broken; in this case, ratio is derived from measurements of canine root immediately beneath cervix.

**12. Mandibular P4 cuspiform entoconid: (0) absent; (1) present**

P4 entoconid is scored as present if a distinct cusp is present on inside trailing margin of tooth. If only a crest is present, there is no cuspiform entoconid. Entoconid as a distinct cusp is characteristically present in *Aotus* (contra Kay and Williams, 1994). Whether entoconid is present in *Apidium* could not be determined from our sample; we followed Kay and Williams (1994) in rating it as absent.

**13. Mandibular Ms, crenulation of: (0) absent; (1) present**

In pitheciines and some *Callicebus*, occlusal surfaces of mandibular molars are deeply crenulated.

The single available lower molar of *Antillothrix* is too worn for assessment.

**14. Mandibular M1, projection of distobuccal quadrant (DB complex): (0) not projecting; (1) projecting (crown sidewall hidden)**

The DB complex comprises hypoconid apex and associated cristids (oblique cristid and posthypoconid). In *Alouatta*, *Stirtonia*, and *Brachyteles*, M1 DB complex is buccally projecting to such an extent that the distobuccal sidewall of crown is not visible from occlusal aspect. In other platyrrhines, there is no or little projection and the sidewall is fully visible. This is also true of Fayum anthropoids, but some living catarrhines with strong loph development (e.g., *Nasalis*) are similar to platyrrhines with the DB complex. Although this feature is probably neomorphic in this group, consistency requires that living catarrhines be scored as polymorphic.

**15. Mandibular M1, intersection of oblique cristid and protoconid: (0) intersects protoconid buccally, directly distal to apex of protoconid (medial protocristid apparently longer than lateral protocristid); (1) intersects protoconid more lingually, distolingual to apex of protoconid (medial and lateral protocristids are subequal)**

The oblique cristid varies across taxa in the manner in which it meets the distal wall of the trigonid. Contra Kay and Williams's (1994) assessment, we find that *Saimiri* is directly distal, CS 15(0). It should be noted that expression of this character can vary through the molar row: compared to M1, cristid tends to be more buccal in M2 and M3 in many species.

**16. Mandibular M1, hypoconulid and distal fovea: (0) absent; (1) present**

The hypoconulid is seldom present in New World monkeys (e.g., some *Ateles*, *Saimiri*, *Cebus*, *Callithrix*), but distal fovea is said to be always absent (Kay, 1980). The fovea is interpreted as being absent in *Antillothrix* by MacPhee and Woods (1982), although condition of M1 in the Trou Woch Sa Wo mandible (UF 28038) admittedly makes this uncertain. However, this fovea (but not the hypoconulid) is clearly present in *Paralouatta*.

**\*17. Mandibular M3, mesiodistal length compared to that of M2: (0) M3 absent; (1) M3 less (95% of M2 length or less); (2) M3 subequal (96–104% of M2 length); (3) M3 greater (105% of M2 length or more)**

**18. Maxillary I1, lingual cusp: (0) absent; (1) present**

Character states define whether or not there is a distinct cusp (as opposed to a ridge or cingulum) on lingual aspect of I1 crown.

**19. Maxillary I2, orientation: (0) nonprognathous; (1) prognathous**

In pitheciines, maxillary incisors are markedly prognathous, jutting out at a very sharp angle from alveolar border of lower face. In other taxa, these incisors either do not project past vertical plane of alveolar border, or do so to a lesser degree. Pitheciines are further distinguished by the fact that I2 is always prognathous (in some other taxa, I1 is occasionally projecting, but I2 never is).

**20. Maxillary C, prominence of root: (0) as prominent as root of I2; (1) more prominent than root of I2**

In most anthropoid skulls, canine root is so large that it has a marked effect on relief in the lower face. In the few anthropoids with very small canines (e.g., *Homo*), lower face is not conspicuously ridged by prominence of canine alveolus. To have a comparative basis for judging relief caused by canine root, we compared prominence of alveoli of canine and lateral incisor. Only in *Paralouatta* and *Callicebus* (both sexes) is the canine alveolus no more prominent than that of lateral incisor.

**21. Maxillary C and P4, comparative size of alveoli: (0)  $C > P4$ ; (1)  $C \leq P4$**

Basis for CS discrimination is area (length  $\times$  width) of alveoli. (Partial alveolus known for *Antillothrix*.)

**22. Maxillary P4, lingual cingulum: (0) absent; (1) present, with lobate projection mesially; (2) present, but no mesial projection**

In examining specimens, we assumed that no cingulum was present if profile of lingual sidewall of P4 crown was uninterrupted even in unworn teeth. (Scoring needs to be conducted on young animals, because lingual cingula can be obliterated by wear at an early age. Thus in *Callithrix* the P4 cingulum was consistently present only in young animals with newly erupted teeth.)

Any evidence of a lingual cingulum is considered sufficient to warrant a score of "present," but CS 22(1) requires a lobate projection. In *Paralouatta* and *Antillothrix* only, P4 lingual cingulum is large and projects mesially in such a way that a definite concavity is created by this lobe along the mesial profile of tooth, as seen in occlusal aspect. In other anthropoids, the P4 lingual cingulum is not mesially deviated, whether or not it is large.

**23. Maxillary P4, protocone position relative to position of widest buccolingual dimension of trigon: (0) mesial to widest dimension; (1) on widest dimension**

CS 23(0) is limited to atelids and *Paralouatta*.

**24. Maxillary P4, cuspidiform hypocone: (0) absent from trigon; (1) present on margin of trigon**

Cuspidiform hypocone counted as present if a distinct cone occurs on distal trigon margin; if position occupied only by a raised ridge, it was regarded as absent, CS 24(0). However, even by this definition *Alouatta* is ambiguous; Kay (1990) considered feature to be present, but we rarely found anything other than a raised ridge. We score this character as polymorphic for this taxon. In *Saimiri* there is a cusp, but in distinction to other cases, this hypocone is isolated on the lingual cingulum and makes no contribution to delimitation of trigon. We do not follow Kay (1990) in considering this to be the homolog of cuspidiform hypocones of other anthropoids. However, we accept Kay's scorings for *Apidium* and *Aegyptopithecus* because our material was not adequate for determination.

**25. Maxillary P4/M1, relative buccolingual breadth: (0)  $P4 < M1$ ; (1)  $P4 \geq M1$**

Maximum buccolingual dimensions utilized for each tooth. Within-genus results were quite uniform, despite considerable differences in crown dimensions in some cases (e.g., *Cebus apella* vs. *C. olivaceus*). For *Paralouatta*, exact tracings of broken and worn cheekteeth on right and left sides of holotype skull were superimposed and measured; relative size determinations are based on these composites.

**26. Maxillary M1, postmetacrista orientation: (0) directed distobuccally; (1) directed distally or distolingually**

Postmetacrista, as it slopes distally away from apex of metacone, tends to swing slightly buccally, CS 26(0), or lingually, CS 26(1). For purposes of this character analysis, whether slope is directly distal or slightly distolingual is not distinguished and both are scored as CS 26(1).

**27. Maxillary M1, alignment of protocone and hypocone relative to midsagittal plane: (0) alignment parallel, (1) alignment not parallel (hypocone lingually displaced relative to protocone)**

In most taxa with hypocones, protocone and hypocone are linearly arranged relative to midsagittal plane, CS 27(0). However, *Stirtonia*, *Paralouatta*, *Antillothrix*, and *Apidium* differ in that hypocone is lingually displaced relative to proto-

cone. In these taxa, hypocone tip is aligned mesiodistally with bottom of valley between lingual cingulum and protocone. *Saguinus* and *Callithrix* (scored as “?”) lack hypocones.

**28. Maxillary M1, mesostyle: (0) absent; (1) present; (2) converted into or replaced by mesoloph**

For CS 28(1), a definite cusp has to be fully present, not merely a bulge in cingulum. A mesostyle that has become incorporated into the ectoloph (=ectocrista) between paracone and metacone, as a kind of buccal extension of this shearing blade, is a mesoloph (but cf. Kinzey, 1973). The mesoloph is best seen in *Alouatta* and *Stirtonia*, but we find that it is present in *Brachyteles* also (except that, in the latter, the mesostyle is not incorporated into the ectoloph until wear has begun, as is also true of occasional specimens of *Alouatta*).

**\*29. Maxillary M1, pericone/lingual cingulum: (0) absent; (1) lingual cingulum only; (2) distinct pericone on lingual cingulum**

*Callicebus* has a polycuspidate lingual cingulum, but no definable pericone. It was therefore scored as CS 29(1).

**\*30. Maxillary M1, prehypocrista/hypocone complex: (0) hypocone present, prehypocrista present; (1) hypocone present, prehypocrista absent; (2) hypocone absent (and prehypocrista absent)**

Prehypocrista is distinctly present in M1 of *Paralouatta* (fig. 1B), and just as distinctly absent in *Antillothrix* (fig. 1A), although both taxa possess hypocones. In *Alouatta*, hypocone and protocone are usually closely appressed, but in specimens in which there is slight separation, no prehypocrista can be detected. (Hypocone can gain a sharp, bladelike lingual margin as a result of wear produced by lingual slope of protoconid, but this is secondary.) In *Cebus*, reorganization of cristae

makes homology recognition difficult, but we conclude that prehypocrista is absent.

**31. Maxillary M2, cristae on distal margin of trigon: (0) cristae form distinct, continuous wall between protocone and metacone; (1) cristae interrupted by a fossette or do not form a distinct wall; (2) cristae absent or differently organized**

Postprotocrista is primitively a distinct blade that sweeps buccodistally from protocone, to encounter a metaconule or a crest on the lingual slope of the metacone (sometimes identified as hypo-metacrista). In this way a continuous distal wall for the trigon is created. In the majority of anthropoids, an essentially continuous wall is present in unworn teeth, 31(0), although its height varies (cf. *Ateles* vs. *Paralouatta*). In some taxa the postprotocrista is barely definable or is interrupted by a fossette, such that the trigon basin broadly opens distally into the posttalon basin (if present), 31(1). Taxa presenting this latter character state on M2 include *Aegyptopithecus*, *Antillothrix*, *Callicebus*, *Alouatta*, *Stirtonia*, and pitheciines. Postprotocrista is judged to be absent in *Apidium*, where its position is filled by an enlarged metaconule, and in *Nasalis*, in which its homolog (if present) cannot be recognized, CS 31(2). In *Cebus*, the major distal crest runs between the metacone and the hypocone (rather than the protocone). This is somewhat different from the feature in other platyrrhines, but the end result is that the trigon basin is not completely walled off distally. In specimens of *Brachyteles* available for study, the feature is too worn for accurate determination.

**32. Maxillary M2, cuspiform hypocone: (0) absent; (1) present**

Character states describe whether or not there is a distinct cusp (as opposed to a ridge or cingulum).

APPENDIX 2  
Character/Taxon Matrix<sup>a,b</sup>

Taxa	Characters											
	1				1111111112				222222223 33			
	1234567890	1234567890	1234567890	12	1234567890	1234567890	1234567890	12	1234567890	1234567890	1234567890	12
<i>Stirtonia</i>	???????	000	010110???	1	0000001211	11						
<i>Alouatta</i>	1010010000	0101103101	0000000201	11								
	1			1								
<i>Lagothrix</i>	1110110000	0100001101	0001010001	01								
<i>Ateles</i>	1110110000	0000001101	0001010001	01								
<i>Brachyteles</i>	1110110000	0101001101	0000010201	?1								
<i>Paralouatta</i>	11110?1010	11001020?0	1100101120	01								
<i>Antillothrix</i>	????1??0??	???010????	0110101021	11								
<i>Saguinus</i>	0110211100	0000100001	021000?012	00								
			1									
<i>Callithrix</i>	0110211100	1000000001	021000?012	00								
			1									
<i>Aotus</i>	0101211000	0100001001	0210010000	01								
	1		1									
<i>Callicebus</i>	1110211010	1100001100	1211010011	11								
		1										
<i>Saimiri</i>	0100210000	0100001001	0210100021	01								
			1									
<i>Cebus</i>	0100211000	0100001001	0210110001	11								
<i>Cacajao</i>	0110211001	0110001111	0010110011	11								
			1									
<i>Pithecia</i>	0110211001	0110001111	0010010010	11								
			1									
<i>Chiropotes</i>	0100211001	0110001111	0010110011	11								
	1		1									
<i>Apidium</i>	????10?010	1000113?01	1011011121	21								
<i>Aegyptopithecus</i>	000000?000	1000013001	0211000111	11								
Living catarrhines	0000001000	0000002001	0010010001	01								
	1	1 1 131	1	2								
	2											

<sup>a</sup> The code “?” means that the feature(s) necessary to define a character state in a given taxon are missing or uninterpretable (in this matrix, 6% of all entries are in this category).

<sup>b</sup> Polymorphies are stacked vertically (below row).

APPENDIX 3  
Specimens Examined

Extinct Primates	
<i>Aegyptopithecus zeuxis</i> (casts):	CGM 40237 (skull); CGM 26901, DUPC 3014 (mandibles)
<i>Antillothrix bernensis</i> (casts):	CENDIA 1 (maxilla); UF 28038 (mandible)
<i>Apidium phiomense</i> (casts):	YPM 21016, DUPC 1048, 1117, 1102, 1104 (mandibles); DUPC 23947 (maxilla)
<i>Paralouatta varonai</i> (originals):	MNHNH V 194 (holotype skull, formerly MNHNH 25-90), V 195 (mandible), isolated teeth (additional to specimens listed in figs. 1 and 2)
<i>Soriacebus</i> sp. (cast):	MACN-SC 67 (maxilla)
<i>Stirtonia tatacoensis</i> (cast):	UCMP 38989 (mandible)
<i>Stirtonia victoriae</i> (casts):	Duke University/INGEOMINAS 85-400 (maxilla)
Extant Primates <sup>a,b</sup>	
<i>Alouatta caraya</i> (n = 1):	211512 f
<i>Alouatta palliata</i> (n = 4):	140335 m, 24437 m, 18933 f, 18934 m
<i>Alouatta seniculus</i> (n = 4):	64091 m, 130485 m, 230805 f, 78489 m
<i>Aotus azarae</i> (n = 1):	36508 f
<i>Aotus lemurinus</i> (n = 4):	37814 m, 38112 ?, 37811 ?, 36478 f
<i>Ateles paniscus</i> (n = 2):	76026 f, 100076 m
<i>Ateles geoffroyi</i> (n = 4):	128113 f, 29845 f, 145206 m, 145201 f
<i>Brachyteles arachnoides</i> (n = 2):	260 ?, 128 ?
<i>Cacajao calvus</i> (n = 3):	183286 ?, 76648 f, 98397 f
<i>Callicebus caligatus</i> (n = 2):	98102 ?, 98767 f
<i>Callicebus cupreus</i> (n = 2):	98388 m, 75987 m
<i>Callicebus moloch</i> (n = 2):	76420 m, 37498 f
<i>Callicebus torquatus</i> (n = 3):	78468 f, 78467 m, 78477 f
<i>Callithrix argentata</i> (n = 3):	133709 m, 94941 m, 94938 m
<i>Cebus apella</i> (n = 5):	260864 f, 133911 ?, 76872 m, 133645 f, 133664 m
<i>Cebus olivaceus</i> (n = 1):	32053 f
<i>Chiropotes albinasus</i> (n = 1):	93717 m
<i>Chiropotes satanas</i> (n = 4):	94124 m, 78963 f, 95872 f, 94127 m
<i>Hylobates syndactylus</i> (n = 3):	102725 m, 102728 m, 102191 f
<i>Hylobates muellerei</i> (n = 2):	106328 f, 106330 m
<i>Lagothrix lagotricha</i> (n = 5):	33889 m, 76796 m, 98332 m, 98335 ?, 78560 m
<i>Nasalis concolor</i> (n = 2):	103369 m, 103368 m
<i>Nasalis larvatus</i> (n = 3):	103402 ?, 212960 ?, 85173 f
<i>Pithecia pithecia</i> (n = 1):	94148 m
<i>Pithecia hirsuta</i> (n = 2):	73539 m, 92824 m
<i>Pithecia monachus</i> (n = 1):	98365 m
<i>Saguinus oedipus</i> (n = 6):	70023 f, 22871 ?, 38075 m, 70027 f, 48217 f, 69589 f
<i>Saimiri sciureus</i> (n = 4):	73426 m, 73418 f, 73425 m, 73430 m

<sup>a</sup> Taxonomic names and contents follow Groves (1993).

<sup>b</sup> Abbreviations: m, male; f, female; ? gender unknown. All specimens from AMNHM collection.





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