Postcranial Remains of the Extinct Monkeys of the Greater Antilles, with Evidence for Semiterrestriality in Paralouatta 1

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CONTENTS

ABSTRACT

This paper describes postcranial remains pertaining to the endemic xenotrichin callicebines of the Greater Antilles, all of which are extinct: *Xenothrix mcgregori* (Jamaica), *Antillothrix bernensis* (Hispaniola), and *Paralouatta varonai* and *P. marianae* (Cuba). These monkeys differed considerably in body size and inferred locomotor behavior. *Xenothrix* and *Antillothrix* are estimated to have weighed 2–5 kg, which is well within the middle range of body sizes found in extant South American monkeys, but *Paralouatta* (~9–10 kg) would have been nearly as large as the largest living platyrrhines. In line with previous studies, we interpret *Xenothrix mcgregori* as a rather short-limbed, slow-moving arboreal quadruped possessing some unusual features not otherwise seen in platyrrhines (e.g., adductor process or "fourth trochanter" of the femur). Its closest locomotor analog among living primates remains uncertain. *Paralouatta varonai* also exhibits features not seen in other platyrrhines, but in this case there are intriguing resemblances to certain Old World monkeys (e.g., retroflexed medial epicondyle and narrow trochlea on humerus, stabilization features of talocrural joint, short digital rays), especially so-called semiterrestrial cercopithecines whose locomotor repertoire includes a significant amount of movement on the ground (e.g., *Cercopithecus lhoesti*). At the same time, the Cuban monkey conspicuously lacks most features uniquely connected with suspensory activities, otherwise seen in all living platyrrhines of large body size. The locomotor and postural repertoire of *Antillothrix* is unresolved, as the only element currently available for analysis is a distal tibia. The tibia of the Hispaniolan monkey is not very informative from a functional standpoint, although it exhibits less emphasis on talocrural stabilization than does the equivalent element in *Paralouatta* (e.g., size of medial malleolus). The diverse postcranial specializations exhibited by xenotrichins are consistent with their long isolation (at least since Oligocene) on land masses in the Caribbean Sea.

INTRODUCTION

The amount of fossil evidence pertaining to Xenotrichini, a clade of extinct callicebine monkeys endemic to the Greater Antilles, has grown substantially over the past quarter century (MacPhee and Woods, 1982; MacPhee, 1984, 1996; Ford, 1986a, 1986b, 1990; Ford and Morgan, 1986; MacPhee et al., 1989, 1995, 2003; MacPhee and Fleagle, 1991; Jaimez Salgado et al., 1992; MacPhee and Iturralde-Vinent, 1995, 2000; Horovitz, 1997; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2002, 2004). With the exception of specimens of the Hispaniolan species *Antillothrix bernensis* (= "*Saimiri*" *bernensis*), under study by others, the only xenotrichin fossils not yet adequately described consist of postcranial elements of *Xenothrix mcgregori* (Jamaica) and *Paralouatta varonai* (Cuba) collected in recent years by American Museum teams and collaborators (tables 1, 2). Here we present brief descriptions of this material and evaluate its significance for understanding the functional morphology of this vanished group of island primates. As this is meant to be an interpretive paper, the best preserved and most instructive elements receive the bulk of attention; fragmentary specimens and elements already known from published material are given cursory treatment.

In previous work, MacPhee and Fleagle (1991) showed that the known postcranium of *Xenothrix* was distinctively different from the postcrania of other New World monkeys in a number of ways. *Paralouatta* is, if anything, even more distinctive—but in ways that converge to some extent on living Old World monkeys that spend significant amounts of time on the ground. To what degree *Paralouatta* may have actually resembled these cercopithecids in locomotor and postural behaviors is a complicated question that will be taken up in the Discussion. However, the fact that at least one lineage of platyrrhines might have experimented with semiterrestriality as early as the Early Miocene is only slightly less surprising than the fact that the lineage in question evolved in an island context.

BODY SIZE IN XENOTRICHINI

Body size or mass (BM) is an important variable when considering functional attributes of extinct species, especially when such species have few or no modern analogs for their inferred locomotory or positional behav-

TABLE 1
Postcranial Specimens: *Xenothrix mcgregori*[a]

AMNHM	Element	Locality[b]	Description
259900	femur (R)	Long Mile	complete except head
259901	humerus (R)	Long Mile	proximal end
259902	tibia (R)	Long Mile	proximal end
259903	tibia (L)	Long Mile	proximal end
259904	os coxae (L)	Long Mile	acetabulum, parts of ilium, ischium
259905	humerus (R)	Long Mile	shaft only
259906	humerus (L)	Long Mile	shaft and distal end
259907	ulna (R)	Long Mile	proximal end
259908	sacrum	Long Mile	partial sacrum
268002	humerus (R)	Drum	proximal end
268003	femur (R)	Somerville	distal end
268005	humerus (L)	New (?)	proximal end
268008	humerus (R)	Drum	complete except head
268009	os coxae (R)	Skeleton	acetabulum, parts of ilium, ischium, pubis
268010	ulna (R)	Somerville	proximal end

[a] For original descriptions of craniodental material not discussed here, see: Williams and Koopman (1952), holotype mandible; Rosenberger (1977), redescription of holotype; MacPhee and Horovitz (2004), skull and additional mandibular remains.

[b] Long Mile Cave, collector H. E. Anthony, 1920; New Cave, collectors K. Koopman and M. Hecht, ca. 1950; all other sites worked by AMNH/CMC expeditions in 1990s. Except for AMNHM 268003, which was found in surface debris, all specimens were recovered in course of excavations.

TABLE 2
Postcranial Specimens: *Paralouatta varonai*[a]

MNHNCu[b]	Element[c]	Description
76.1010	humerus (R)	complete except head, capitulum
76.1011	humerus (L)	diaphysis
76.1012	humerus (R)	head only, damaged
76.1013	humerus (R)	distal articular end
76.1014	ulna (R)	triceps process only
76.1015	radius (L)	proximal end
76.1016	ulna (L)	proximal end, damaged
76.1017	ulna (L)	proximal end, damaged
76.1018	femur (L)	proximal end, severely damaged
76.1019	femur (L)	distal epiphysis
76.1020	calcaneus (L)	talar facet area only, damaged
76.1021	middle cuneiform (R)	complete
76.1022	MC1 (R)	complete
76.1023	MC2 (R)	complete
76.1024	humerus (L)	distal articular end, partial trochlea only
76.1025	MT1 (L)	complete
76.1026	MT1 (R)	proximal end
76.1027	MT3 (L)	complete
76.1028	MT3 (R)	complete
76.1029	proximal phalanx, DR1 (R)	complete, ?pes
76.1030a–c	3 proximal phalanges, DR2–5	*a* complete, *b* distal end, *c* proximal end
76.1031a–l	12 middle phalanges, DR2–5	most specimens complete
76.1032a–d	4 distal phalanges	complete, with expanded tips
76.1033	1 distal phalanx, DR2–5	complete but water-rolled, unexpanded
76.1034	tibia (R)	shaft and distal end
76.1035	humerus (L)	shaft and distal end
76.1036	os coxae (R)	acetabular area, part of iliac blade
76.1037	talus (R)	body, damaged

[a] For additional descriptions of material, see: Rivero and Arredondo (1991); Horovitz (1997), Horovitz and MacPhee (1999), and MacPhee and Iturralde-Vinent (1995).

[b] Current MNHNCu catalog numbers differ from those previously in use. It is especially important to note that the (a) *P. varonai* skull (holotype), previously published under the MNHNCu numbers V90-25 and V194, is now cataloged as 76.2565; (b) *P. marianae* talus (holotype), previously P3059, is now 76.3059; (c) *P. varonai* partial talus, previously V205 and later P2565, is now 76.1037; (c) *P. varonai* partial jaw V195 is now 76.1213; (d) and mandibular molar specimens V123, 138, 144, 145 are now numbered serially from 76.1214 through 76.1217.

[c] All specimens listed in this table are from Cueva Alta, except humerus MNHNCu 76.1035 and MT3 MNHNCu 1027 which are from Cueva del Mono Fosíl. Material is currently housed in MNHNCu and was collected in collaboration with members of Grupo Espeleologico "Pedro A. Borrás" of La Habana, Cuba.

ior within their phylogenetic group (Martin, 1990). To provide a consistent basis for estimating BMs among xenotrichins, we selected Conroy's (1987) ordinary least squares approach, which relates $\log_e$ of average m1 area (independent variable) to BM (dependent variable). We acknowledge that, as a predictive technique, any regression approach has limitations, especially when (as here) the target taxa are not actually part of the reference sample (Jungers, 1990). Evaluations of results in table 3 are provided in following paragraphs.

For *Antillothrix*, the least known of the three known xenotrichins, BM has to be based for the present on a single jaw fragment containing m1 (MacPhee and Woods, 1982). The tooth is worn, but its sidewalls are intact and thus appropriate for measurement. In the case of *Xenothrix*, the m1s of AMNHM 268001 and 268004, two recently described mandibles (MacPhee and Horovitz, 2004), are severely

damaged. Measurements are therefore based on the type, AMNHM 148198, whose m1 is fortunately well preserved. For *Paralouatta*, measurements are based on a sample of five teeth, four of which represent isolated finds (MNHNCu 76.1214–1217) and are identifiable only as "m1 or 2" (Horovitz and MacPhee, 1999: their table 1). The fifth m1 is present in a beautifully preserved partial jaw, MNHNCu 76.1213 (Horovitz and MacPhee, 1999), and its locus is therefore certain. The fact that most of the teeth in the sample were isolated finds is important; first and second lower molars are homomorphic in *Paralouatta*, and in practice they cannot be metrically or morphologically discriminated. Thus, even though m2s are doubtless present in our sample, in principle they should not affect BM estimations based on the measurements employed in Conroy's (1987) regression expressions.

We utilized Conroy's expressions for "all primates," "anthropoid grade," and "monkey grade" (table 3). Although on grounds of narrow allometry the "monkey grade" estimates might be preferred, all three expressions produced rather similar results. In the case of *Paralouatta*, estimates are in the range of 9–10 kg, with MNHNCu 76.1213 producing the largest result. BMs in this range are large for platyrrhines; the implication is that *Paralouatta* groups with the largest living taxa, such as *Brachyteles arachnoides* and large species of *Ateles* and *Alouatta*, all of which meet or exceed 10 kg in BM (Fleagle, 1999: table 5.4). However, as we note later (see Cheiridia), compared to other platyrrhines, *Paralouatta* has a relatively large m1 for its

talar length, which suggests in turn that one should be conservative in accepting a very large BM estimate for this monkey.

For *Antillothrix*, the calculated estimates of 4.5–5.0 kg also seem large, but it is hard to have a good sense of the size of this primate because the only other published craniodental fossil of this species is the type maxilla. Rímoli (1977), the type's discoverer, thought that it represented a squirrel monkey (hence "*Saimiri*" *bernensis*), but allowed that its owner would have been closer to a living capuchin in BM. Ford (1986a) suggested that *Chiropotes* was an equally good size proxy, but had in mind a body weight closer to 3 kg.

The estimates for *Xenothrix*, 5.5–6.5 kg, also seem large and moreover are in conflict with the 2–4-kg range predicted by MacPhee and Fleagle (1991) using Ruff's (1987) femoral cortical cross-section method on AMNHM 259900. (Unfortunately, this method could not be used as an independent check on dentition-based BM estimates for *Paralouatta* because there are no suitable femoral specimens in the current hypodigm.) An obvious possibility is that Conroy's (1987) method yields over-estimates not only when an unknown is in the upper range of tooth sizes for its group (as he acknowledged), but also when the molar row is reduced—the theory being, in the case of *Xenothrix* at least, that m1 is larger than would be "typically" expected. An analogous issue may affect estimates for "big-toothed" species like *Cebus apella*, whose "monkey grade" predicted range of 4.0–5.5 kg (Conroy, 1987: his table 1) lies well beyond

TABLE 3
Body Size Estimates: *Antillothrix*, *Xenothrix* and *Paralouatta*[a]

Taxon	Mandibular m1 specimens	BL × MD	Log$_e$ m1 area	Body size estimates (g):		
				All primates	Anthropoid "grade"	Monkey "grade"
Antillothrix bernensis	UF 28038	4.9 × 5.5	3.2940	4520.9	5174.8	5176.6
Xenothrix mcgregori	AMNHM 148198	5.1 × 6.1	3.4372	5840.4	6476.8	6482.9
Paralouatta varonai	MNHNCu 76.1213–1217	5.7 × 7.0[b]	3.6863	9104.2	9581.7	9551.3
Paralouatta varonai	MNHNCu 76.1213 only	5.6 × 7.4	3.7242	9740.6	10,168.7	10,133.0

[a] Based on ordinary least squares regression expressions published by Conroy (1987).
[b] Mean values for these five specimens.

its empirical average of 2.5–3.6 kg (cf. Silva and Downing, 1995; Fleagle, 1999).

In summary, we suspect that average BM in *Paralouatta* could have been as much as 9 kg, but may well have been somewhat less. This is still, of course, very large for a platyrrhine monkey. With regard to *Xenothrix*, it seems quite unlikely that the Jamaican monkey could have exceeded 5 kg in view of its general similarity in long bone lengths to monkeys such as *Cebus*. The conclusion is the same for *Antillothrix*, whose dental measurements are slightly smaller. We continue to prefer the 2–4 kg range originally predicted by MacPhee and Fleagle (1991) for *Xenothrix*, which means that this monkey would have been approximately one-half to one-third the size of *Paralouatta* as currently estimated. Interestingly, at 0.9–1.3 kg (Silva and Downing, 1995; Fleagle, 1999), the only extant callicebine, *Callicebus*, is but one-tenth the estimated size of the Cuban monkey.

MATERIAL AND METHODS

The comparative set of taxa employed by MacPhee and Horovitz (2004) for evaluating the craniodental morphology of *Xenothrix* was essentially limited to extant pitheciids and *Aotus*. Adequate appreciation of the unusual postcranial morphology of Antillean primates requires wider comparisons, and the comparative set has been broadened accordingly (see appendix 1), with special attention given to species of the following genera (platyrrhines: *Callicebus*, *Chiropotes*, *Ateles*, *Brachyteles*, *Alouatta*, and *Cebus*; catarrhines: *Trachypithecus*, *Erythrocebus*, *Lophocebus*, and *Theropithecus*). Incidental observations on other anthropoids are also provided where appropriate. We have accepted species designations as they appear on specimen labels, although it is clear that, given the current drive to relimit numerous species of primate taxa (e.g., Groves, 2005), the AMNHM collection stands in need of major revision.

Although the primate collections of the AMNHM are very extensive, for not a few species there is little postcranial material; worse, even for some well represented species, so much postcranial material has been ''lost'' over the years that it is now hard to find intact individuals. For this study, the necessary compromise was to use the best of what there is, even if the specimens in question lacked provenance data. In some cases, species in the same genus have been combined when there was not enough material to make up an adequate sample.

Obviously, providing equal coverage in the figures for so wide a range of taxa is not possible, nor even particularly useful unless noted resemblances have some significant correlation with function. In this paper we concentrate on illustrating major limb bones (especially the humerus, ulna, and tibia), using for comparative purposes a set of New and Old World monkeys which are predominantly quadrupedal in their locomotor behavior (whether in the trees or on the ground). BMs for the comparative set are as follows (data of Fleagle [1999], male/female BMs in kilograms): (1) tufted capuchin, *Cebus apella* (2.5/3.7 kg), a medium-sized arboreal quadruped; (2) red howler monkey, *Alouatta seniculus* (5.2/6.7 kg) a large-bodied arboreal quadruped with some arm swinging capability; (3) gray-cheeked mangabey, *Lophocebus albigena* (6.0/8.3 kg), a predominantly arboreal quadruped in the size range of *Alouatta seniculus*; (4) patas monkey, *Erythrocebus patas* (5.7/10.6 kg), an agile ground-foraging species, and (5) gelada, *Theropithecus gelada* (11.7/19.0 kg), a very large Old World monkey whose locomotor activities are conducted almost exclusively on the ground. The last two species are markedly sexually dimorphic. Other elements are much more poorly represented in the xenotrichin collection and are accordingly given less attention in this paper. In general, the usual run of biomechanically important ratios emphasized in functional morphology (e.g., Anapol et al., 2005) could not be taken on highly incomplete fossil material, although we have tried to fashion a few others that seem to have some interpretative significance. Appropriate comparative illustrations of conditions in other primates for some elements (femur, os coxae) can be found in the paper by MacPhee and Fleagle (1991).

MacPhee and Fleagle's (1991) study should also be consulted for additional comparative observations and illustrations, as well as

measurements and ratios not defined here. Anatomical names mostly conform to the most recent *Terminologia anatomica* (Federative Committee of Anatomical Terminology, 1998), except in instances where homologs in *Homo sapiens* are not obvious or another term is to be preferred.

ABBREVIATIONS

Anatomical

ac	anterior crest (tibia)
ap	adductor process (femur)
apl	abductor pollicis longus m. (insertion)
BL	buccolingual
BM	body size
br	brachialis m. (insertion)
brf	brachialis flange
bt	bicipital tuberosity
CC	craniocaudal
cf	coronoid fossa
cp	coronoid process
cpt	capitulum
ctf	cotylar fossa (talus)
df	dorsal epitrochlear fossa
DP	distal phalanx
dpe	deltopectoral eminence
DR	digital ray (unspecified)
DR1	digital ray of thumb or big toe
DR2–5	other digital rays (manus or pes)
DV	dorsoventral
ef	entepicondylar foramen
ff	fabellar facet (femur)
fdp	flexor digitorum profundus m. (origin)
ftp	fossa for tibialis posterior m. (origin)
gt	greater tubercle (humerus)
gtr	greater trochanter
ib	interosseous border
if	iliac fossa
ig	intertubercular groove (sulcus)
ip	iliac planum
is	ischial spine
it	ischial tuberosity
lc	lateral condyle (femur)
le	lateral epicondyle
lsr	lateral supracondylar ridge
lt	lesser tubercle (humerus)
ltc	lateral cuneiform
ltr	lesser trochanter
lw	lateral "wing" of the olecranon surface of the trochlear notch (ulna)
m., mm.	muscle, muscles
m1, 2	mandibular molar + locus
me	medial epicondyle

MC	metacarpal (with or without digital ray specified)
ML	mediolateral(ly)
mltr	medial lip of trochlea (humerus)
mm	medial malleolus
msr	medial supracondylar ridge
MT	metatarsal (with or without digital ray specified)
mw	medial "wing" of the olecranon surface of the trochlear notch (ulna)
nv	navicular
ol	olecranon
olf	olecranon fossa
OSTN	olecranon surface of trochlear notch
PP	proximal phalanx
ps	patellar surface
pt	peroneal trochlea (talus)
rf	radial fossa
rn	radial notch
sc	supinator crest
scf	semicondylar facet (tibia)
srp	superior ramus (pubis)
st	sustentaculum tali
tcj	talocrural joint surface
tm	teres major m. (insertion)
tn	trochlear notch
tp	triceps process (ulnar)
tro	trochlea

Measurements

AdjMDW	adjusted maximum distal width (of long bone)
APW	anteroposterior
DR2L	total length of second digital ray (including MC2)
DVW	dorsoventral width
MaxL	maximum length (of limb bone)
MLW	mediolateral width (of limb bone)
MC2L	maximum length of second metacarpal
MEPD	posterior deviation of medial epicondyle (of humerus)
TPL	total phalangeal length (i.e., finger/toe length)

Other

asl	above sea level
bp	before present (i.e., before radiocarbon datum, AD 1500)
L	left side
PCA	principal components analysis
R	right side
rev.	sides photographically reversed (in figures)

UF	Florida Museum of Natural History, Gainesville, FL
MNHNCu	Museo Nacional de Historia Natural, La Habana, Cuba
AMNHM	American Museum of Natural History (Mammalogy)
USNMM	United States National Museum of Natural History (Division of Mammals)

JAMAICAN FOSSILS AND LOCALITIES

Although it is easy to appreciate the difficulty of assigning isolated bones to individual species of primates in contexts in which there are several possible choices, assignment can be problematic even when there is only a single conceivable choice. The gradual accretion of the hypodigm of *Xenothrix mcgregori* is a case in point. The describers of the Jamaican monkey, Williams and Koopman (1952), reported that they found several unusual mammalian postcranials in H.E. Anthony's 1919/1920 Jamaican faunal collections, but decided that no conclusive allocation of these elements was then possible. After examining this same material, MacPhee and Fleagle (1991) concluded otherwise: Some of the unusual postcranials could, they thought, be assigned to *Xenothrix* on general morphological grounds, even though the bones in question did not greatly resemble those of any other platyrrhine or even any other anthropoid. Other elements had to be excluded from consideration because they were either too incomplete or too ambiguous morphologically to assign to any particular mammalian group. Since then, renewed collecting has produced both new craniodental material of *Xenothrix* (MacPhee and Horovitz, 2004) as well as the postcranial remains described in this paper. Although these specimens are unassociated and damaged to a greater or lesser extent, they have helped to clear up some mysteries as well as to reinforce the likelihood that the majority of allocations made by MacPhee and Fleagle (1991) were correct.

To date, six localities (figs. 1, 2; table 1) have yielded remains attributable to *Xenothrix*: Long Mile, Skeleton, Somerville, Drum, Lloyd's, and "New" Caves. With the exception of the first and (possibly) the last, these sites are concentrated on the western end of Portland Ridge, a prominent elevated limestone area in the southernmost part of Jamaica, near Jackson's Bay (17°45′N, 77°15′W) in southern Clarendon Parish. New Cave is known only from a manuscript notation and has not yet been relocated. The only site on the north side of the island that has yielded *Xenothrix* remains is the type locality, Long Mile Cave. Descriptions of these caves and their speleological, paleontological, and paleoenvironmental significance can be found in papers by MacPhee (1984), Fincham (1997), McFarlane et al. (2002), MacPhee and Flemming (2003), MacPhee and Horovitz (2004), and references cited therein.

A nearly complete humerus (AMNHM 268008) of *Xenothrix* was recovered from a position just above layers dated to 11,220 ± 100 bp and 10,250 ± 80 bp in the Brown Dust Passage of Drum Cave (fig. 2A; McFarlane et al., 2002). This establishes that the Jamaican monkey lived in the vicinity of Jackson's Bay—now one of the driest regions on the island—at least as early as the close of the Pleistocene. Dates reported by MacPhee (1984) on nonprimate bone scrap from levels in Long Mile Cave that produced monkey remains indicate that *Xenothrix* was present on the north coast late in the Holocene. These are the only radiometric dates available, and are likely to remain so for the foreseeable future. Because of the scantiness and fragility of the new *Xenothrix* material, it was decided to treat all specimens with a consolidant (Butvar). The type jaw had earlier been treated with a varnish or resin of some sort, presumably by Anthony. Thus all specimens of *Xenothrix* in the current hypodigm are contaminated with recent carbon, and they will therefore never produce reliable ^{14}C dates. This is of little paleontological consequence because it is beyond doubt that this monkey survived very late, perhaps even into early European colonial times (MacPhee, 1984, 1996). Although it would be of interest to ascertain more precisely when its extinction took place (cf. Steadman et al., 2005), this kind of inquiry can only be adequately conducted through the discovery of many more specimens than exist at present.
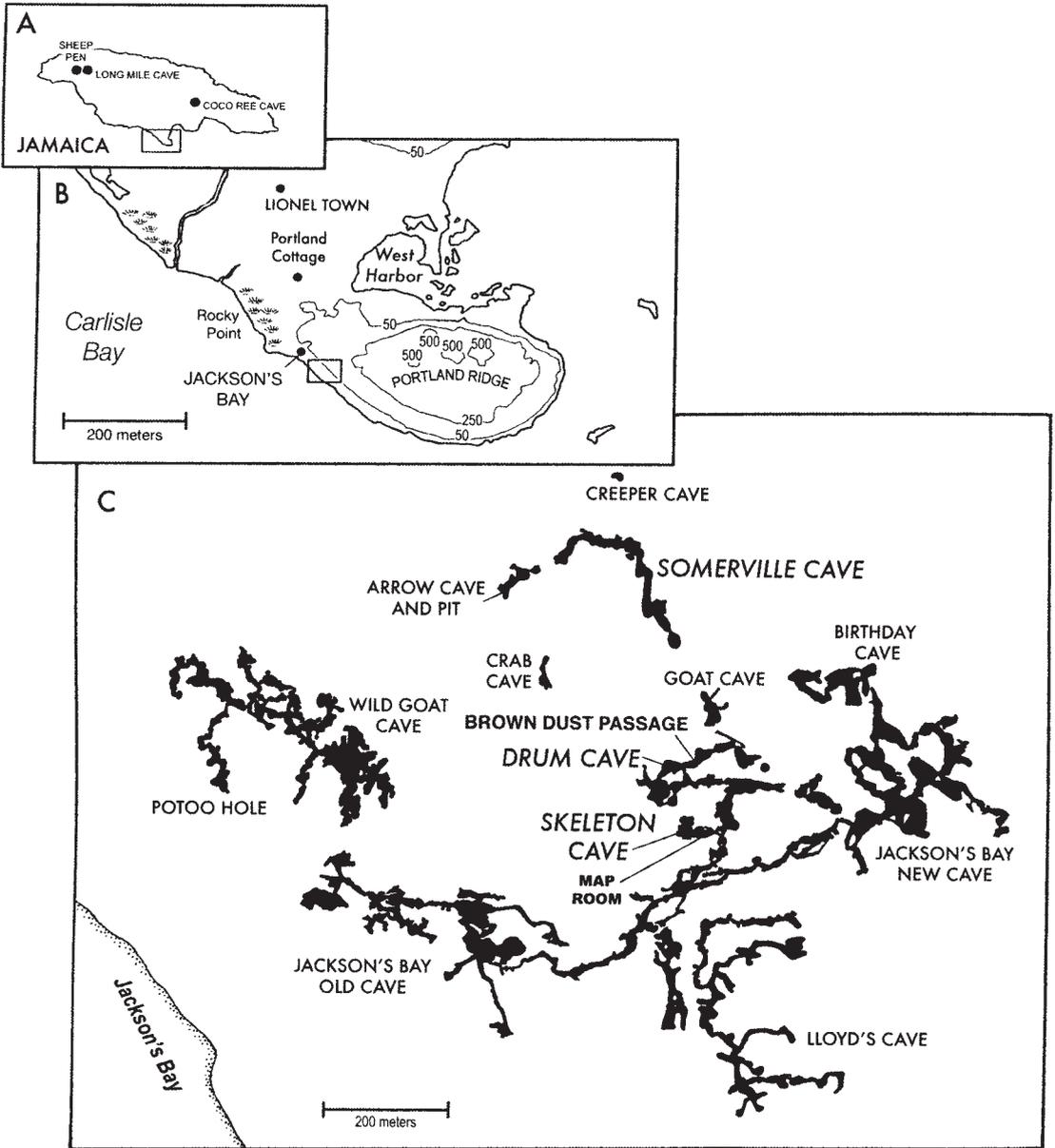
Fig. 1.   Jamaican localities: Locator maps for sites mentioned in text. The greatest concentration of xenotrichin sites is in southern Clarendon Parish, near Jackson's Bay (**A**, **B**). Caves in this area that yielded postcranial remains discussed in this paper are in capital italics (**C**); for other localities, see MacPhee and Horovitz (2004). The location of "New Cave" is not known but is believed to lie on Portland Ridge; Sheep Pen and Coco Ree are not definite xenotrichin sites (see text). Map **B** based on Sheet H, Series E721 (D.O.S. 410), U.K. Directorate of Overseas Surveys for the Jamaica Government; map **C** after Fincham (1997).
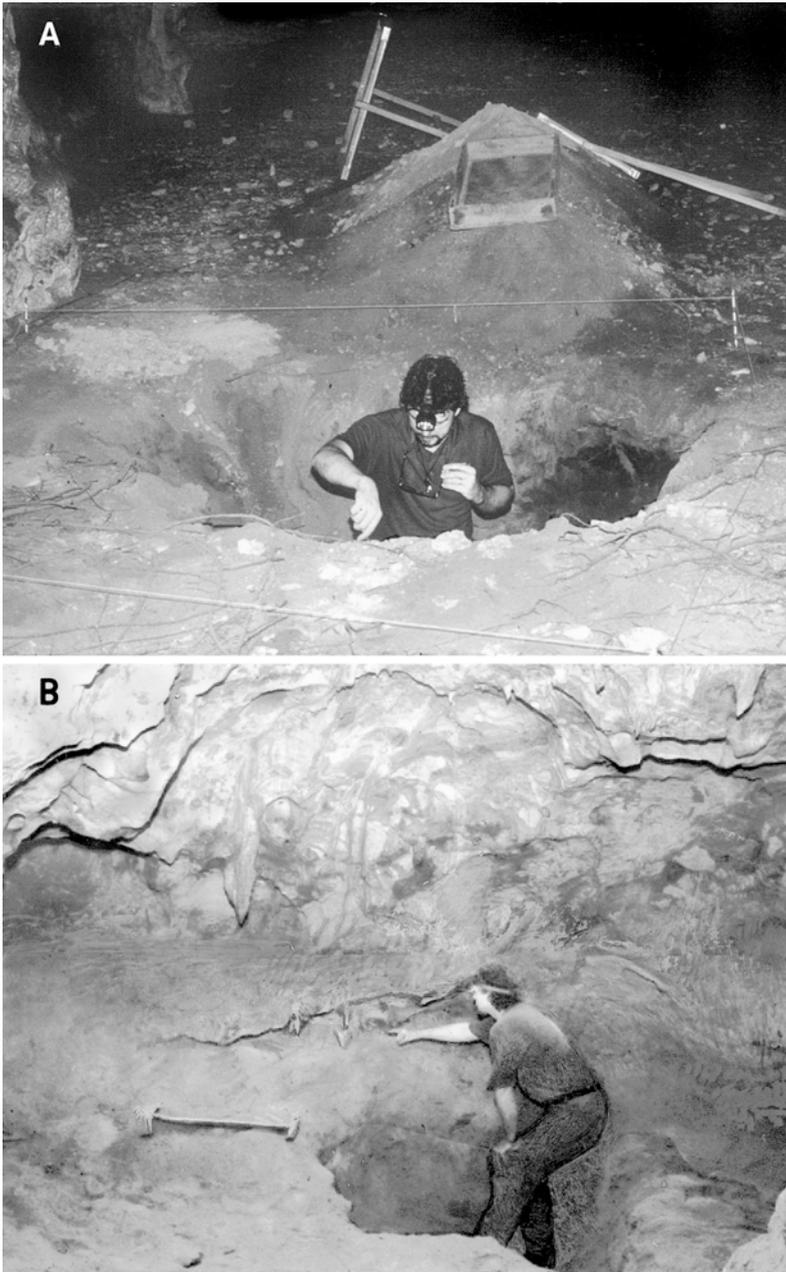
Fig. 2.   Jamaican localities: **A**, Drum Cave, excavation in Brown Dust Passage near entrance #3. **B**, Skeleton Cave, showing rear of Map Room after excavation of most of the upper part of the fill (sediment stain line can be seen to left of individual's head). Drum Cave has yielded two humeri of *Xenothrix* (AMNHM 268002, 268009) as well as the holotype jaw of the ?heptaxodontid rodent *Xaymaca fulvopulvis* (MacPhee and Flemming, 2003). Excavations at Skeleton Cave produced an os coxae (AMNHM 268008) as well as the two new jaws of *Xenothrix* described by MacPhee and Horovitz (2004), one of which was found where individual is pointing in **B**. The paleoecology of this locality is discussed by McFarlane et al. (2002).

CUBAN FOSSILS AND LOCALITIES

As discussed in detail elsewhere (Jaimez Salgado et al., 1992; Horovitz and MacPhee, 1999), all known fossils of *Paralouatta varonai* come from what amounts to a point source— a pair of caves in the Sierra de Galeras, prov. Pinar del Río, western Cuba (figs. 3, 4; table 2). Although these localities—Cueva del Mono Fosíl and nearby Cueva Alta (fig. 3A; Rivero and Arredondo, 1991; Jaimez Salgado et al., 1992)—are nominally distinguished, they open on the same hillside and lie within the opening of a still larger cave system, Caverna Constantino (22°39′18″N, 83°48′35″W; 56 m asl). Most or all of the monkey fossils are now believed to have originally come from a fissure of complicated form that cuts through both caves. In Cueva Alta (figs. 3C, 4B), the ultimate source of bones is a narrow, chimney-like feature just inside the cave entrance, related to the fissure and plugged with a bone-bearing matrix. In Cueva del Mono Fosíl (fig. 3B), monkey bones (type skull of *P. varonai* and a humerus) were found at one of the lowest levels of the cave. The fissure can be traced vertically to a higher elevation on the hillside, where it intersects yet another, very small cave. No fossils were recovered at the latter site, nor in any of the numerous other
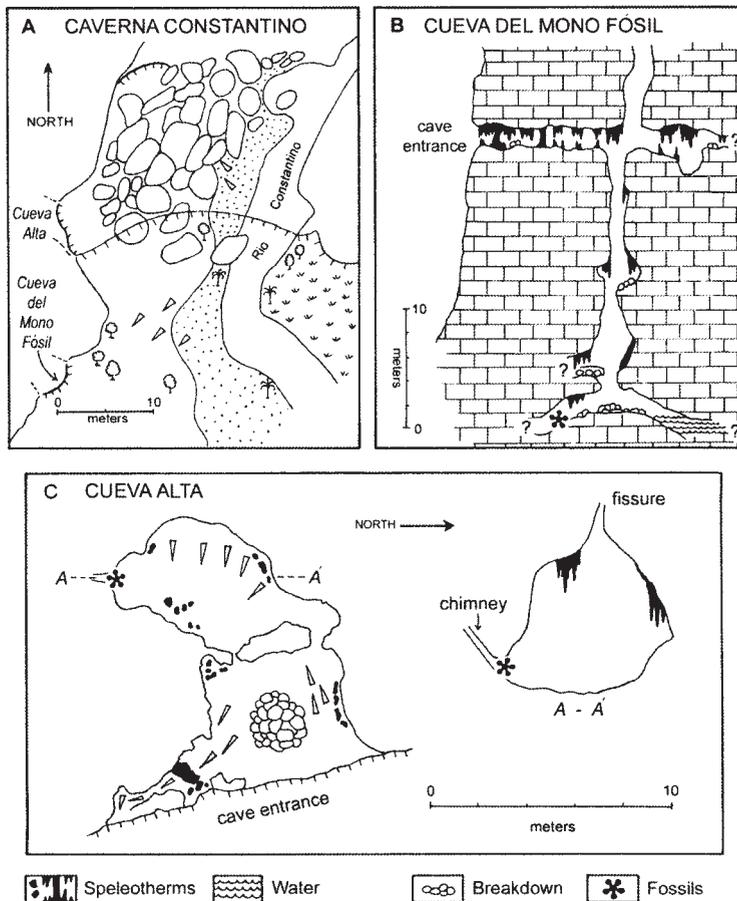
Fig. 3. Cuban localities: **A**, Caverna Constantino, plan of main entrance; **B**, Cueva del Mono Fosíl, section; **C**, Cueva Alta, plan and section (A–A′), all after Jaimez Salgado et al. (1992). In Cueva del Mono Fosíl, type skull of *P. varonai* was found at bottom of fissure that transects the cave (**B**, asterisk). In Cueva Alta, monkey fossils were originally detected in matrix that had eroded from chimney feature (**C**, asterisk); excavation of chimney resulted in recovery of ~70 cranial and postcranial fossils of *Paralouatta*.
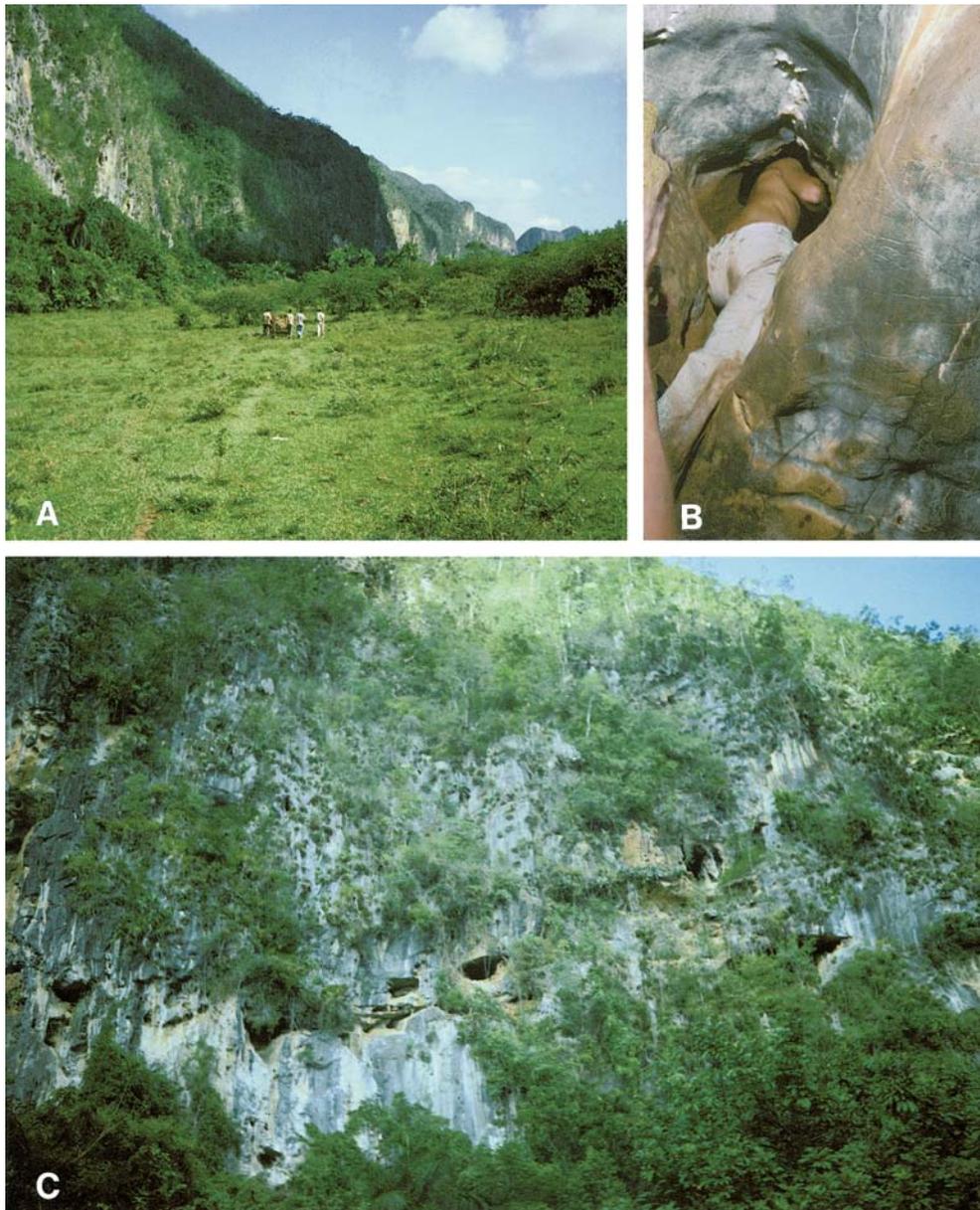
Fig. 4.   Cuban localities: **A**, South side of Sierra de Galeras, near Cueva del Mono Fosíl. Valley follows strike of major fault; substantial cave development is common in surrounding hills of Late Jurassic limestone. **B**, Looking up the chimney that produced many fossils of *Paralouatta varonai*, including most of the postcranial remains described in this paper. Brown stain on walls around individual's head and torso marks former extent of fossiliferous matrix that plugged chimney, which was removed and screened. Passage becomes further constricted and subvertical immediately above individual's head. **C**, Hanging cave entrances above valley floor in vicinity of Cueva del Mono Fosíl, Sierra de Galeras. Solutional features (passages) appear to mark a previous phreatic level that can be traced elsewhere in the sierra. Movements along fault which resulted in this exposure are of unknown age but may well predate Pleistocene. Many other caves in this sierra have produced faunal remains, but to date none has yielded monkey material.

caves that riddle the Sierra de Galeras (fig. 4C). Work conducted by the AMNHM and Grupo Espeleologico ''Pedro A. Borrás'' was devoted to removing and screening as much matrix as possible from the Cueva Alta chimney. Additional work in these caves in recent years, conducted by Inés Horovitz and Grupo Borrás (I. Horovitz, personal commun., 2001), has not resulted in any further monkey finds.

Although certainty is clearly not possible, in terms of minimum numbers of individuals the totality of monkey remains from Cueva Alta may represent only a few individuals—perhaps as few as two adults (a larger and a smaller) and one or more juveniles with nearly complete dentitions. This conclusion is supported by the low number of duplicate elements in the same size and ontogenetic ranges in the postcranial collection from the cave. It is also supported by the dental remains, which, although relatively plentiful in number, amount to only a few representatives per locus, including a few unerupted and milk teeth (cf. Horovitz and MacPhee, 1999). The relatively large number of phalanges and other small cheiridial elements found in the chimney at Cueva Alta indicate that remains of these individuals could not have been widely dispersed after death. The type skull (MNHNCu 76.2565), an incomplete humerus, and an isolated MT3 were recovered deep within Cueva del Mono Fosíl and presumably represent at least one other adult. Interpretations of morphology and measurements made on elements belonging to different individuals have to be offered cautiously, especially when (as in the case of Antillean monkeys) fossils are few and the scale of intersexual and intrapopulational variation is unknown. Although more individual parts of the skeleton are represented in the collection for *Paralouatta* than the one for *Xenothrix*, there are very few complete (or even nearly complete) bones in either set.

The geological age of the *Paralouatta* fossils remains an open question. A Quaternary age has been assumed more or less by default for material from these caves because most faunal elements appear to belong to taxa known from Pleistocene/Holocene contexts elsewhere on the island (cf. Rivero and Arredondo, 1991; Jaimez Salgado et al., 1992). The only excep-

tions recognized to date are an owl, interpreted as an extinct species of the extant genus *Bubo* (Arredondo and Olson, 1994), and a sloth, *Galerocnus jaimezi*, based on an incomplete and poorly preserved femur (Arredondo and Rivero, 1997). As far as may be ascertained, the new sloth appears to be a megalonychid, possibly related to the Quaternary Cuban genus *Neocnus*. Thus the lack of distinctive elements within the faunule from the monkey caves makes the unique occurrence of *Paralouatta varonai* all the more egregious. If this faunule is Quaternary, why don't monkey fossils occur in same-age localities elsewhere in Cuba?

Most specimens from the monkey caves, whether primate or nonprimate, are very thoroughly fossilized. Collagen was absent from test pieces, which precluded their being dated by radiocarbon. However, the significance of this is ambiguous because in hot, wet cave environments bone proteins disappear relatively quickly, even in material of unquestionably recent origin. It is also worth recording that many of the mammal, bird, and reptile bones are waterworn, as though the material had been lagged in a high energy environment such as a fast-flowing stream or even a beach. Turbulent circulation within cave channels is a possible agent, of course, but the remarkable level of wear on bones and teeth—many of which have been reduced to semispherical bits of gravel—differs greatly from what is seen in cave collections made elsewhere on the island. Passage of bones and teeth through the gut of crocodiles would have left a different signature (cf. Fisher, 1981; *contra* Jaimez Salgado et al., 1992). On the other hand, a fair number of fossils, including most of the ones depicted in this paper, seem to have escaped excessive damage, indicating that more than one depositional regime may be represented.

An additional age-related complication is that a second species of *Paralouatta*, *P. marianae*, has recently been named on the basis of a single talus from the securely dated Early Miocene locality of Domo de Zaza (MacPhee et al., 2003). The element in question differs in subtle ways from that of *P. varonai* from the monkey caves, but less so than one might otherwise expect given the

time interval nominally separating these species. Although it is possible that the fossils from Sierra de Galeras are much older than previously thought, testing of this proposition will have to await discoveries in dated temporal contexts.

Finally, it needs to be briefly noted that changes in cataloguing schemes in use at the MNHNCu, where the *Paralouatta* hypodigm is housed, have resulted in some specimens being published under different museum numbers (see table 2). All *Paralouatta* specimens have now been placed in a single lot, MNHNCu 76.

HISPANIOLAN FOSSILS
AND LOCALITIES

Although a number of monkey postcranial specimens were collected in the 1980s by Woods (1989) at Trou Woch Sa Wo in western Haiti, except for Ford's (1990) brief mention of their existence, nothing has been published on this material. The only other specimen from Hispaniola that has been recognized as primate is a distal tibia (USNMM 254682; fig. 24) from a kitchen midden on the small island of Naranjo Abajo in Bahia de Samaná, Dominican Republic, described by Miller (1929). Because this element is given brief treatment in this paper, a few notes on the history of its interpretation are in order.

Miller (1929) was perplexed by the Samaná tibia. He was unable to match it to any known species of extant primate, but could not quite bring himself to conclude that it belonged to a true endemic. In the end, he cited vague similarities to cercopithecid monkeys as a reason for assuming that it belonged to a monkey recently imported from Africa. Ford (1986a) made a detailed study of USNMM 254682, but concluded instead that it bore features consistent with its being a callitrichid. This was a surprising finding, inasmuch as the specimen is comparatively large and very robust, whereas no extant callitrichid weighs more than a few hundred grams. Ford (1986a) offered the explanation that perhaps the Dominican monkey was a member of a callitrichid lineage that had colonized Hispaniola and later evolved toward gigantism. MacPhee et al. (1995) did not directly address the issue

of the callitrichid features of the Samaná tibia, but simply followed Rosenberger (1978) in stating that it was more likely than not that the element belonged with a partial maxilla from Cueva Berna in eastern Dominican Republic originally described by Rímoli (1977). But in their cladistic analysis (based on craniodental features only), MacPhee et al. (1995) found that *Antillothrix* displayed no homologous similarities to callitrichids; instead, the Hispaniolan monkey grouped with a clade consisting of *Callicebus*, *Xenothrix*, and *Paralouatta*. Unfortunately, some of the characters supporting this clade as a whole could not be assessed in *Antillothrix* because of the lack of pertinent fossil evidence. The evidence for the placement of *Antillothrix* in or near Xenotrichini is therefore somewhat inconclusive, and is likely to remain so until new material is described.

POSTCRANIAL ELEMENTS
ATTRIBUTED TO *XENOTHRIX*,
PARALOUATTA, AND *ANTILLOTHRIX*

For efficiency in presentation, descriptions and appropriate comparisons will be presented element by element for *Xenothrix* and *Paralouatta* (and *Antillothrix*, in connection with the Samaná tibia only). While most of the individual specimens discussed in this paper are immediately recognizable as primate, we were careful to consider other alternatives when undertaking initial sorting and identification. Limb bones of the smaller arboreal megalonychid sloths that lived in Cuba (e.g., *Nesocnus*) are rather gracile, and incomplete elements may occasionally seem somewhat primatelike (see White, 1993, for a useful atlas of Antillean megalonychid limb bones). It is often hard to place small bones (e.g., phalanges) when dealing with poorly known extinct species, and to establish secure identifications we always compared doubtful cases to well identified museum specimens.

It may be briefly noted here that the faunal collections from Cueva del Mono Fosíl and Cueva Alta contain a few other elements, not discussed in this paper, that may belong to *Paralouatta*. Among them are several partial vertebrae that cannot be allocated to any other Antillean mammal and appear to be in

the correct size range for the monkey. All of them are in very poor condition and do not warrant description or illustration here. There are likewise several shaft fragments, lacking articular ends, that could be parts of monkey postcranials if they do not belong to small sloths. None could be fitted to the isolated articular ends described in this paper.

HUMERI

Xenothrix AMNHM 268002,
268005, and 268008

The humerus is the best represented long bone in the *Xenothrix* hypodigm (*N* = 6; figs. 5, 6; table 4). In 1991, the only known examples of this element were immature or highly incomplete, and none seemed conclusively primate (as opposed to large rodent). Now that several humeri of the same type have been recovered, including one nearly intact specimen, allocation is no longer in doubt. AMNHM 268008, an adult right humerus lacking only the proximal articular surface (fig. 5), is obviously primatelike and can be immediately distinguished from that of the Jamaican coney (*Geocapromys brownii*) and most other caviomorphs by the lack of a large, flaring deltopectoral crest. The less complete specimens (fig. 6A–D) clearly represent the same species. Like AMNHM 268008, AMNHM 268002 was found at Drum Cave, but in another area (Molehole Passage). AMNHM 268005 is an unexpected addition to the hypodigm: it was found serendipitously while examining Jamaican faunal collections housed in the AMNH's Department of Mammalogy. The specimen was retrieved from a small box containing an assortment of rodent bones and and a note reading "South Side New Cave, Jamaica—Karl Koopman, Max Hecht, 1950". All of the rest of the material in the box was found to belong to *Geocapromys*. As the location of the cave and its local name are not recorded in any of Koopman's notes, the only course available is to accept the box's labeling and identify the site as "New Cave", location currently unknown.

Considering these specimens as a group, among New World monkeys the humerus of *Xenothrix mcgregori* may be said to have roughly the size and proportions of the equivalent element of a small individual of *Cebus apella* (fig. 11A–C). There are, however, notable differences. Compared to the brown capuchin, in *X. mcgregori* (1) the diaphysis is more robust overall and more concave posteriorly, (2) the deltopectoral eminence is larger and more projecting, (3) the crest for insertion of teres major m. is more projecting, (4) the medial epicondyle is smaller, and (5) the lateral border of the intertubercular sulcus is much less distinct. In many other regards they are similar, such as in (1) the relative size and conformation of proximal and distal articular surfaces, (2) the presence of the entepicondylar foramen, (3) the size and disposition of the tubercles, and (4) the moderate development of the brachialis flange. Several of these contrasts, which hold for other similar-sized platyrrhines such as *Chiropotes satanas* and *Pithecia pithecia* (Fleagle and Meldrum, 1988), are discussed further under Functional Considerations.

The proximal articular end, not well preserved on AMNHM 268008, is complete in AMNHM 268002 and 268005 (fig. 6A–D; see also AMNHM 259901 in MacPhee and Fleagle, 1991). In proximal aspect, the articular end appears ovate rather than rounded, much as in *Cebus*, and in posterior aspect its distal margin appears rather tapered, as in *Cacajao* and *Saimiri*. It is also less hemispherical overall (cf. ratio A, table 4) than that of *Lagothrix* or *Brachyteles*. The new material also helps to clarify the height relationship between the proximal articular surface and the tubercles (the scapular articulation rises above the level of the tubercles, but only slightly; fig. 6C). The tubercles themselves are as described previously, being moderately prominent and separated by the broad intertubercular groove. These features of the proximal end of the humerus are correlated in other anthropoids with limited shoulder movement outside of the extension–flexion plane (cf. Rose, 1997). The deltopectoral eminence is broad, V-shaped, and somewhat laterally displaced, so that in anterior view the lateral margin of the shaft bows slightly outward (fig. 5A), as in arboreal quadrupedal primates generally (cf. fig. 11). The specimen is robust for its length (ratios C and D, table 4), and there is no torsion of the head.
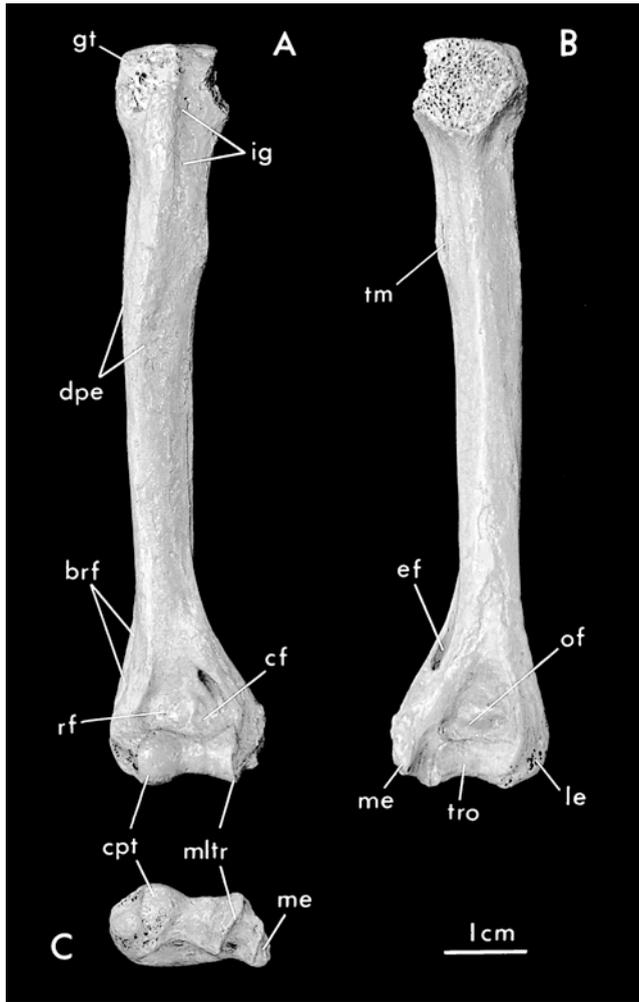
Fig. 5. *Xenothrix mcgregori*, nearly complete humerus: AMNHM 268008 (R) in anterior (**A**), posterior (**B**), and distal (**C**) aspects. Specimen esentially intact except for damage to head; note overall robusticity, slight lateral convexity of shaft, presence of entepicondylar foramen, and moderate posterior projection (retroflexion) of medial epicondyle. Recovered just above a dated level in Drum Cave (see text), AMNHM 268008 is the only specimen of *Xenothrix* known to be of definite Pleistocene (as opposed to indefinite Quaternary) age.

The distal articular surface (fig. 5C) bears a relatively broad capitulum; it is quasispherical and distolaterally extensive, indicating a large range of extension and rotation at the elbow joint (Meldrum et al., 1990). The capitulum and lateral epicondyle are only moderately rolled ventrally, relative to the long axis of the diaphysis, and the broad, shallow radial fossa is distinctly separated from the coronoid fossa (fig. 5A). Qua-

drupedal primates in which the elbow is habitually held in a semiflexed position usually exhibit this complex of features (Napier and Davis, 1959).

The lateral lip of the trochlea is indistinct in *Xenothrix*, and the medial lip is likewise only moderately prominent in both distal and anterior directions. A prominent medial lip is characteristic of arboreal quadrupeds such as *Saimiri* and *Cebus*, in which it functions to
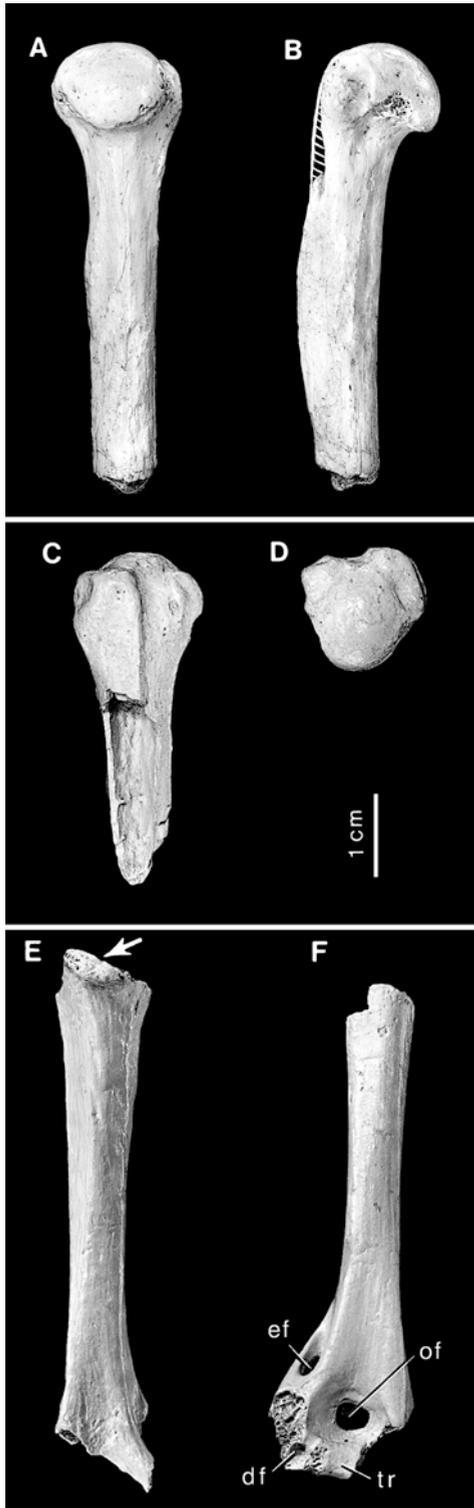
resist adducting torques generated by the digital and carpal flexors when the forearm is pronated during quadrupedal progression (Jenkins, 1973; Fleagle and Simons 1978). Platyrrhines employing greater frequencies of suspensory and clinging positional behaviors, such as *Ateles* or *Pithecia* (Fleagle and Meldrum, 1988), exhibit a trochlea that is more cylindrical, with a less prominent medial lip.

The medial epicondyle is relatively short, tapered, and posteriorly (dorsally) directed (~54°; see table 6). Platyrrhines with posteriorly directed medial epicondyles (e.g., *Cebus*, fig. 11A–C) are more quadrupedal in behavior than those in which the epicondyle projects directly medially. Functionally, posterior inclination redirects the line of pull of the digital and carpal flexors toward the dorsal trochlea (Jolly, 1967; Jenkins, 1973).

The olecranon fossa is moderately deep but is unfenestrated, whereas it often is in *Cebus apella* (fig. 11A). The depth and shape of the olecranon fossa are determined by the interaction of several factors, primarily the depth of the trochlear notch and the prominence of its posterior border.

As already noted, AMNHM 259906 (fig. 6E) from Long Mile Cave is clearly subadult because there is evidence that the proximal epiphysis was unfused at the time of death (MacPhee and Fleagle, 1991). However, the individual must have been close to adulthood because the distal epiphysis is completely fused in the other small humerus of similar size, AMNHM 259905 (fig. 6F).

Because of the generally poor condition of the Long Mile specimens, it is difficult to define measurements that permit useful size comparisons with the single complete humerus, AMNHM 268008. However, one comparison of relevance can be managed by reference

←

Fig. 6. *Xenothrix mcgregori*, other humeri: AMNHM 268002 (R) in posterior (**A**) and medial (**B**) aspects; AMNHM 268005 (L [rev.]) in anterior (**C**) and proximal (**D**) aspects; and AMNHM 259906 (L) (**E**) and AMNHM 259905 (R) (**F**), both in posterior aspect. **E** and **F** after MacPhee and Fleagle (1991). In **B**, dashed line indicates presumed original contour of damaged area. To same scale.

TABLE 4
Humerus: *Xenothrix mcgregori*, Dimensions (in mm) and Ratios[a]

	AMNHM 259901	AMNHM 259905	AMNHM 259906	AMNHM 268002	AMNHM 268005	AMNHM 268008
Dimensions						
1. Length (as preserved)	—	—	—	—	—	93.7
2. Head. MLW	12.7	—	—	12.7	11.5	—
3. Head, APW	—	—	13.8	12.6	—	—
4. Bitubercular width, maximum	15.5[b]	—	—	15.2	15.5	—
5. Midshaft circumference (below deltopectoral eminence)	—	20.0	19.9	26.5	—	24.9
6. Shaft, minimum APW	—	5.0	4.9	—	—	6.5
7. Maximum distal epiphysis width	—	—	—	—	—	19.6
8. Trochlea, minimum MLW in anterior aspect (excluding capitulum)	—	—	—	—	—	12.4
9. Olecranon fossa depth	—	4.2	—	—	—	3.6
10. Partial shaft length (see text)	—	—	46.5	—	—	54.3
Ratios						
A. Ratio 2/3 ("head sphericity")	0.88	—	—	0.92	0.91	—
B. Ratio 8/7 ("trochlea size")	—	—	—	—	—	0.63
C. Ratio 5/1 ("robusticity1")	—	—	—	—	—	0.26
D. Ratio 5/10 ("robusticity2")	—	—	0.11	—	—	0.46

[a] Measurements 1–8 as in MacPhee and Fleagle (1991); measurement 9 as in Schultz (1969).
[b] Incorrectly recorded as "14.5" by MacPhee and Fleagle (1991, table 2).

to the entepicondylar foramen, permitting measurement of "partial shaft length" (edge of proximal epiphyseal line on diaphysis to proximal border of bridge of entepicondylar foramen). Comparing these lengths in AMNHM 259906 and 268008 (table 4) reveals that the partial shaft of the Long Mile humerus is approximately 23% shorter than the comparable region of the Drum Cave specimen, even though the former is presumably fairly close to adult size. This accords with one's general impression that the Long Mile partial humeri are more gracile than the Drum or New Cave specimens.

Paralouatta MNHNCu 76.1010–
76.1013, 76.1024, and 76.1035

Although the humerus is also well represented in the *Paralouatta* postcranial collection ($N = 6$; figs. 7–10; table 5), only two of the specimens are appreciably complete. MNHNCu 76.1010 is very nearly entire, although there are losses to the head, tubercles, and the lateral part of the distal epiphysis (capitulum and lateral epicondyle). MNHNCu

76.1035 is missing its shaft proximal to the level of the deltopectoral tuberosity as well as the lateral part of the distal epiphysis. MNHNCu 76.1011 is much smaller in all dimensions and is judged to be juvenile. The other accessioned specimens are more fragmentary, but in some cases they provide useful information on parts not represented in the two more complete specimens. All are figured here save for MNHNCu 76.1024, a badly damaged distal articular end.

The humerus of *Paralouatta* is not simply a relatively longer version of that of *Xenothrix*: the diaphysis is less posteriorly concave, and for its length it is more gracile (cf. ratios C and D, tables 4 and 5). It also displays marked contrasts in the conformation of the distal articular end (see Functional Considerations).

Although MNHNCu 76.1035 gives the impression of being considerably more robust than MNHNCu 76.1010, this is mainly due to the size of its medial and lateral supracondylar ridges. Midshaft circumference, which is taken above the termination of these lines, is very similar in the two specimens, as is minimum
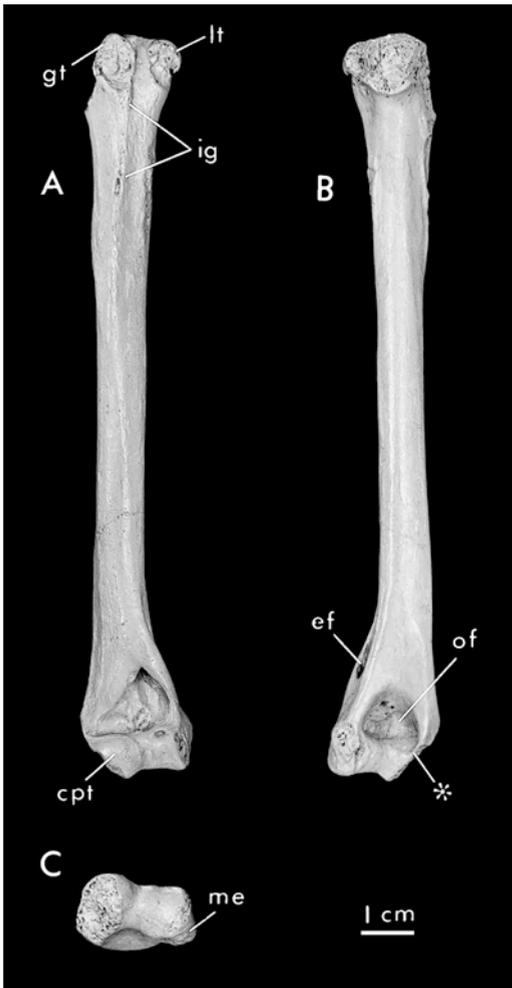
Fig. 7. *Paralouatta varonai*, nearly complete humerus: MNHNCu 76.1010 (R) in anterior (**A**), posterior (**B**), and distal (**C**) aspects. Except for the capitular region the distal end appears to be reasonably intact, but in fact all edges and surfaces are strongly abraded or broken. Reduction of medial lip of trochlea by abrasion should be especially noted; cf. MNHNCu 76.1013 (fig. 10), which is undamaged in this area. Asterisk indicates short continuation of OSTN articular surface onto lateral sidewall of olecranon fossa.

Fig. 8. *Paralouatta varonai*, distal humerus: MNHNCu 76.1035 (L [rev.]) in anterior (**A**), posterior (**B**), and distal (**C**) aspects. Although this specimen is less complete than MNHNCu 76.1010 (fig. 7), it is much less abraded. Asterisk indicates short continuation of OSTN articular surface onto lateral sidewall of olecranon fossa.

shaft width (table 5). The deltopectoral eminence ends in both examples in a distinctive "V" shape, presumably defined by the line of origin of the medial head of triceps m. Compared to MNHNCu 76.1010, the shaft of MNHNCu 76.1035 is relatively flatter above the level of the olecranon fossa, and

the medial epicondyle is more prominent and less abraded.

The one striking contrast between these specimens that requires comment is the entepicondylar foramen, present in MNHNCu 76.1010 but not MNHNCu 76.1035. It is also clearly present in the diaphyseal specimen, MNHNCu 76.1011 (fig. 9C, D), and a slight depression just above the shallow coronoid fossa in MNHNCu 76.1013 (fig. 10A) hints at an additional occurrence. According to Fleagle (1983), the entepicondylar foramen is found in about half of the extinct platyrrhine taxa for which the humerus is known. Among living platyrrhines foramen presence can be variable even within species (e.g.,

Fig. 9. *Paralouatta varonai*, humerus: proximal epiphysis MNHNCu 76.1012 (R) in oblique posterior (**A**) and medial (**B**) aspects; and ?immature diaphysis MNHNCu 76.1011 (L [rev.]) in anterolateral (**C**) and posterior (**D**) aspects. Note that the summit of the articular surface rises slightly above the level of the tubercles.

Aotus, *Callicebus*, and *Alouatta*; J. Meldrum, unpubl. obs.; consistently absent in *Callithrix* and *Leontopithecus* but not *Saguinus*; Ford, 1986a, 1986b; Meldrum, 1990). In view of the overarching similarity of all of the humerus specimens from the monkey caves (and, not incidentally, the teeth; Horovitz and MacPhee, 1999), we conclude that, like
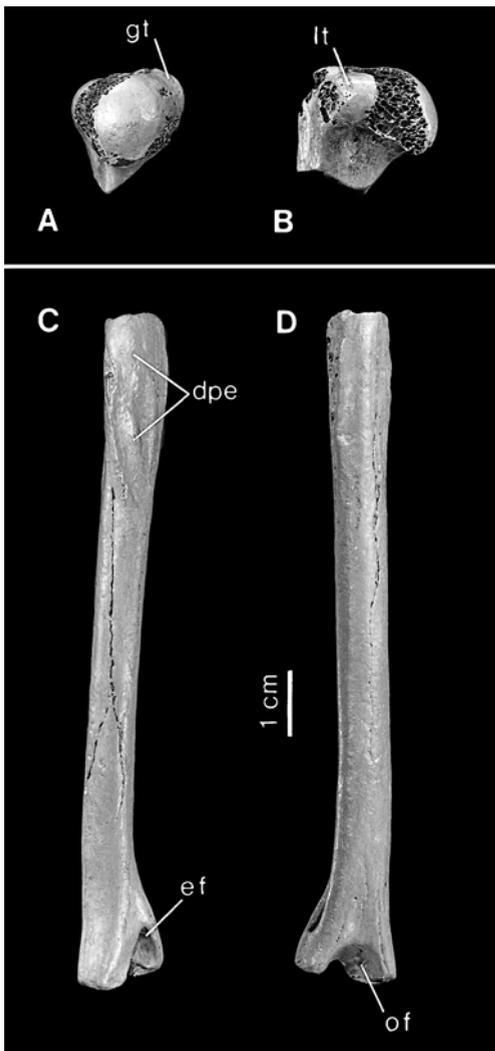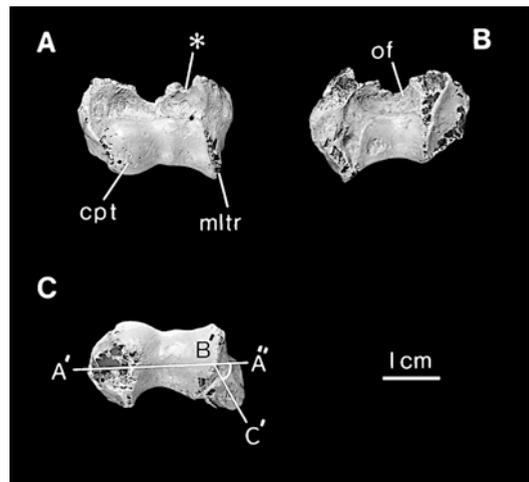

Fig. 10. *Paralouatta varonai*, distal epiphysis of humerus: MNHNCu 76.1013 (R) in anterior (**A**), posterior (**B**), and distal (**C**) aspects. Orientation is based on distal end of MNHNCu 76.1035 (fig. 8). Asterisk indicates apparent distal limit of groove bordering entepicondylar foramen. Indicated in **C** are planes and landmarks for measuring posterior deviation of the medial epicondyle (MEPD, table 6; see text).

several extant platyrrhine species, *P. varonai* was variable for entepicondylar foramen development, and that only one kind of primate is represented in the hypodigm.

Among humeri in the comparative set, MNHNCu 76.1010 is approximately as long as that of *Alouatta seniculus* and *Trachypithecus pileatus* (fig. 11D–F, G–I). It resembles these taxa in having a comparatively straight shaft, but is more like *Erythrocebus* and *Theropithecus* (fig. 11M–O, P–R) in exhibiting a ML narrow distal epiphysis. The overall appearance of the posterior aspect of the distal humerus is also somewhat cercopithecidlike in the lack of medial projection of the medial epicondyle, the proportions of the posterior extension of the trochlear surface, and the depth of the lateral margin of the olecranon fossa. The capitulum is wider (in anterior aspect) than the trochlea, although this is hard to measure accurately because the waist defining their respective limits is indistinct on these specimens (fig. 10A). In *Alouatta* (fig. 11E) and other large-bodied atelids, the posteromedial edge of the trochlea ends in a long medial lip that is aimed medially

TABLE 5
Humerus: *Paralouatta varonai*, Dimensions (in mm) and Ratios[a,b]

	MNHNCu				
	76.1010	76.1011	76.1012	76.1013	76.1035
Dimensions					
1. Length (as preserved)	142.7	—	—	—	—
2. Head, MLW	—	—	*14.5e*	—	—
3. Head, APW	*13.0e*	—	*15.0e*	—	—
4. Bitubercular width, maximum	*6.6*	—	—	—	—
5. Midshaft circumference (below deltopectoral eminence)	29.6	24.7	—	—	31.4
6. Shaft, minimum APW	8.4	7.5	—	—	8.5
7. Distal epiphysis, maximum MLW	*21.6e*[c]	—	—	26.5	*26.3e*[c]
8. Trochlea, minimum MLW in anterior aspect (excluding capitulum)	8.5	—	—	9.2	10.7
9. Olecranon fossa depth	6.1	—	—	—	6.0
10. Partial shaft length (see text)	112.0	—	—	—	—
Ratios					
A. Ratio 2/3 ("head sphericity")	—	—	*0.97e*	—	—
B. Ratio 8/7 ("trochlea size")	*0.39e*	—	—	0.35	*0.41e*
C. Ratio 5/1 ("robusticity1")	0.21	—	—	—	—
D. Ratio 5/10 ("robusticity2")	0.26	—	—	—	—

[a] Measurements 1–8 as in MacPhee and Fleagle (1991); measurement 9 as in Schultz (1969).

[b] Measurements/ratios in italics are not precise (*e* = estimate, due to damage or breakage).

[c] Although the lateral part of the distal epiphysis is not preserved in this specimen, the lateral supratrochlear line (which is often the point of maximum distal width in primate humeri) is present and was used as a replacement landmark for this measurement.

more than ventrally. In *Trachypithecus*, *Lophocebus*, *Erythrocebus*, and *Theropithecus* the homologous area is directed inferiorly (fig. 11H, K, N, Q). In *Paralouatta* conditions are intermediate (fig. 10A).

The olecranon fossa is notably deep in the two most complete specimens. The floor of the fossa is intact in MNHNCu 76.1010 but perforated in MNHNCu 76.1035 (which affects measurement). Whether the perforation is natural or due to postmortem breakage is difficult to say. Under high magnification, involved edges are not smooth and show a thin layer of cancellous tissue sandwiched between compact bone surfaces, suggesting that material has spalled off.

Functional Considerations

RELATIVE MEDIAL EPICONDYLE SIZE AND ORIENTATION: In both *Xenothrix* and *Paralouatta* the medial epicondyle is posteriorly directed or retroflexed, as may be clearly seen in the least damaged specimens (cf. fig. 5C, 10C). Fleagle and Simons (1978: 705) pointed out that medial rotatory torques on the radiohumeral and ulnohumeral joints are increased if the medial epicondyle projects directly medially (as in *Alouatta* and *Lagothrix*) rather than posteriorly (as in *Cebus* and Old World monkeys). They explain retroflexion of the medial epicondyle as an adaptation "enhancing the actions of the pronators and flexor muscles when the elbow is already pronated as in pronograde quadrupedalism."

Only the distal epiphysis MNHNCu 76.1013 retains an unabraded medial epicondyle (fig. 10); in the two more complete humeri the epiphysis is damaged. Nevertheless, it is clear in all three specimens that the epicondyle's mass is directed posteriorly, quite unlike the situation in the majority of platyrrhines (including all New World species of large BM)
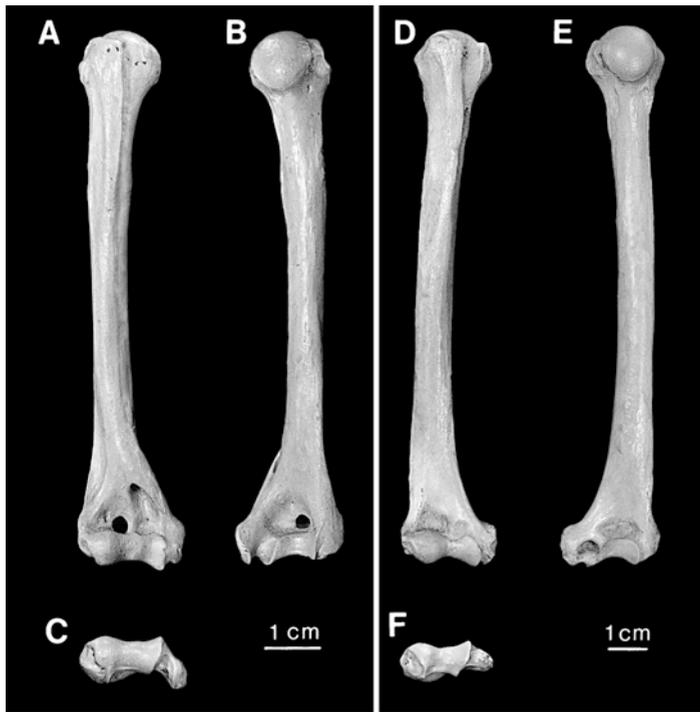
Fig. 11. Comparative set, right humerus in anterior, posterior, and distal aspects: *Cebus apella* AMNHM 209927 (**A–C**); *Alouatta seniculus* AMNHM 23377 (**D–F**); *Trachypithecus pileatus* AMNHM 43071 (**G–I**); *Lophocebus albigena* AMNHM 52627 (**J–L**); *Theropithecus gelada* AMNHM 60568 (**M–O**); *Erythrocebus patas* AMNHM 34709 (**P–R**). Note differences in scale.

in which the epicondyle juts almost directly medially. The size of the medial epicondyle relative to the maximum (biepicondylar) width of the distal end of the bone can be expressed as a ratio (MEPR) by dividing maximum distal width by adjusted distal width (i.e., by deducting the medial epicondyle's contribution). The higher the ratio, the less the medial epicondyle contributes to total width. In the case of our comparative set, MEPR is of limited value because it does not provide good discrimination even between suspensory and terrestrial species (table 6). The ratio is affected by the size of other features, especially the lateral epicondyle. Among measured taxa, xenotrichines display some of the highest values because of the limited contribution of the medial epicondyle to distal width. However, *Brachyteles* and *Lagothrix* are not far behind, despite the fact that they have relatively large, flaring medial epicondyles.

Posterior deviation (retroflexion) of the medial epicondyle (MEPD; table 6) is a more subjective measurement, due to the difficulty of deciding where the center of the epicondyle is located in distal aspect. There is variation within locomotor groupings, although some interesting consistencies can be identified. Large-bodied Old World species that spend significant periods on the ground tend to have very large deviations ($>80°$), up to an extreme of $\sim100°$ in the case of *Theropithecus*. Smaller-bodied forms, however, do not show so great a degree of deviation. Gebo and Sargis (1994) did not mention medial epicondyle retroflexion as an informative character in their ecomorphological evaluations of *Cercopithecus mitis* and *C. lhoesti*.

New World suspensory species display the opposite trend in MEPD, from $29°$ in *Brachyteles arachnoides* to $0°$ in *Ateles belzebuth* (although both values are based on single

Fig. 11.   Continued.

TABLE 6
Medial Epicondyle of Humerus: Posterior Deviation (MEPD) and Participation Ratio (MEPR) in *Xenothrix*, *Paralouatta*, and Selected Living Primates[a]

Taxon (N)	MEPD (degrees)[b,c]	MDWHum (I)[b,d]	AdjMDWHum (II)[b,e]	MEPR (II/I)
Theropithecus gelada (3)	**98** (96–100)	**35.6** (36.1–35.5)	**29.8** (29.2–30.1)	**0.84**
Macaca nemestrina (3)	**90** (95–85)	**34.6** (34.4–35.0)	**29.6** (28.0–30.4)	**0.86**
Erythrocebus patas (2)	**88** (87, 88)	**27.6** (22.9, 32.2)	**23.7** (20.3, 27.1)	**0.86**
Lophocebus albigena (3)	**75** (71–80)	**28.2** (26.2–29.9)	**23.4** (21.7–24.4)	**0.83**
Paralouatta varonai MNHNCu 76.1013	**68**	**26.5**	**23.7**	**0.89**
Paralouatta varonai MNHNCu 76.1035	*65e*	*26.3e*	*23.9e*	*0.91e*
Trachypithecus pileatus (3)	**63** (62–65)	**27.9** (26.1–29.0)	**24.0** (23.6–24.8)	**0.86**
Cebus apella (3)	**51** (46–54)	**20.7** (20.3–21.1)	**17.6** (17.5–17.7)	**0.85**
Xenothrix mcgregori AMNHM 268008	**54**	**19.6**	**17.5**	**0.89**
Chiropotes satanus (2)	**48** (46, 50)	**21.4** (19.5, 23.2)	**17.0** (14.9, 19.0)	**0.79**
Colobus guereza (1)	**45**	**25.0**	**21.4**	**0.86**
Saguinus midas (1)	**36**	**12.3**	**9.6**	**0.78**
Brachyteles arachnoides (1)	**29**	**32.4**	**26.7**	**0.82**
Lagothrix lagotricha (3)	**26** (23–27)	**27.9** (24.9–30.4)	**24.3** (20.4–28.6)	**0.87**
Alouatta seniculus (3)	**24** (20–28)	**29.2** (27.5–32.6)	**21.4** (19.9–24.5)	**0.73**
Callicebus moloch (3)	**22** (20–24)	**13.5** (13.4–13.7)	**9.1** (8.8–10.5)	**0.67**
Aotus sp. (2)	**9** (8, 10)	**13.3** (13.1,13.4)	**10.3** (9.7, 10.8)	**0.77**
Ateles belzebuth (1)	**0**	**33.0**	**24.3**	**0.74**

[a] Measurements in italics are not precise (*e* = estimate, due to damage or breakage).

[b] Values given in bold are means followed by range in parentheses.

[c] MEPD, posterior deviation of medial epicondyle of humerus. Method: on a camera lucida tracing of the distal aspect of each humerus (see fig. 10C), (1) divide the distal surface into two moieties, as equally as possible, by means of a line A′–A″; (2) where A′–A″ intersects the medial lip of the trochlea, define point B′; (3) run a line B′–C′ from the latter point to the tip of the medial epicondyle. MEPD is dihedral angle A″B′–C′.

[d] MDWHum, maximum biepicondylar width of distal end of humerus (in distal aspect).

[e] AdjMDWHum, adjusted maximum width, minus contribution of medial epicondyle (i.e., lateral epicondyle to medial rim of trochlea, in distal aspect).

specimens). Small arboreal quadrupeds (*Aotus infulatus*, *Callicebus moloch*) also show little medial epicondyle deviation, 9–22°. The largest posterior deviation among living platyrrhines—51°—occurs in *Cebus apella* (range, 46–54°). This converges on the single value for *Xenothrix* (AMNHM 268008, 54°), but does not overlap with *Paralouatta* (65–68°, based on the two least abraded examples).

In summary, with respect to medial epicondyle retroflexion, although *Xenothrix* and *Paralouatta* do not differ radically from generalized platyrrhine arboreal quadrupeds like *Cebus*, at the same time they also show some similarity to cercopithecids who spend considerable time on the ground or in lower tree branches.

TROCHLEAR ORGANIZATION: As noted, the capitulum is separated from the trochlea by an indistinct waist, the lateral margin of the trochlea, in *Xenothrix* and *Paralouatta* (figs. 5, 10). According to Gebo and Sargis (1994), the lateral margin is very pronounced in highly arboreal *Cercopithecus mitis* but not in more terrestrial *C. lhoesti*. However, in their figures the contrast appears less marked than their description indicates. In any case, this margin is very strongly modeled in *Theropithecus* (fig. 11M–O) and is therefore by itself not a strong correlate of arboreality. A more significant functional indicator is the short ML width of the trochlea in *Paralouatta*, which is relatively much shorter than in *Xenothrix* (ratio B in tables 4, 5) and also large-bodied atelids such as *Alouatta* (fig. 11D, F). *Cercopithecus lhoesti* and *C. mitis* contrast in the same manner, as Gebo and Sargis (1994) noted. The narrow trochlea is important functionally because it tends to constrain the motion of the forearm on the arm to fore/
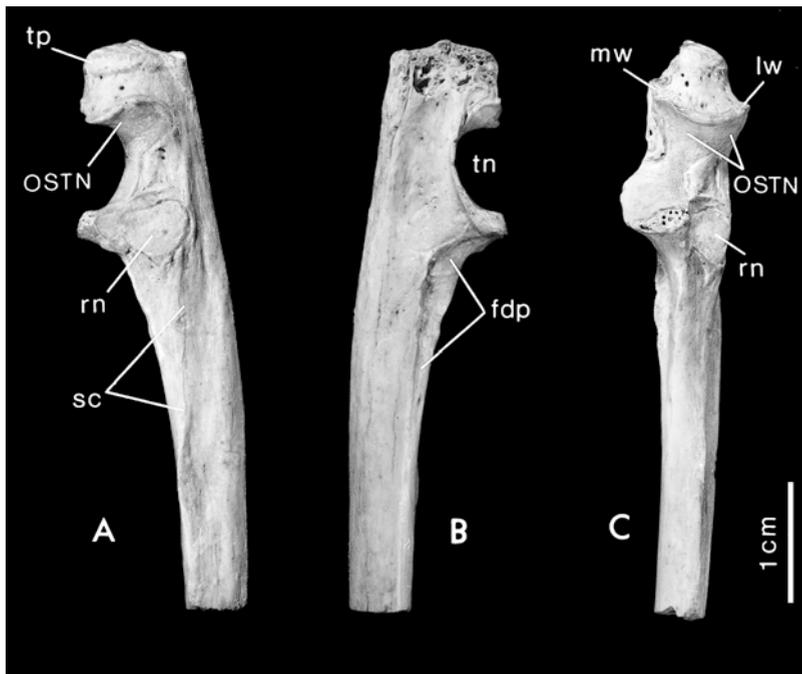
Fig. 12.   *Xenothrix mcgregori*, proximal ulna: AMNHM 268010 (R [rev.]) in lateral (**A**), medial (**B**), and anterior (**C**) aspects. Note the markedly ''inset'' condition of the radial articular surface, which is unabraded. Both medial and lateral ''wings'' of the olecranon surface of the trochlear notch are large and flaring (cf. *Paralouatta*, fig. 13).

aft movements, with little or no ulnar deviation (cf. *Theropithecus*, fig. 11M, O).

ULNA AND RADIUS

Xenothrix AMNHM 268010

The ulna from Somerville Cave, AMNHM 268010 (fig. 12; table 7), agrees in detail with AMNHM 259907, the immature specimen from Long Mile Cave described by MacPhee and Fleagle (1991: their fig. 14). Also, the trochlear notch of AMNHM 268010 articulates reasonably well with the complete humerus AMNHM 268008, which helps to corroborate the view that they belong to the same species. Because breakage occurs in approximately the same place in both ulnae, the new find adds little to what is already known. However, because AMNHM 268010 is from an adult and is less abraded than earlier finds it provides a better sense of the size and disposition of proximal joint surfaces and muscle markings. (In fig. 12, note

prominent scars for supinator, brachialis, and flexor digitorum superficialis mm.)

It is difficult to estimate the degree of shaft curvature in incomplete ulnae. In the case of *Xenothrix* AMNHM 268010, the remaining proximal section of the posterior border (fig. 12B) is straight, but distally there is the beginning of a slight curvature, probably much as in *Cebus apella* (fig. 14B). It appears that the epiphysis of the triceps process of *Xenothrix* was small and tablike: in the new fossil there is no visible metaphyseal ''line'' in the cancellous bone fortuitously exposed by breakage on the medial side of the olecranon region (fig. 12B). Posteromedial slant of the process, which is characteristic of both arboreal and terrestrial Old World monkeys (to differing degrees) is not indicated (fig. 14I, J, M; table 7). A deep trochlear notch, with a sharply projecting coronoid as seen in *Xenothrix*, is characteristic of primates that emphasize quadrupedalism (Knussman, 1967) (cf. *Cebus apella*, fig. 14B).

TABLE 7
Ulna: *Xenothrix mcgregori*, *Paralouatta varonai*, and Selected Living Primates, Dimensions (in mm) and Ratio [a,b]

	Xenothrix mcgregori AMNH 268010	*Paralouatta varonai* MNHNCu 76.1014	*Paralouatta varonai* MNHNCu 76.1016	*Paralouatta varonai* MNHNCu 76.1017	*Callicebus moloch* (3)	*Chiropotes satanus* (2)	*Ateles belzebuth* (1)	*Brachyteles arachnoides* (1)	*Lagothrix lagotricha* (3)	*Alouatta seniculus* (3)	*Cebus apella* (3)	*Trachypithecus pileatus* (3)	*Erythrocebus patas* (2)	*Macaca nemestrina* (3)	*Lophocebus albigena* (3)
Dimensions															
1. Length	—	—	—	—	**75.1** (67.6–82.3)	**112.6** (104.1, 121.1)	**223.0**	**221.5**	**175.2** (158.1–187.1)	**158.7** (149.1–169.4)	**109.4** (103.9–114.7)	**159.7** (157.2–167.6)	**191.7** (165.4, 210.0)	**222.4** (213.7–229.0)	**167.5** (175.7–156.3)
2. Triceps process height above olecranon, anterior aspect[c]	6.5	8.4	—	—	**6.0** (5.1–7.1)	**8.8** (7.9, 9.7)	9.4	9.8	**11.4** (9.4–13.1)	**13.4** (11.1–15.3)	**8.8** (8.0–9.4)	**10.6** (8.9–11.6)	**8.0** (5.0, 11.1)	**11.8** (9.9–12.8)	**10.8** (10.5–11.0)
3. Trochlear notch height, coronoid to olecranon	8.2	—	9.5	—	**6.0** (5.0–7.3)	**8.9** (8.2, 9.5)	9.4	11.8	**12.4** (11.9–13.4)	**10.5** (10.0–10.8)	**8.2** (6.5–9.4)	**12.7** (11.9–13.8)	**12.8** (13.5, 12.1)	**13.8** (12.8–14.4)	**10.6** (10.8–9.9)
4. Trochlear notch width, olecranon section (OSTN)	8.3	*10.5e*	7.2	—	**4.9** (4.3–5.2)	**8.5** (7.4, 9.6)	13.5	10.4	**9.9** (9.0–10.4)	**9.3** (8.9–9.7)	**7.8** (7.4–8.0)	**9.7** (9.3–10.3)	**9.1** (8.6, 9.6)	**10.3** (9.7–11.2)	**9.7** (8.7–10.5)
5. Upper shaft, MLW[d]	5.0	—	5.6	7.5	**2.6** (2.4–2.7)	**4.9** (4.3, 5.5)	8.8	5.9	**6.2** (5.0–7.5)	**6.4** (5.9–6.9)	**5.1** (4.1–6.0)	**7.8** (6.5–8.8)	**8.4** (7.1, 9.7)	**13.2** (11.7–14.7)	**8.1** (7.5–8.6)
6. Upper shaft, APW[d]	7.8	—	11.9	12.7	**5.1** (4.2–6.1)	**9.3** (8.4, 10.1)	11.6	9.7	**11.1** (10.1–12.2)	**10.9** (9.4–12.4)	**8.6** (8.4–8.8)	**11.9** (10.9–13.4)	**14.6** (12.4, 16.7)	**19.2** (18.8–20.5)	**12.7** (11.8–13.5)
Ratio															
A. 4/3 ("trochlear notch proportion")	1.01	—	0.76	—	0.82	0.95	1.44	0.88	0.80	0.89	0.95	0.76	0.71	0.75	0.92

a Measurements/ratios in italics are not precise (e = estimate, due to damage or breakage).
b Values cited in bold are means (or single observation, if N = 1) followed by range in parentheses.
c Triceps process height: superior margin of trochlear notch to summit of triceps process in anterior aspect.
d Upper shaft measurements (5 and 6): immediately beneath plane of coronoid process/radial notch, regardless of the disposition of crests in this area.

The nonarticular areas on the trochlear surface are well marked in AMNHM 268010 (fig. 12C): They extend onto the central part of the notch medially and especially laterally, but do not extend across the notch's whole face. The radial notch is "inset" on the lateral aspect of the bone, being almost flush with it and extending onto and even slightly under the coronoid process. This feature, which has an interesting distribution, is discussed further below.

The radius of *Xenothrix* is not yet known.

Paralouatta MNHNCu 76.1014, 76.1016, and 76.1017

The ulnae in the hypodigm are highly incomplete (fig. 13A–I). Even so, the size contrast between both MNHNCu 76.1014 and 76.1017 on the one hand and MNHNCu 76.1016 on the other is quite noticeable, the former being larger for given linear measurements by ~20–25%. MNHNCu 76.1014 and 76.1017 are from opposite sides of the body, but in size they are very similar and quite possibly represent the same animal.

Although the posterior border of the ulna was evidently rather straight in its upper moiety, as in *Xenothrix*, too little is left of the shaft to ascertain whether the distal section was straight or bowed. As in *Xenothrix*, muscle scars around the coronoid process are well marked. Of interest is the fact that the supinator crest is displaced relatively posteriorly, as in *Cebus*, *Lophocebus*, and *Theropithecus*, but unlike *Alouatta* (or other large-bodied platyrrhines) in which the indistinct supinator crest lies closer to the interosseous crest (fig. 14).

The preserved part of the shaft in MNHNCu 76.1016 and 1017 is anteroposteriorly as wide as, or wider than, in other large-bodied platyrrhines such as *Alouatta* (fig. 14D–F; table 7) and *Brachyteles*. Mediolaterally it is compressed into a knife edge, whereas in other large-bodied platyrrhines the shaft tends to be more rounded in this dimension. This feature is possibly correlated with the extensive fossa beneath the radial notch, which recalls a similar feature seen in *Macaca* and some other cercopithecids in the comparative set (e.g., *Erythrocebus*, *Theropithecus*; fig. 14J–M). In these last taxa, the fossa is needed in order to give free passage to the bicipital tuberosity during movements of supination/pronation, because the tuberosity is located relatively higher on the shaft than in large-bodied platyrrhines. *Xenothrix* lacks this feature. In *Lagothrix* the ulna is compressed in this region, but it too lacks the fossa.

MNHNCu 76.1014 (fig. 13A) provides evidence that the triceps process of *Paralouatta* was not especially large and was built as in other platyrrhines (i.e., the process was not posteromedially retroflexed as in some cercopithecids; cf. fig. 14L).

The proximal articular areas are incomplete to some degree in all *Paralouatta* specimens. The trochlear notch is moderately deep, intermediate between the conditions seen in suspensory platyrrhines and terrestrial cercopithecids. As in *Xenothrix*, the triceps process is not medially twisted or deviated. The disposition of the nonarticular areas within the trochlear notch are hard to interpret because of damage to joint surfaces. In MNHNCu 76.1016, however, on the lateral side there is evidence that the nonarticular surface penetrated rather far into the notch. It is clear that the radial articular facet was relatively "inset" on the lateral aspect of the ulna, as in *Xenothrix* (cf. figs. 12, 13). In this feature, both xenotrichins agree with other platyrrhines, and in particular with the large-bodied taxa in which the elbow joints emphasize mobility (e.g., *Alouatta*, fig. 14F).

In Old World monkeys (fig. 14I, J, M), even in highly arboreal *Colobus*, the radial articular facet is more "outset," projecting at a sharp angle out of the plane of the shaft's lateral aspect and thereby imparting a strong curve to the radial notch (Fleagle, 1983). In the comparative set, projection reaches a maximum in *Theropithecus*, *Erythrocebus*, and *Macaca*, in which the radial notch is divided in two by an intervening nonarticular area (e.g., fig. 14K). The "outset" condition and presence of a subdivided radial facet are evident in many ground-dwelling cercopithecids. In *Trachypithecus pileatus* and *Colobus guereza* there is only one radial facet, but in *Cercocebus galeritas* there are two, practically conjoined, whereas in *Lophocebus albigena* there are clearly two and they are quite separate (fig. 14G). This variation implies that the subdivided radial notch is not
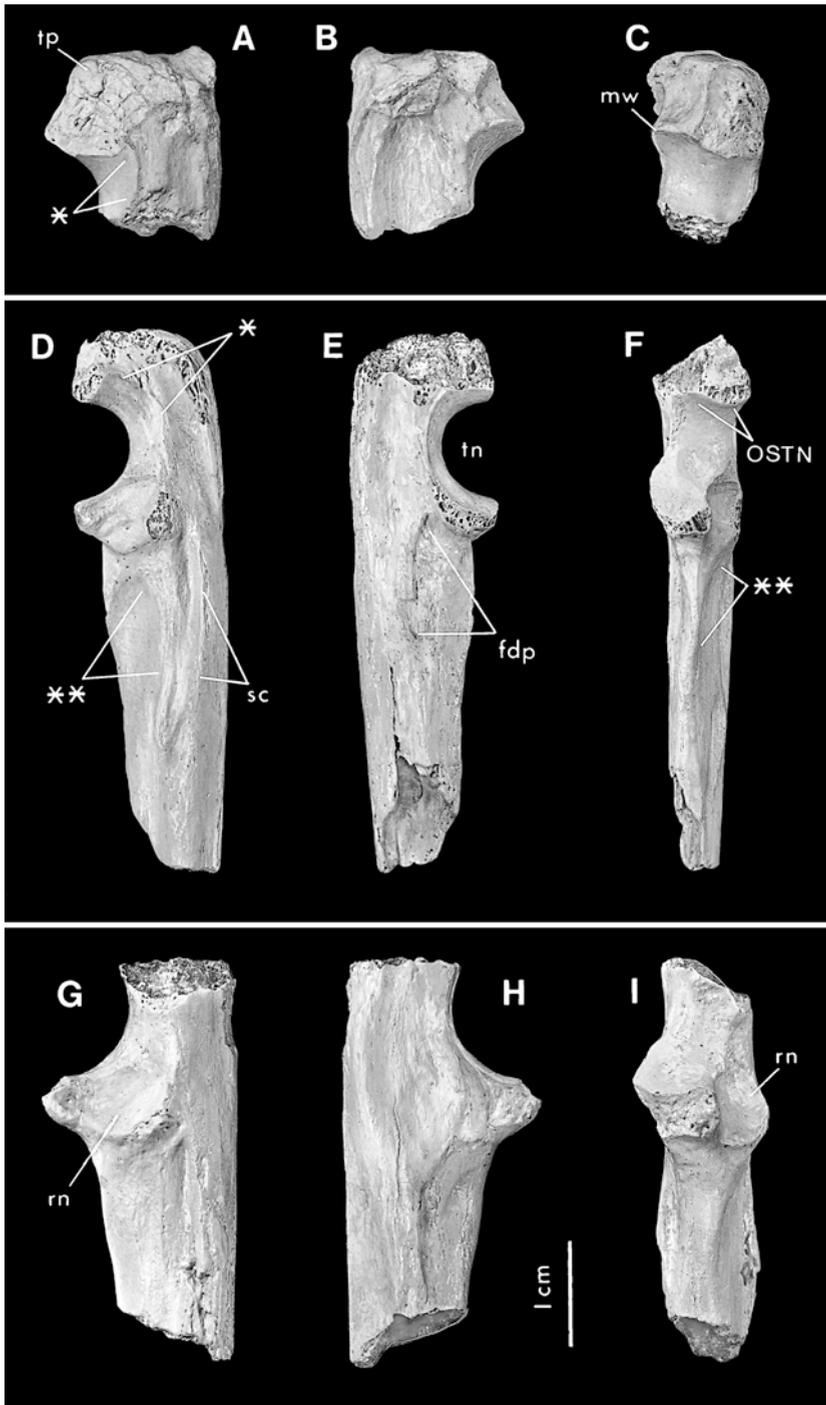
Fig. 13. *Paralouatta varonai*, proximal ulnae in lateral, medial, and anterior aspects: MNHNCu 76.1014 (R [rev.]) (**A–C**), MNHNCu 76.1016 (L) (**D–F**), and MNHNCu 76.1017 (L) (**G–I**). Note the ''inset'' condition of the radial articular surface in **I**, which appears exaggerated in **F** because facet edges are markedly abraded. Only the medial wing (mw) of the olecranon surface of the trochlear notch is present in

completely diagnostic of preferred substrate. The fact that platyrrhines are all quite similar for the "inset" version of this feature suggests that it is not strongly correlated with any single locomotor style.

The radius (MNHNCu 76.1015; fig. 15; table 8) attributed to *Paralouatta* consists only of the proximal end and a small portion of the shaft, and extensive interpretation or comparison is not warranted. Most of the articular circumference is chipped away, but there is no reason to think that it was not extensive, as in primates generally. The short neck and rather high positioning of the long, contoured bicipital tuberosity strongly recalls radii of some Old World monkeys, such as *Lophocebus* and *Erythrocebus*.

Functional Considerations

OLECRANON SURFACE OF TROCHLEAR NOTCH: In many primates, including *Xenothrix*, the upper or olecranon surface of the trochlear notch (OSTN) is saddle shaped, with medial and lateral wings flaring from it to a roughly equal extent. In large-bodied platyrrhines with wide but shallow olecranon fossae (e.g., *Alouatta*, fig. 14D–F), the medial and lateral surfaces of the OSTN have sharp, nonreflected margins without facets, because nowhere along the ulna's range of motion do they impinge on the low borders of the humeral trochlea/olecranon fossa.

By contrast, in *Erythrocebus* (fig. 14J) and *Theropithecus* (fig. 14K–M), the lateral "wing" does not really exist as such. This side of the OSTN is molded instead into a flat, crescentic facet on the surface of the triceps process, and throughout the range of motion it remains in contact with the large, continuous lip formed by the lateral margins of the trochlea and the olecranon fossa. In *Theropithecus*, both lateral and medial wings of the OSTN are abbreviated to mesh with the posteriorly narrowing trochlea. In *Erythrocebus* only the lateral wing is abbrevi-

ated; its short external margin is reflected and turned upward to articulate with the lateral lip, which is, in effect, a continuation of the trochlear surface into the olecranon fossa. Together, these surfaces increase the articular area of the ulnohumeral joint, and by their conformation provide stability against laterally directed forces when the arm is extended.

Paralouatta appears to have had a somewhat intermediate arrangement. In MNHNCu 76.1016, which is well preserved in the relevant area, there is no lateral shelf of the OSTN; the articular area is flush with and continues onto the triceps process (asterisk, fig. 13D), more or less as in *Theropithecus* or *Erythrocebus*. In MNHNCu 76.1014 most of the relevant area is damaged, although it is possible to identify the distal part of the reflected facet (fig. 13A). Unfortunately, the condylar portions of the humeri MNHNCu 76.1010 and 1035 are incomplete laterally to about the same degree (figs. 7, 8), although it is possible to see that the well-defined lateral margin of the trochlea bears a short, striplike continuation of the articular surface onto the sidewall of the olecranon fossa. In *Alouatta*, by contrast, the indistinct lateral margins of the trochlea and the olecranon fossa are only weakly connected (fig. 11E). These comments apply in equal measure to *Ateles*, *Brachyteles*, and *Lagothrix* and all other platyrrhines in the comparative set.

Ratio A in table 7 compares the height of the trochlear notch to its width across the OSTN section. *Theropithecus* and *Erythrocebus* have very narrow OSTN sections and correspondingly low ratios (0.65, 0.71). Highly arboreal New World monkeys, whether predominantly quadrupedal or suspensory, have flaring medial and lateral OSTN wings and ratios above 0.80. (This is also true of *Colobus guereza*, data not shown). *Paralouatta* has a relatively low value (0.76) in the table, but only one specimen could be measured for both width and height and it is somewhat damaged. However, it is unlikely that in an

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←
Paralouatta (**C**). On the lateral side there is instead a narrow facet (single asterisk in **A** and **D**), flush with the sidewall of the triceps process, which articulates with the continuous crest formed by the lateral margins of the trochlea and olecranon fossa. Double asterisks in **D** and **F** indicate position of large fossa on shaft distal to radial notch. To same scale.

Fig. 14. Comparative set, right ulna in lateral, medial, and anterior aspects: *Cebus apella* AMNHM 209927 (**A–C**); *Alouatta seniculus* AMNHM 23377 (**D–F**).

intact specimen the ratio would have exceeded 0.80 significantly. Interestingly, *Xenothrix* has a very high ratio (1.01), higher than any other member of the comparative set except *Ateles belzebuth* (1.44).

Os Coxae

Xenothrix AMNHM 268009

AMNHM 268009, the Skeleton Cave coxal specimen (fig. 16A–C; table 9), is as incomplete as AMNHM 259904 from Long Mile Cave (fig. 16D–F) described by MacPhee and Fleagle (1991). The only noteworthy feature that is better preserved in the former is the superior ramus of the pubis. MacPhee and Fleagle (1991) inferred on the basis of the

Long Mile specimen that, in the intact state, the superior ramus would have jutted at a wide angle from the coxal body; the new specimen confirms this. By superimposing images of AMNHM 2599004 (more complete ischium) on AMNHM 268009 (more complete pubis), it can be established that in *Xenothrix* the superior ramus departs the coxal body at somewhat less than a right angle (75–80°). Old and New World monkeys alike, especially larger species, display broadly similar angles (MacPhee and Fleagle, 1991; Meldrum, 1993; Meldrum and Kay, 1997).

In the new specimen (fig. 16A), the superior ramus is notably gracile, flat, and craniocaudally narrow. The maximum distance from the approximate center of the acetabulum to the medial end of the pubis as preserved is

Fig. 14. (Continued).   *Lophocebus albigena* AMNHM 52627 (**G–I**); *Erythrocebus patas* AMNHM 34709 (**J**, anterior aspect only); *Theropithecus gelada* AMNHM 60568 (**K–M**). White pointers in **C** and **J** indicate lateral olecranon surface of trochlear notch. In **C** and **F** this area is built out into a prominent wing, but in **J** and **M** the articular surface spreads onto the sidewall of the triceps process and the wing feature is reduced or absent. White arrows in **F** and **M** indicate, respectively, "inset" and "outset" conditions of radial notch (asterisk in **D**). Note differences in scale.

27.3 mm. On the broken medial margin no rugosities or other features are present which might serve to indicate that part of the true symphyseal surface is preserved. Evidently, in the intact state the complete ramus would have been longer still. On the underside of the superior ramus there is another broken surface (arrow, fig. 16A), the site of the inferior ramus of the pubis. Although the shape of the obturator foramen cannot be inferred from the evidence at hand, it must have been relatively large, as the root of the inferior ramus lies at a considerable distance from obturator margin of the acetabular region.

The acetabulum is notably wide in both specimens. Acetabular depth is approximately one-half of acetabular diameter (ratio A, table 9), as is typical for primates (Schultz, 1969). Owing to the condition of the new specimen, in which the sciatic margin is broken away (fig. 16C), dorsal and medial acetabular wall dimensions could not be taken. However, the ventral wall is intact and its measurement resembles that of AMNHM 259904 (table 9).

MacPhee and Fleagle (1991) noted previously that the locomotor correlates of the Long Mile os coxae were indeterminate; the Skeleton Cave specimen sheds no new light on
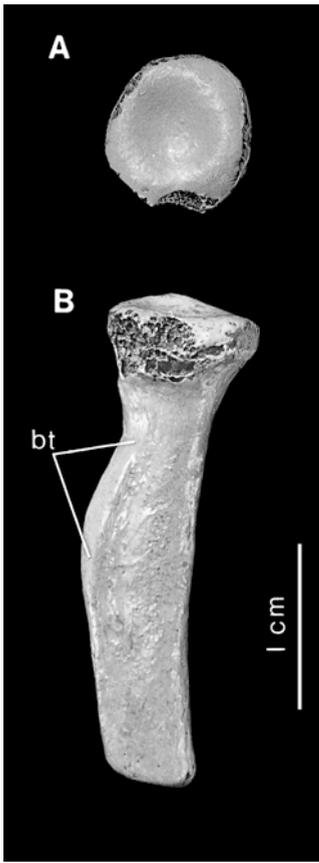
Fig. 15. *Paralouatta varonai*, proximal radius: MNHNCu 76.1015 (L) in proximal (**A**) and lateral (**B**) aspects.

TABLE 8
Radius: *Paralouatta varonai*, Dimensions (in mm)[a]

Dimensions	MNHNCu 76.1015
1. Length (as is)	*31.6e*
2. Head, APW	*10.2e*
3. Head, circumference	*30.4e*
4. Biceps, (radial) tuberosity length	15.0
5. Shaft, minimum APW	5.0

[a] Measurements in italics are not precise (*e* = estimate, due to damage or breakage).

margin. The broad iliac blade is reflected laterally in such a way that the dorsal surface is noticeably concave, as in large *Ateles belzebuth* or *Lagothrix lagotricha*. The ischium is broad and appears to have supported a wide and perhaps slightly laterally flaring tuberosity. Nothing, however, in the anatomy of the part preserved suggests that the tuberosity was built out into a platform, as in Old World monkeys. The acetabulum is conspicuously large and slightly more downward-facing than in living large-bodied platyrrhines.

The longest dimension, as preserved, is 115 mm. However, the proportions of the os coxae suggest that it might have exceeded 140 mm in maximum length when intact, which is within the range of coxal lengths found in the largest living platyrrhines.

Functional Considerations

ACETABULAR WALLS: Since the acetabulum and its walls are the only well preserved parts of this specimen, functional remarks will concentrate on this area. Fleagle and Simons (1979) showed that, with some prominent exceptions, nonhuman anthropoids with subequal dorsal and ventral acetabular walls tended to utilize limb suspension in locomotion (and exhibit typically high values for ratio B, cf. table 9). Those with relatively thicker dorsal acetabular walls tended to be more pronograde (with lower values), possibly because in these taxa this part of the os coxae is expanded as an adaptation for weight bearing.

The ratio for *Xenothrix* AMNHM 259904 calculated by MacPhee and Fleagle (1991) is 0.61, indicating that the Jamaican monkey falls at the low end of the anthropoid

this question. However, they noted that the expanded iliac planum is consistent with slothlike slow quadrupedalism or climbing, as is the gracile and apparently elongated pubic ramus.

Paralouatta MNHNCu 76.1036

Although abrasion has affected most edges of this specimen, reducing the accuracy of measurements, it is clear that the os coxae was large and robustly built in the Cuban monkey, with wide iliac surfaces and a massive dorsal acetabular wall (fig. 17; table 9). The pubis is shorn off at its acetabular root, and only a small portion of the ischium is preserved. The iliac portion includes most of the sacral articular surface, but nothing remains of its rostral
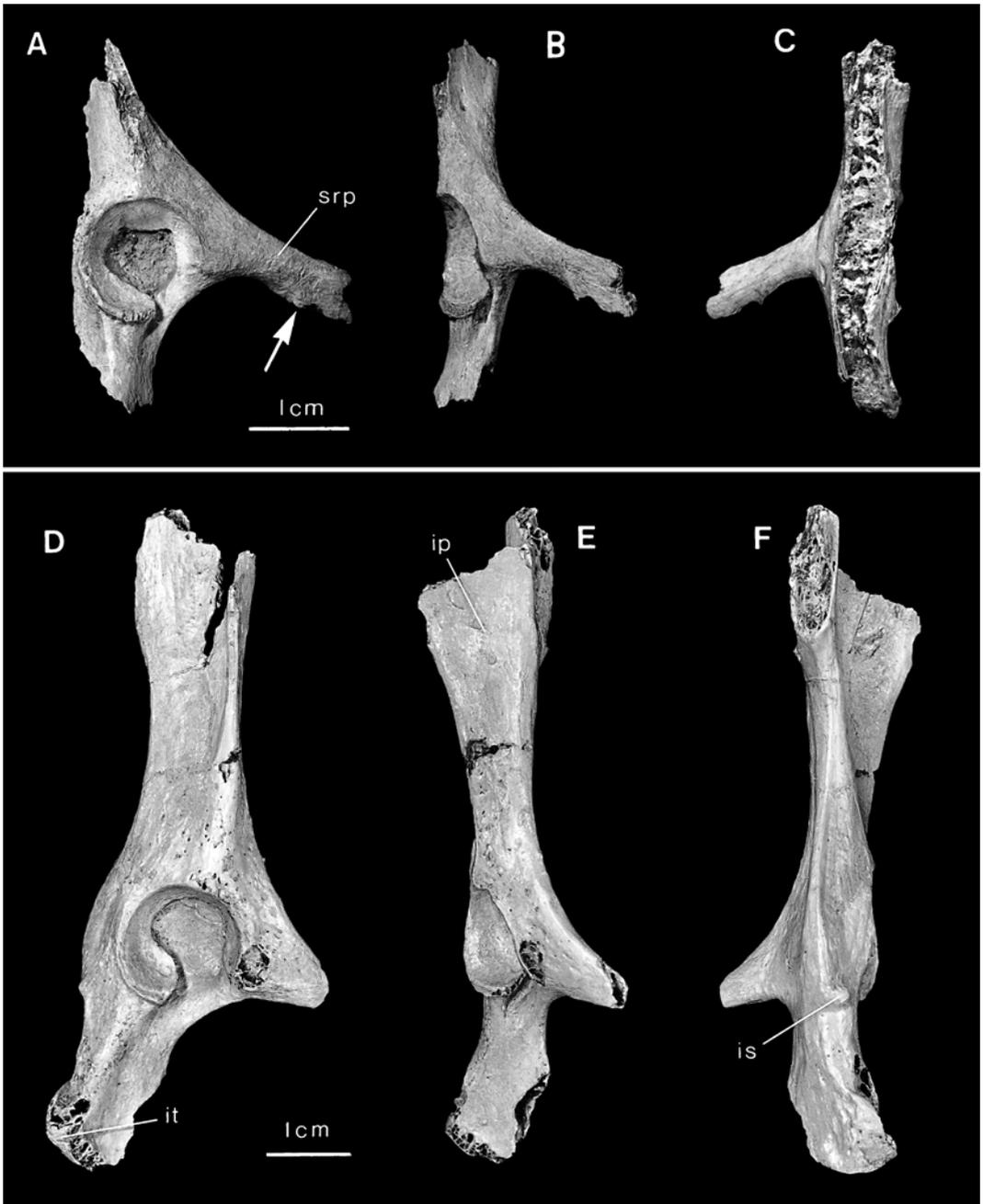
Fig. 16.   *Xenothrix mcgregori*, partial os coxae: AMNHM 268009 (R) (**top**) and AMNHM 259904 (rev.) (**bottom**) in lateral (**A, D**), ventral (**B, E**), and dorsal (**C, F**) aspects. Arrow in **A** indicates lateral margin of broken inferior pubic ramus/medial border of obturator foramen. Note that **A** and **D** are oriented slightly differently in this figure.

TABLE 9
Os Coxae: Xenothrix mcgregori, Paralouatta varonai, and Selected Living Primates, Dimensions (in mm) and Ratios [a,b]

	Xenothrix mcgregori AMNH 259904	Xenothrix mcgregori AMNH 268009	Paralouatta varonai MNHNCu 76.1036	Callicebus moloch (2)	Chiropotes satanus (2)	Ateles belzebuth (1)	Brachyteles arachnoides (1)	Lagothrix lagotricha (3)	Alouatta seniculus (3)	Cebus apella (3)	Trachypithecus pileatus (3)	Erythrocebus patas (2)	Macaca nemestrina (3)	Lophocebus albigena (3)	Theropithecus gelada (3)
Dimensions															
1. Acetabulum, depth	8.5	7.5	10.7	4.4 (4.2, 4.3)	5.7 (4.7, 6.7)	10.8	9.8	8.1 (7.6–9.0)	7.5 (7.1–8.0)	5.9 (6.2–5.6)	10.1 (8.8–11.4)	10.5 (8.3, 12.7)	13.7 (12.5–15.3)	10.8 (10.0–11.3)	15.3 (14.7–16.1)
2. Acetabulum, maximum DV diameter	13.2	12.9	18.3	8.6 (7.4, 9.8)	12.3 (10.7, 13.9)	23.3	19.8	18.0 (18.4–19.1)	16.6 (15.8–17.7)	11.2 (10.8–11.6)	17.9 (16.7–18.7)	15.9 (14.0, 17.7)	20.4 (20.0–20.7)	17.5 (16.7–18.3)	22.8 (20.3–25.0)
3. Acetabulum, maximum CC diameter	14.0	14.1	19.6e	9.2 (8.0, 10.3)	12.2 (10.9, 13.5)	24.0	20.8	18.4 (17.0–19.6)	17.3 (16.5–17.9)	11.3 (10.5–12.3)	19.2 (18.0–20.2)	16.8 (15.2, 18.4)	22.4 (21.7–23.3)	18.2 (17.0–19.3)	23.8 (21.5–25.6)
4. Ventral acetabular wall, breadth	6.3	6.2	8.5	3.4 (3.3, 3.5)	5.3 (4.6, 6.0)	13.4	7.7	8.4 (7.0–10.3)	8.3 (8.2–8.3)	5.5 (4.3–6.2)	9.9 (8.2–11.3)	7.9 (7.7, 8.1)	10.1 (13.0–15.5)	7.4 (6.5–8.1)	11.4 (10.3–12.2)
5. Dorsal acetabular wall, breadth	10.3	—	17.6e	4.7 (4.2, 5.2)	7.3 (6.5, 8.0)	14.1	11.5	10.1 (8.3–11.7)	8.0 (7.3–9.1)	7.9 (7.5–8.3)	14.1 (12.1–15.2)	15.7 (13.0, 18.3)	18.8 (17.5–19.9)	13.5 (13.2–13.7)	18.4 (18.3–18.5)
6. Medial acetabular wall, breadth	24.2	—	33.9	12.8 (10.5, 15.0)	9.0 (8.3, 9.6)	36.7	29.5	27.6 (25.5–31.8)	23.9 (20.7–27.7)	19.9 (18.6–20.6)	28.2 (25.5–31.5)	31.1 (28.4, 33.8)	39.6 (34.1–48.4)	28.9 (28.5–29.6)	34.4 (32.4–35.5)
7. Lower ilium length	32.1	—	52.1	19.8 (17.7, 21.8)	31.5 (29.5, 33.4)	55.2	53.7	41.5 (39.5–44.6)	44.5 (48.0–40.2)	31.4 (29.0–33.8)	42.8 (39.0–52.1)	43.1 (41.8, 44.4)	49.9 (46.2–52.0)	46.9 (45.7–47.5)	55.0 (52.3–57.1)
Ratios															
A. Ratio 1/3 ("acetabular size")	0.61	0.53	0.55e	0.48	0.43	0.45	0.47	0.44	0.43	0.52	0.53	0.63	0.61	0.59	0.64
B. Ratio 4/5 ("acetabular wall robusticity")	0.61	—	0.48e	0.72	0.73	0.95	0.67	0.83	1.04	0.70	0.70	0.50	0.54	0.55	0.62
C. Ratio 3/(4 + 5 + 6)	0.35	—	0.33e	0.44	0.56	0.37	0.43	0.40	0.43	0.33	0.37	0.31	0.33	0.37	0.37

[a] Measurements/ratios in italics are not precise (e = estimate, due to damage or breakage).
[b] Values cited in bold are means (or single observation, if N = 1) followed by range in parentheses.

Fig. 17. *Paralouatta varonai*, partial os coxae: MNHNCu 76.1036 (R) in lateral (**A**), ventral (**B**), and dorsal (**C**) aspects (cf. fig. 16). Because of breakage, it is difficult to appreciate the substantial width of the incomplete dorsal border of the acetablum (indicated by double-headed arrow in **A**) and the flaring iliac fossa/planum.

spectrum. (Unfortunately, the sciatic margin of AMNHM 268009 is too broken for accurate measurement.) This index was lower than in any platyrrhine specimen measured by Schultz (1969), who recorded the lowest values (0.66–0.68) for this group in female *Cebus* and *Callithrix*. However, we found in spot-checking material in the AMNHM collection that *Cebus apella* expresses indices as low as 0.52, which is similar to the lowest values in Schultz' (1969) data for cercopithecoids. Conversely, we also found that the only specimen of *Brachyteles arachnoides* available for study also yielded a relatively low index (0.67), whereas *Ateles belzebuth* and *Alouatta seniculus* yielded much higher values (0.95 and 1.04, respectively). The difference among these taxa is due not so much to variability in the thickness of the dorsal wall as to the remarkable gracility of the sparlike ventral wall in the measured specimen of *Brachyteles*.

Remarkably, ratio B may be even lower in *Paralouatta* than in *Xenothrix*. The dorsal acetabular wall measurement for MNHNCu 76.1036 had to be taken at a relatively craniad position, rostral to the damaged area on the sciatic margin (fig. 17). However, in many primates this part of the dorsal wall is actually narrower than at the figurative equator of the acetabular cup. Abrasion of the cup's margins also affects measurement, and for this reason the ratio's value (0.48) in table 9 should be treated with caution. Nevertheless, even after allowances are duly made, we conclude that ratio B is low in this specimen of *Paralouatta*, perhaps as low as the lowest scores Schultz (1969) recorded in his study for male members, species unspecified, of *Macaca* (58.4), *Papio* (55.0), and *Cercocebus* (52.8) (cf. equivalently low scores for *E. patas*, *L. albigena*, and *M. nemestrina* in table 9). It is noteworthy that, in Schultz' (1969) study,
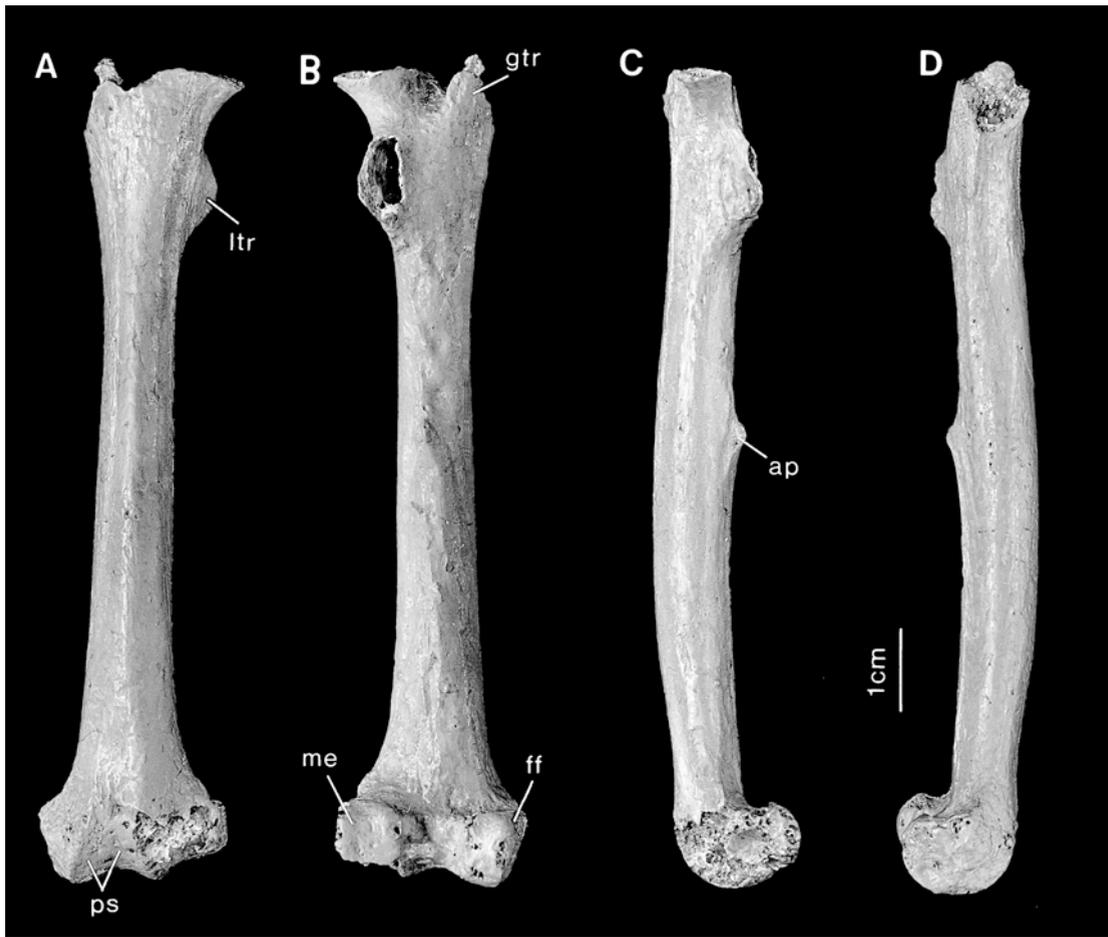
Fig. 18. *Xenothrix mcgregori,* nearly complete femur: AMNHM 259900 (**R**) in anterior (**A**), posterior (**B**), medial (**C**), and lateral (**D**) aspects (partly after MacPhee and Fleagle, 1991: fig. 4A,C).

females were consistently found to have higher indices than males within the same taxon, indicating that this ratio is affected by sexual dimorphism (Fleagle and Simons, 1979).

All of the cercopithecid genera just mentioned include species that spend an appreciable portion of their time on low substrates within the canopy, as well as on the ground. However, this ratio is not decisive for separating ground-preferring primates from all others. Although *Gorilla* and *Pan* exhibit ratios in the mid-60s, as already noted so does the one specimen of *Brachyteles arachnoides* available for this study (table 9). Furthermore,

decidedly terrestrial *T. gelada*, not included in Schultz' (1969) study, has a comparatively high index of 0.62.

According to Fleagle and Simons (1979), ratio C (table 9) is less satisfactory than ratio B for separating quadrupedalists from other locomotor types. Nevertheless, even given the suspect quality of available measurements for *Xenothrix* and *Paralouatta*, they clearly group at the low end of the spectrum. Unfortunately, other ratios of interest such as lower ilium length/ischium length could not be computed for *Paralouatta* because of specimen incompleteness.

TABLE 10
Femur: *Xenothrix mcgregori* and *Paralouatta varonai*, Dimensions (in mm) and Ratios [a,b]

	Xenothrix mcgregori AMNHM		*Paralouatta varonai* MNHNCu	
	268003	259900	76.1018	76.1019
Dimensions				
1. Length, as preserved	*66.5e*	*96.2e*	*43.5e*	—
2. Lateral condyle/trochanteric fossa length	—	91.0	—	—
3. Midshaft, MDW	7.1	8.9	*11.2e*	—
4. Head, APW	—	—	—	—
5. Medial condyle width (posterior aspect)	8.1	7.5	—	11.9
6. Lateral condyle width (posterior aspect)	5.7	5.5	—	*>8.5e*
7. Maximum distal width (of distal epiphysis)	22.1	22.2	—	*31.1*
8. Patellar surface length	10.0	9.4	—	*12.3e*
9. Lateral condyle length	12.1	12.9	—	16.5
10. Midshaft, circumference	26.3	29.5	—	—
11. Intercondylar fossa, width	6.1	6.2	—	—
Ratios				
A. Ratio 3/2 (''robusticity'')	—	0.10	—	—
B. Ratio 7/2 (''distal epiphysis size'')	—	0.24	—	—
C. Ratio 6/5 (''condylar proportionality'')	0.70	0.73	—	*0.71e*
D. Ratio 8/7 (''patellar surface size'')	0.45	0.42	—	*0.41e*
E. Ratio 9/7 (''compression of distal epiphysis'')	0.55	0.58	—	0.53

[a] Measurements 1–11 as in MacPhee and Fleagle (1991).
[b] Measurements/ratios in italics are not precise (*e* = estimate, due to damage or breakage).

FEMUR

Xenothrix AMNHM 268003

The highly distinctive femur of *Xenothrix* was originally described on the basis of AMNHM 259900, a relatively intact specimen from Long Mile Cave (MacPhee and Fleagle, 1991; fig. 18; table 10). This specimen presents an odd combination of features: some are primatelike, such as large greater and lesser trochanters, but others are rare or absent in other members of the order, such as the ''fourth'' trochanter or adductor process on the posterior aspect of the bone. As with the os coxae, functionally significant features of the femur suggests that *Xenothrix* was a slow, quadrupedal climber with no obvious adaptations for more energetic forms of locomotion such as leaping.

The Somerville specimen (AMNHM 268003; fig. 19) is much less complete, although for the parts represented it is actually in a better state of preservation. The femur was found in a small pile of bones on the surface of an exposed ledge on the north side of the large pit fall that represents the entrance to the cave (for a plan, see Fincham, 1997). It is thus possibly very recent in age. No additional primate elements were found among these other bones, which seem to have fallen or weathered out of openings (?owl roosts) situated about a meter above the ledge.

The shaft of the new specimen is somewhat more gracile than that of AMNHM 259900. This feature tends to emphasize the relative bulk of the condyles (fig. 19), which are essentially intact. As noted by MacPhee and Fleagle (1991) on the basis of the less complete Long Mile specimen, the femoral condyles of *Xenothrix* are large, mediolaterally compressed, and define between them a broad, rather flat patellar surface. The area giving rise to the adductor process seen in AMNHM 259900 is not preserved.

For completeness, it may be briefly noted that no additional examples of femora resembling those from Coco Ree Cave (UF 40097) and Sheep Pen (UF 58350) in central

Fig. 19. *Xenothrix mcgregori*, distal femur: AMNHM 268003 (R) in anterior (**A**) and distal (**B**) aspects, showing disproportion of medial and lateral condylar articular surfaces.

and northern Jamaica have been found in recent years (see Ford and Morgan, 1986; Ford 1990; see also MacPhee and Fleagle, 1991: their fig. 2). These specimens—both poorly preserved proximal femora—are of considerable interest because Ford described them as possessing primatelike features. MacPhee and Fleagle (1991) concluded that they differed too greatly from AMNHM 259900 to warrant their placement in the same

hypodigm, but no progress has been made in finding a better attribution for them.

Paralouatta MNHNCu 76.1018 and 76.1019

Proximal femur MNHNCu 76.1018 is badly battered (fig. 20; table 10). Fresh breaks on the specimen's shaft indicate that the bone was probably broken during the course of recovery, although no diaphyseal fragments in the collection can be precisely fitted to the specimen. The head and greater trochanter are missing, evidently because they were still in the epiphyseal stage at the time of death. The lesser trochanter is present but damaged. The shaft quickly tapers distal to the position of the trochanters, as in platyrrhines generally, but too little is left to allow a good estimate of robusticity or midshaft circumference. The femoral head of *Paralouatta* was obviously large and spherical, judging from the dimensions of the acetabular cup in MNHNCu 76.1036 (table 9, ratio A). Although the neck of MNHNCu 76.1018 is partially preserved, its angulation in relation to the shaft cannot be reliably established.

The distal epiphysis MNHNCu 76.1019 (fig. 21), also from an immature animal, pairs well with the proximal femur in terms of relative size, but nothing associates these specimens beyond the fact that they were found in the same chimney fill. As in *Xenothrix* (and many other mammals) there is a small facet on the posterior articular surface of the lateral condyle for a sesamoid, the lateral fabella. The anterior patellar surface, which is deeper than in *Xenothrix*, has lost some material just where the craniad border of the epiphysis would have met the diaphysis; however, the measurement (12.3 mm) of this feature is unlikely to be greatly in error.

The lateral condyle is damaged in MNHNCu 76.1019, and therefore condylar width as defined by MacPhee and Fleagle (1991) cannot be taken directly on this specimen. However, one's visual impression is that the lateral condyle was relatively larger than in *Xenothrix*, and that therefore the condylar proportionality ratio was actually higher than in the Jamaican monkey (see MacPhee and Fleagle, 1991, for additional comparative data and discussion of ratios).
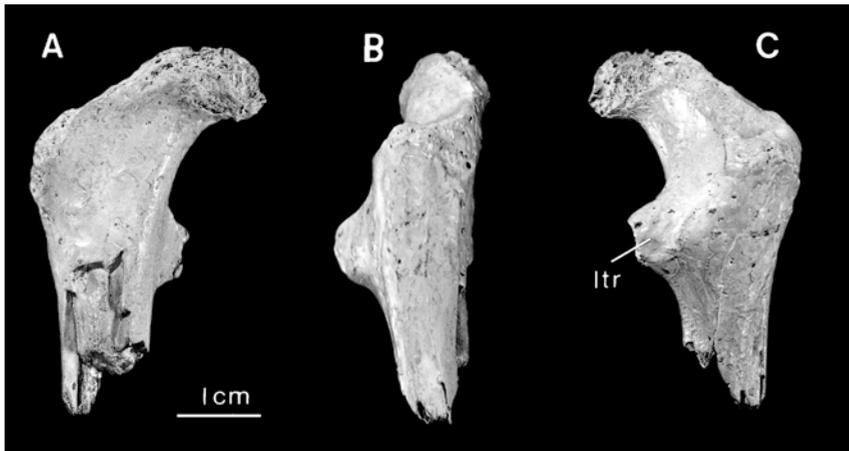
Fig. 20. *Paralouatta varonai*, proximal femur: MNHNCu 76.1018 (L [rev.]) in anterior (**A**), lateral (**B**), and posterior (**C**) aspects.

Functional Considerations

HUMERUS/FEMUR PROPORTIONALITY: The nearly complete humerus AMNHM 268008 and femur AMNHM 259900 of *Xenothrix mcgregori* are from different localities and therefore represent different adults. Nevertheless, assuming that MacPhee and Fleagle's (1991) estimate of the length of the Long Mile femur

Fig. 21. *Paralouatta varonai*, distal epiphysis of femur: MNHNCu 76.1019 (L [rev.]) in distal (**A**) and medial (**B**) aspects.

(~99 mm) is reasonably accurate, and additionally assuming that these two specimens are representative, then femur length in *Xenothrix* was probably only slightly greater (+5%) than humerus length, i.e. the bones were subequal. In New World suspensory taxa, the humerus tends to be slightly longer (*Brachyteles arachnoides, Ateles belzebuth*) than the femur or the bones are subequal (*Lagothrix lagotricha*). In *Alouatta seniculus* the femur is slightly longer. If humerus/femur proportionality were similar to that inferred for *Xenothrix*, then extrapolation from the length of the nearly complete humerus MNHNCu 76.1010 would produce an estimated femur length of ~150 mm for *Paralouatta*, which is similar to *Alouatta seniculus*.

DISTAL EPIPHYSIS ANTEROPOSTERIOR COMPRESSION AND CONDYLAR PROPORTIONALITY: As noted, the architecture of the femoral distal epiphysis is similar in *Xenothrix* and *Paralouatta* in that the distal epiphysis is anteroposteriorly compressed and the condyles are asymmetrical. These are common features of arboreal quadrupeds and climbers. However, in the Antillean monkeys the degree of compression is not as extreme as it is in the suspensory atelines and pitheciines. Arboreal quadrupeds, and to a greater degree terrestrial quadrupeds, have rather tall femoral condyles and narrow patellar grooves (MacPhee and Fleagle, 1991; Meldrum, 1993). The intact portions of the condyles of *Paralouatta* are
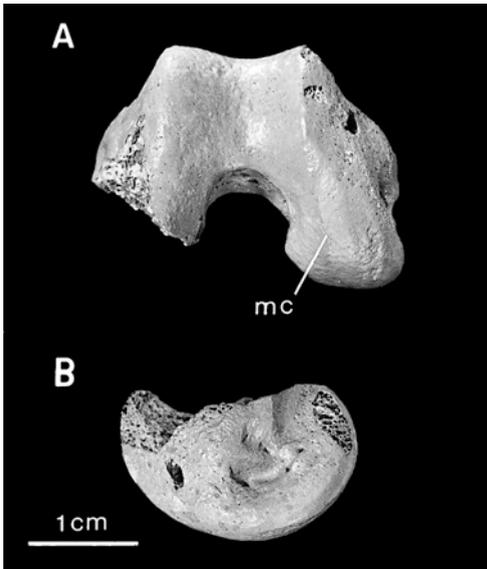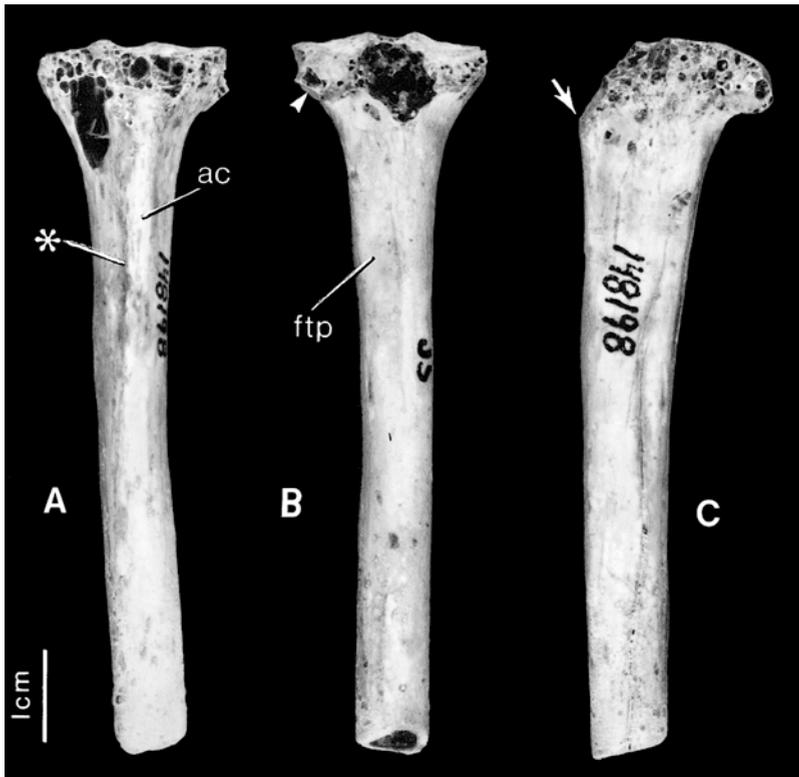
Fig. 22.   *Xenothix mcgregori*, proximal tibia: AMNHM 259903 (L), in anterior (**A**), posterior (**B**), and lateral (**C**) aspects. Asterisk in **A** marks site of insertion of sartorius, gracilis, and semimembranosus mm. Pointer in **B** indicates facet for head of fibula. Arrow in **C** draws attention to projection and high proximal position of tibial tuberosity. Specimen previously numbered AMNHM 148198, the accession number of type jaw (after MacPhee and Fleagle, 1991: fig. 9B–D.)

noticeably taller than those of *Xenothrix*, and the patellar groove has greater relief and depth. However, it is not obvious how to interpret the significance of patellar groove breadth, as it is wider in pitheciines (chiefly climbing locomotion) than it is in atelines (chiefly suspensory locomotion) (Lockwood, 1999). In overall proportions of the distal femur, xenotrichins resemble Miocene platyrrhines such as *Carlocebus* and *Homunculus* (Meldrum and Kay, 1997).

TIBIA

Xenothrix AMNHM 259903

Two proximal tibiae from the Long Mile faunal collection (the more complete of which is illustrated in fig. 22) were assigned to *Xenothrix* by MacPhee and Fleagle (1991).

No additional discoveries have been made in recent years. As preserved the incomplete shafts of the Long Mile specimens are comparatively straight. The medial condylar articular facet is larger in area than the lateral, which is consistent with the asymmetry of the femoral condyles in *Xenothrix*. According to MacPhee and Fleagle (1991), certain features (size and prominence of scars for hamstrings and tibial tuberosity) suggest an animal that was capable of powerful flexion and extension at the knee. However, because of the inferred overall shortness of the hind limb and presence of features indicating slow climbing, exceptional leaping ability is unlikely.

Paralouatta MNHNCu 76.1034

MNHNCu 76.1034 is the distal end of a right tibia, with half (or less) of the shaft

TABLE 11

Tibia: *Paralouatta varonai*, *Antillothrix bernensis*, and **Selected Living Primates, Dimensions (in mm) and Ratio**[a,b,c]

Dimensions	*Paralouatta varonai* MNHNCu 76.1034	*Antillothrix bernensis* USNM 254682[d]	*Callicebus moloch* (3)	*Chiropotes satanas* (2)	*Ateles belzebuth* (1)	*Brachyteles arachnoides* (1)	*Lagothrix lagotricha* (3)	*Alouatta seniculus* (3)	*Cebus apella* (3)	*Trachypithecus pileatus* (3)	*Erythrocebus patas* (3)	*Macaca nemestrina* (3)	*Lophocebus albigena* (3)	*Theropithecus gelada* (3)
1. Length	—	—	**96.7** (86.6–109.5)	**129.2** (119.4, 138.9)	**194.0**	**192.0**	**162.4** (143.0–173.9)	**149.6** (138.8–157.8)	**118.0** (114.2–122.1)	**166.3** (159.4–177.2)	**169.3** (152.5–177.2)	**206.3** (199.0–210.0)	**187.6** (175.7–194.0)	**202.0** (178.0–214.0)
2. Malleolaus, greatest APW[c]	*10.1*	**7.0**	**4.9** (3.8–5.8)	**7.2** (6.4, 8.0)	**11.7**	**10.4**	**9.2** (8.6–9.6)	**8.5** (7.5–9.5)	**6.9** (6.1–7.4)	**11.5** (11.0–12.5)	**11.9** (11.0–12.5)	**14.5** (12.1–16.0)	**11.4** (10.2–12.3)	**11.4** (9.0–14.2)
3. Distal end, APW	*14.2*	**11.8**	**7.4** (7.0–8.1)	**9.6** (8.7, 10.4)	**15.0**	**13.5**	**12.0** (10.7–12.9)	**11.4** (9.8–13.1)	**9.2** (8.9–9.4)	**15.1** (13.3–18.1)	**15.8** (14.0–17.6)	**16.6** (16.4–16.9)	**14.5** (13.6–15.6)	**17.1** (15.0–18.3)
4. Distal end, MLW	*20.5e*	**15.2**	**8.4** (7.5–8.9)	**13.6** (12.4, 14.7)	**27.2**	**21.4**	**20.1** (19.6–20.4)	**18.3** (15.0–20.0)	**12.8** (12.6–13.1)	**17.8** (16.1–19.6)	**18.4** (17.5–20.1)	**21.9** (20.8–22.5)	**18.2** (16.4–19.5)	**23.3** (20.1–25.4)
5. Shaft, minimum APW	*9.8*	**9.0**	**4.5** (3.6–5.1)	**5.5** (5.0, 5.9)	**9.9**	**7.7**	**8.1** (7.0–9.0)	**7.5** (6.5–8.6)	**5.7** (5.6–5.9)	**9.5** (8.8–10.1)	**9.5** (8.1–10.9)	**11.5** (9.9–12.9)	**10.0** (8.8–10.4)	**12.4** (11.3–13.4)
6. Shaft, minimum MLW[f]	*8.1*	**7.2**	**3.8** (3.5–4.4)	**5.1** (4.5, 5.7)	**10.2**	**7.6**	**8.1** (7.1–8.8)	**7.3** (6.0–8.4)	**5.1** (4.7–5.3)	**8.5** (8.0–8.9)	**8.4** (7.6–9.5)	**10.0** (9.0–10.5)	**8.1** (7.6–8.6)	**11.4** (10.8–12.5)
Ratio														
A. 1/2 ("distal end proportion")	*0.69e*	**0.78**	0.88	0.71	0.55	0.63	0.60	0.62	0.72	0.85	0.86	0.76	0.80	0.73

[a] Measurements in italics are not precise (e = estimate, due to damage or breakage).
[b] Values cited in bold are means (or single observation, if $N = 1$) followed by range in roman.
[c] For measurements of proximal tibial specimens of *Xenothrix mcgregori*, see MacPhee and Fleagle (1991).
[d] Cast.
[e] Measured coplanar with tibiotalar articular surface.
[f] Minimum AP width found by sliding calipers along lower third of diaphysis until minimum found; minimum ML usually higher (middle third).
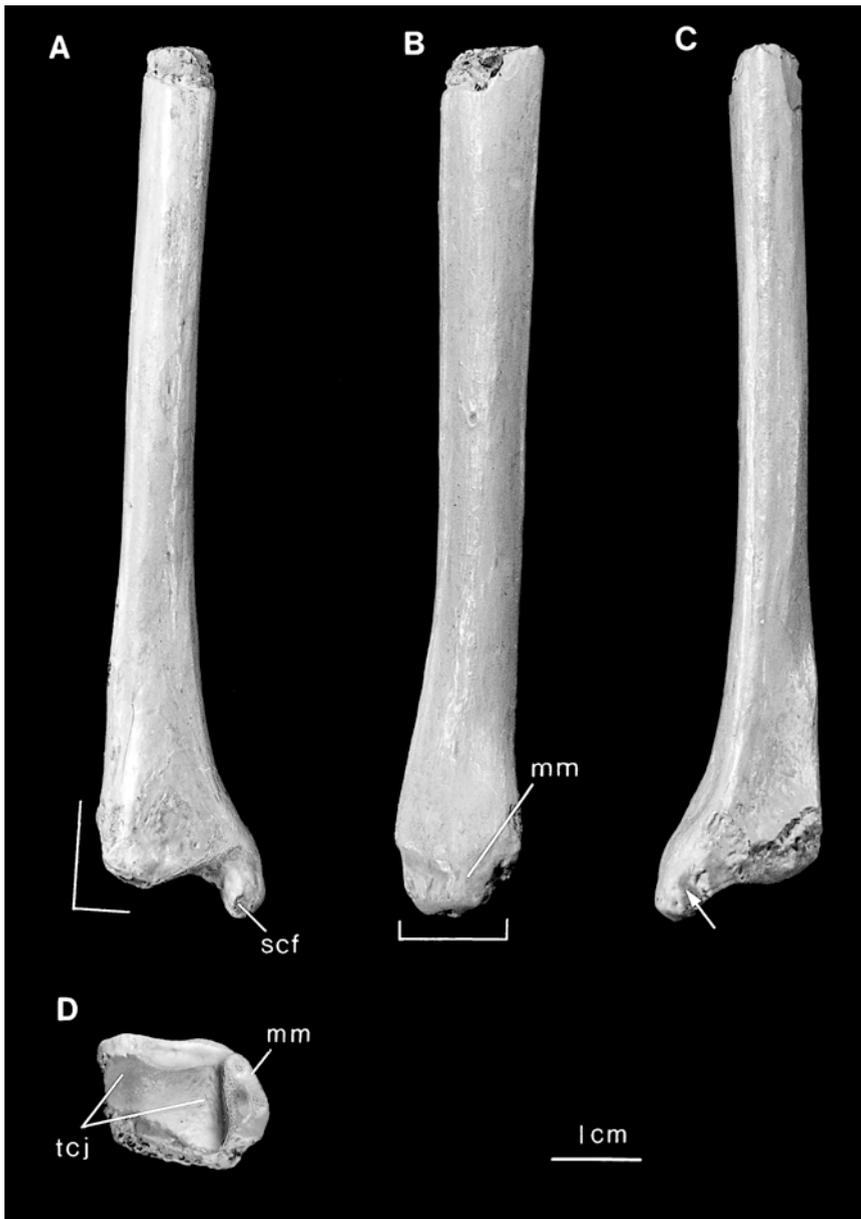
Fig. 23.   *Paralouatta varonai*, distal tibia: MNHNCu 76.1034 (R), in anterior (**A**), medial (**B**), posterior (**C**), and distal (**D**) aspects. Note great anteroposterior breadth; comparatively straight but somewhat abraded interosseous border (suggested by right angle in **A**); and "square" medial malleolus (bracket in **B**). In **C**, groove (arrow) is an artifact, not a channel for tendon of tibialis posterior m.

preserved (fig. 23; table 11). The posterior and lateral aspects of the distal end are damaged, including the area where the fibular notch was situated. The interosseous border is faintly indicated, but otherwise there are no strong lines or muscle markings on the shaft. The anterior "border" is smoothly rounded rather than sharp, as in platyrrhines generally. The

Fig. 24. *Antillothrix bernensis*, distal tibia: USNMM 254682 (R [cast]) in anterior (**A**), medial (**B**), and distal (**C**) aspects. In profile, distal end is laterally expanded (as suggested by obtuse angle in **A**) rather than straight as in *Paralouatta* (cf. fig. 23A). Medial malleolus is large but "triangular" (acute angle in **B**) in medial profile like that of many anthropoids (cf. fig. 25). Arrow points to large furrow for tendon of tibialis posterior m.

diaphysis was probably relatively straight, as it is in most but not all platyrrhines (fig. 25B, F, J), although with only half of the element available this point cannot be settled.

The medial aspect of the distal tibia of *Paralouatta* is distinctive: the shaft is quite massive anteroposteriorly, and terminates distally in a wide, blunt malleolus (fig. 23B). The anterolateral aspect of the malleolus terminates in a poorly defined facet (fig. 23A) for the cotylar fossa of the talus. In primates generally the malleolus tends to be pyramidal rather than rectangular (fig. 25), but the specimens of *Ateles belzebuth* (fig. 25F) and *Lagothrix lagotricha* (fig. 25J) in the comparative set show some approximation to the condition in *Paralouatta*.

Note also that, in posterior view (fig. 23C), the tibia's lateral surface is remarkably straight compared to tibiae of other large-bodied platyrrhines such as *Ateles* and *Lagothrix* (fig. 25G, K), in which the lateral surface of the distal end is slightly projecting. The squared-off appearance of the region of the fibular facet resembles the condition in many catarrhines (Hershkovitz, 1988; cf. *Lophocebus*, fig. 25O). This arrangement may have allowed the distal moiety of the fibular shaft to be closely approximated to the facing surface of the tibia (cf. Meldrum and Kay, 1997). However, it is also clear that, unlike *Lophocebus*, the lateral margin of the distal articular surface is not deeply notched by the fibular facet in *Paralouatta* (fig. 23D). The significance of this is uncertain, because according to Ford (1986a) Old and New World monkeys differ markedly in the size and depth of the fibular facet.

Finally, the malleolus bears a small excavation (fig. 23C) where one might expect a groove for the tendon of tibialis posterior m. (as in *Cebus*, fig. 25C). However, the floor of the groove is rough rather than smooth, and the feature itself is oriented at an angle impossible for the tendon to assume. Bone lateral to this area is badly abraded and it is not clear whether there were grooves for this last muscle or flexor digitorum longus m.; on the whole it seems doubtful that there were.

Antillothrix USNMM 254682

Ford (1986a) described the Samaná tibia (fig. 24) in some detail and compared it to a wide range of other primates, and in regard to basic anatomical details we are in agreement with most of her observations. However, like Hershkovitz (1988) we are not convinced that the morphology of the distal tibia supports a strong case for callitrichid affinities. Indeed, of the numerous tibial characters that Ford (1986a, 1986b) considered in her cladistic analysis, only three strongly implied a callitrichid connection, and two of these are variable within the latter group. The remaining character, strong development of a bony flange for conducting the tendon of tibialis
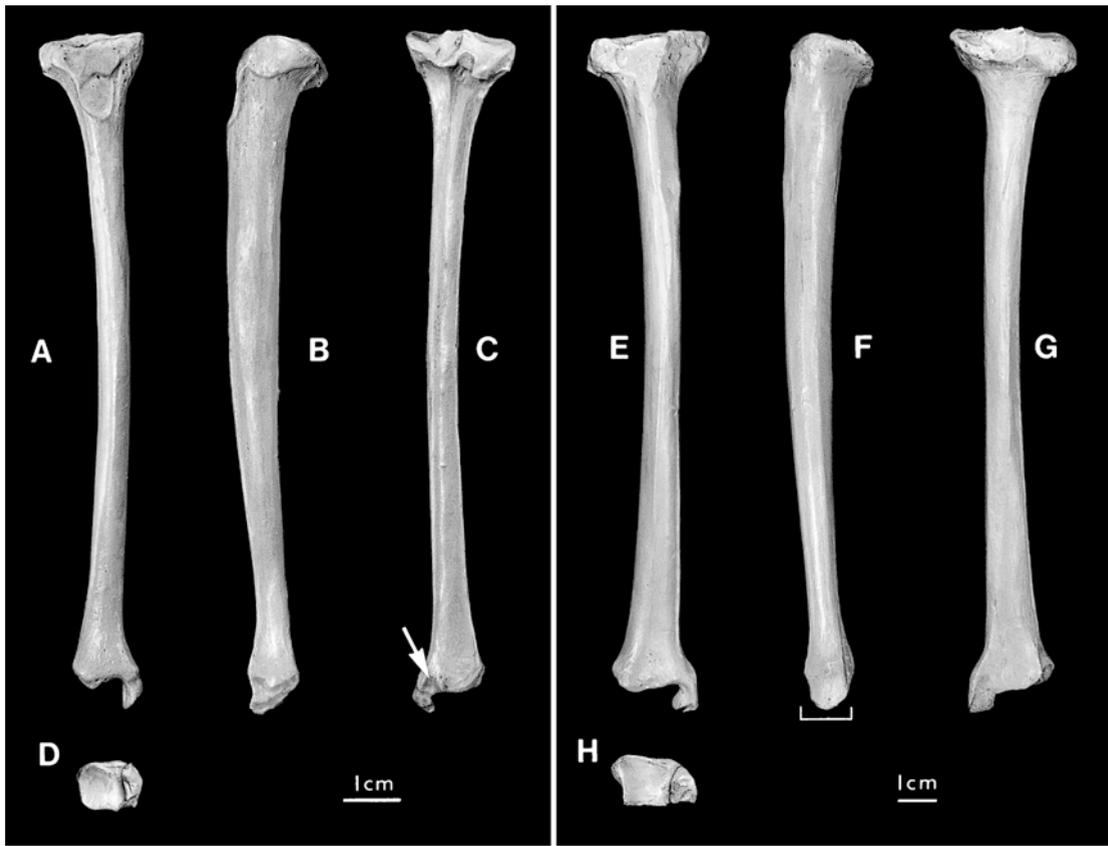
Fig 25. Comparative set, right tibia in anterior, medial, posterior, and distal aspects: *Cebus apella* AMNHM 209927 (**A–D**); *Ateles belzebuth* AMNHM 30192 (**E–H**).

posterior m. into the foot, is produced to about the same degree in the Samaná tibia and *Saguinus* (which are shown as sister taxa in Ford's cladogram). However, this feature, which is not uncommon among mammals generally (MacPhee, 1994), shows about the same amount of development in *Callicebus*. As already noted the flange is absent in *Paralouatta*, making it further doubtful that this is a feature of much systematic valency. Hershkovitz (1988: 383) concluded that the Samaná tibia represented "a platyrrhine distinct from known living forms", possibly the same species as *Antillothrix bernensis*. Although we favor the same conclusion, it is unlikely that there will be any consensus until there is new material to evaluate.

Both *Paralouatta* MNHNCu 76.1034 and the Samaná tibia (fig. 24) are notably robust for their respective sizes, as far as this can be judged, but they differ in several details (e.g., medial malleolus in *Antillothrix* is pyramidal in medial aspect, as in anthropoids generally, whereas in *Paralouatta* it is more massive and rectangular). The cotylar facet is well developed in both.

Functional Considerations

FIBULAR APPRESSION: Appression of the distal parts of the tibia and fibula occurs in several small and medium-sized platyrrhines (*Saimiri*, *Aotus*, *Callithrix*, *Cebuella*, and *Pithecia*) but not in larger taxa (Meldrum and Kay, 1997). The appression of the distal fibula to the tibia of *Paralouatta*, if it occurred, suggests together with other features that the distal tibiofibular syndesmosis may have been extensive. This arrangement, combined with the equally massive medial mal-
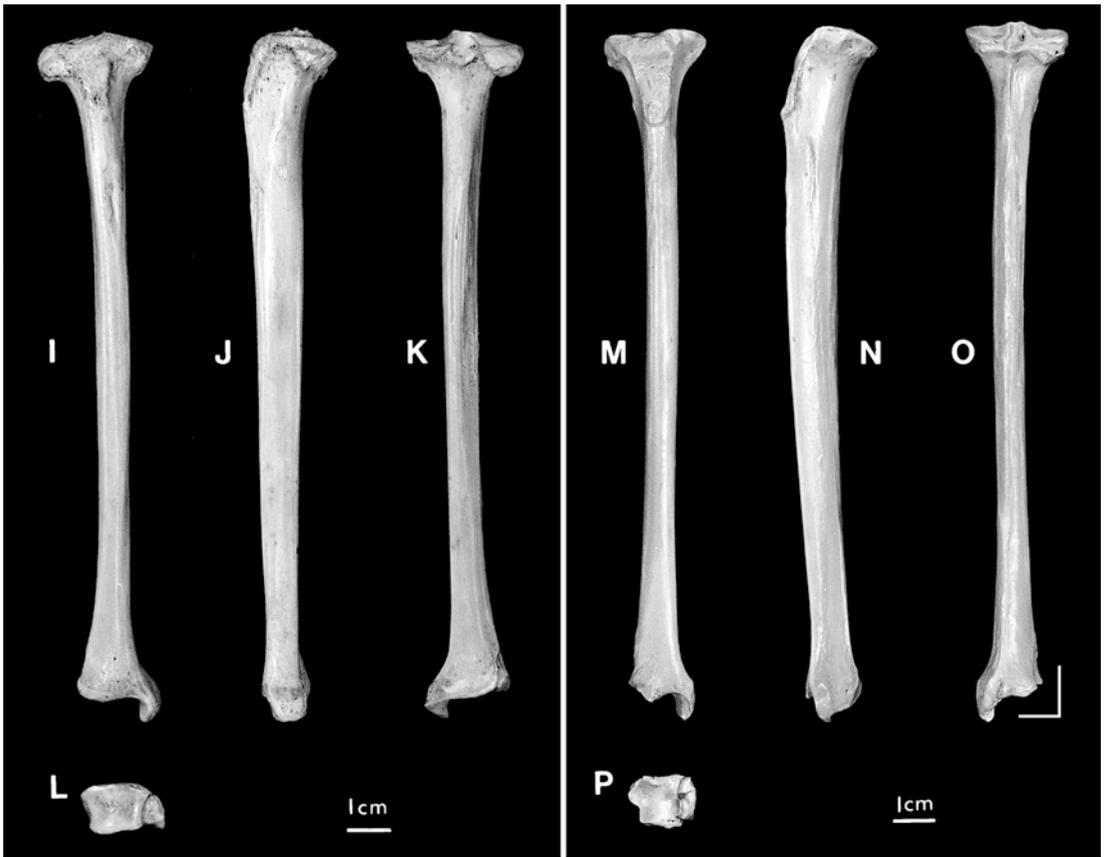
Fig. 25. (Continued). *Lagothrix lagotricha* AMNHM 70404 (**I–L**); *Lophocebus albigena* AMNHM 52627 (**M–P**). Note comparatively blunt medial malleolus in *Ateles* (bracket in **F**) and squared-off lateral border of distal tibial shaft in *Lophocebus* (right angle in **O**). Note difference in scales.

leolus, would have served to strongly resist dislocation by limiting lateral and rotational movement of the talocrural joint. Behaviorally, this morphology is correlated with frequent leaping in small-bodied primates, such as *Saimiri*, or with arboreal or terrestrial quadrupedalism in larger-bodied primates (Meldrum and Kay, 1997). Although the fibula of *Paralouatta* is unknown, one might predict from the size of the lateral surface of the talocrural joint (see below) that the fibular malleolus must have been large as well. The presence of some but not all of these features in large atelines (cf. fig. 25) may indicate that the correlation is with BM.

CHEIRIDIA

A number of distinctive mammalian hand and foot bones were collected in the same caves that yielded remains unquestionably attributable to *Paralouatta*. After careful comparison of these elements to their homologs in other members of the Quaternary fauna, both living and extinct, we are persuaded that they probably belong to the Cuban monkey. For some elements, like the tarsals and distal phalanges, there is not much doubt because they strongly resemble those of other primates. In other cases judgment is more difficult (e.g., proximal and middle phalanges).

No carpals have been yet been recovered for any Antillean primate, and the few tarsal elements available (for *Paralouatta* only) are battered and not especially informative. Accordingly, descriptions and analyses in this section will be brief except for the discussion of digital ray length, which has some functional

significance. Measurements for cheiridial elements can be found in tables 12 and 14.

Paralouatta MNHNCu 76.1037 and 76.3059 (Talus)

Two tali have been referred to *Paralouatta*: one is the partial talus MNHNCu 76.1037 of *Paralouatta varonai* from Cueva Alta (fig. 26A–D); the other is MNHNCu 76.3059 from the Early Miocene locality of Domo de Zaza, which MacPhee et al. (2003) recently made the holotype of a second species, *P. marianae* (fig. 26E–H). These authors noted that the two specimens differ only slightly— a remarkable point, given that 17–18 Ma allegedly separate them (see Introduction)— and for the characters of interest here they are nearly identical. Because MNHNCu 76.1037 is quite incomplete, we feel that it is justified to utilize the Miocene fossil as our basis for genus-level comments in this section.

In an earlier paper, MacPhee and Iturralde-Vinent (1995) concluded that there were no strong matches for the talus of *Paralouatta* among living platyrrhines. In particular, they noted that large-bodied platyrrhines (living atelines and *Alouatta*) differ sharply from *Paralouatta* in possessing a "wedged" trochlear articular surface with overall low trochlear relief. This morphology helps insure maximum mobility at the talocrural joint; by
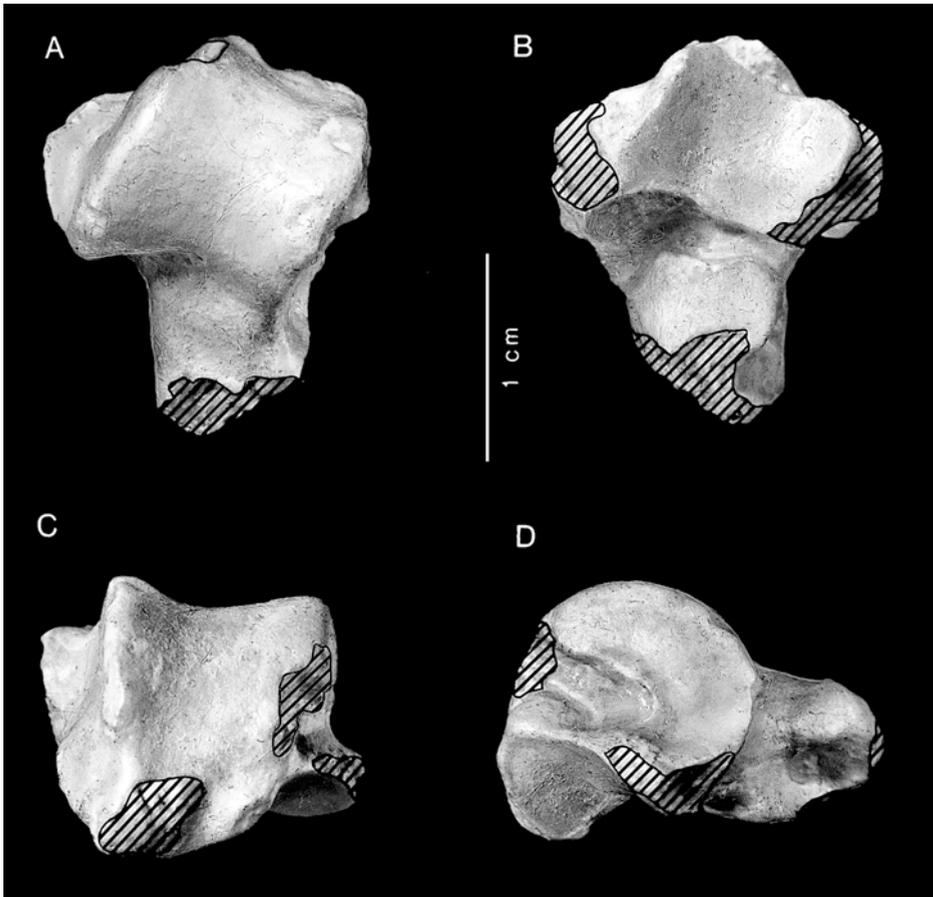

Fig. 26.   *Paralouatta*, partial tali: *P. varonai* MNHNCu 76.1037 (R) in dorsal (**A**), ventral (**B**), posterior (**C**), and lateral (**D**) aspects; *P. marianae* MNHNCu 76.3059 (R) in dorsal (**E**), ventral (**F**), posterior (**G**), and distal (**H**) aspects. Hatchure indicates broken surfaces. To same scale.

TABLE 12
Talus: *Paralouatta varonai*, Dimensions (in mm) [a,b]

MNHNCu	L	HDW	HDH	ACF	PCL	IO	PCW	TW	TH	ATW	PTW	W
76.3059	20.0	*9.7e*	*7.3e*	12.7	9.5	3.0	5.5	11.7	10.8	9.2	9.1	16.5
76.1037	—	—	—	—	*10.0e*	3.1	6.9	*12.0e*	11.9	10.5	*10.5e*	*16.9e*

[a] Measurements in italics are not precise (*e* = estimate, due to damage or breakage).

[b] For measurement acronyms, see figure 27.

contrast, the talus of *Paralouatta* seems to have been built for stability (MacPhee and Iturralde-Vinent, 1995).

Paralouatta tali also present a definite if shallow cotylar fossa fronting a lengthy articular surface for the medial malleolus (fig. 26A, C), thereby providing firm seating for the latter. The limits of the fossa are difficult to make out because of damage to the neck in both specimens. Talar cotylar fossae are insignificant (when present at all) in larger platyrrhines such as *Ateles*, *Chiropotes*, and *Alouatta* but are well developed in Old World monkeys such as *Theropithecus* and *Lophocebus*. According to Gebo and Sargis (1994), there is a similar contrast (but on a lesser scale) between moderately terrestrial *Cercopithecus lhoesti* and highly arboreal *C.*
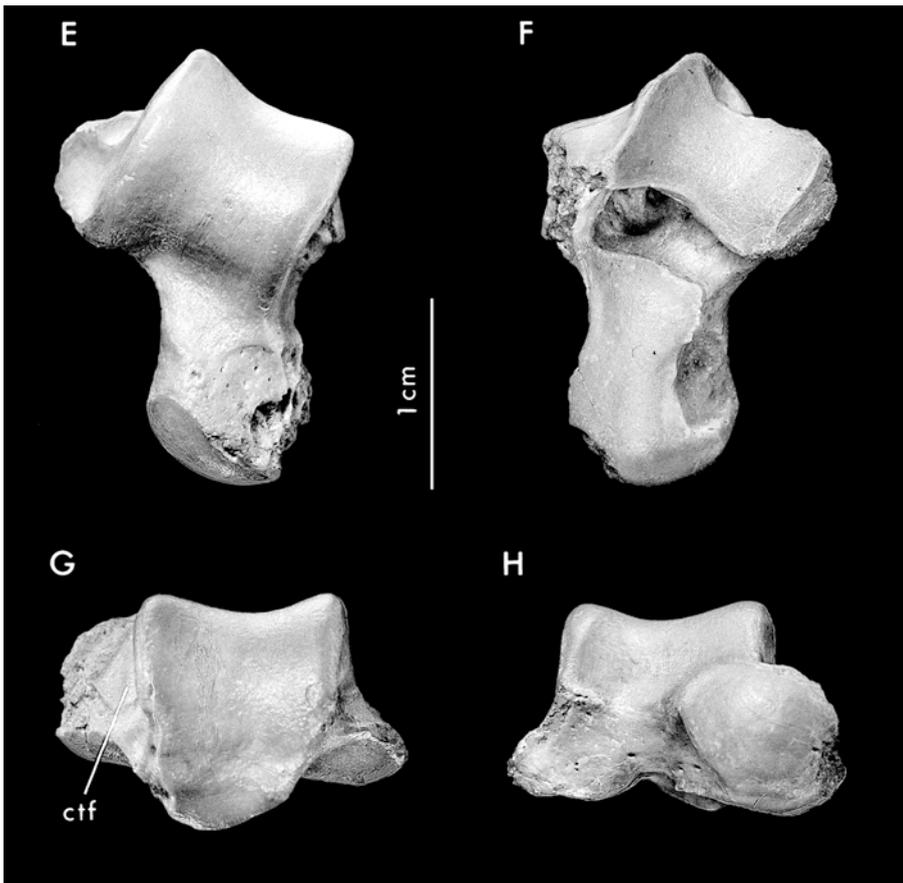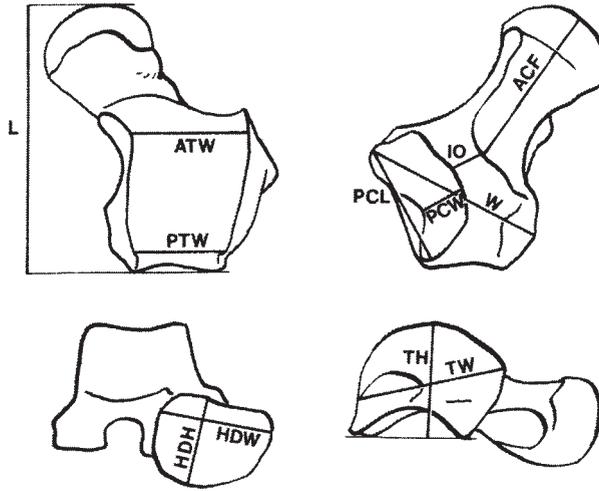

Fig. 26. Continued.

Fig. 27.   Twelve morphometric measurements used in principal components analysis (see fig. 29). Key: ACF, anterior calcaneal facet; ATW, anterior trochlear width; HDH, head height; HDW, head width; IO, interosseus space between the anterior and posterior calcaneal facets; L, length; PCL, posterior calcaneal facet length; PCW, posterior calcaneal facet width; PTW, posterior trochlear width; TH, trochlear height; TW, trochlear width; W, width.
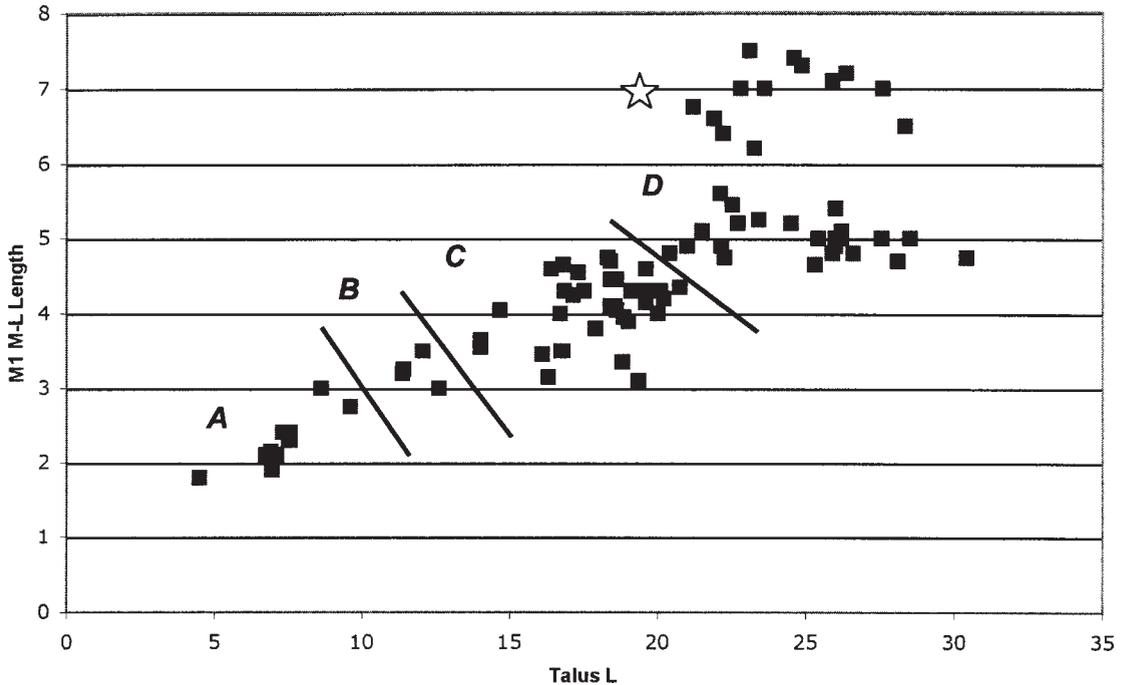

Fig. 28.   Bivariate plot of the mesiodistal length of mandibular M1 versus greatest length of the talus perpendicular to the tangent of the posterior tubercles. Groupings are empirical and have the following content: **A**, *Cebuella*, *Callithrix*, *Saguinus*, *Callimico*, *Leontopithecus*; **B**, *Saimiri*, *Aotus*; **C**, *Callicebus*, *Pithecia*, *Chiropotes*, *Cacajao*, *Cebus*; **D**, *Lagothrix*, *Alouatta*, *Brachyteles*, *Ateles*. The position of *Paralouatta marianae* (MNHNCu 76.3059) is indicated by star. See text for discussion.
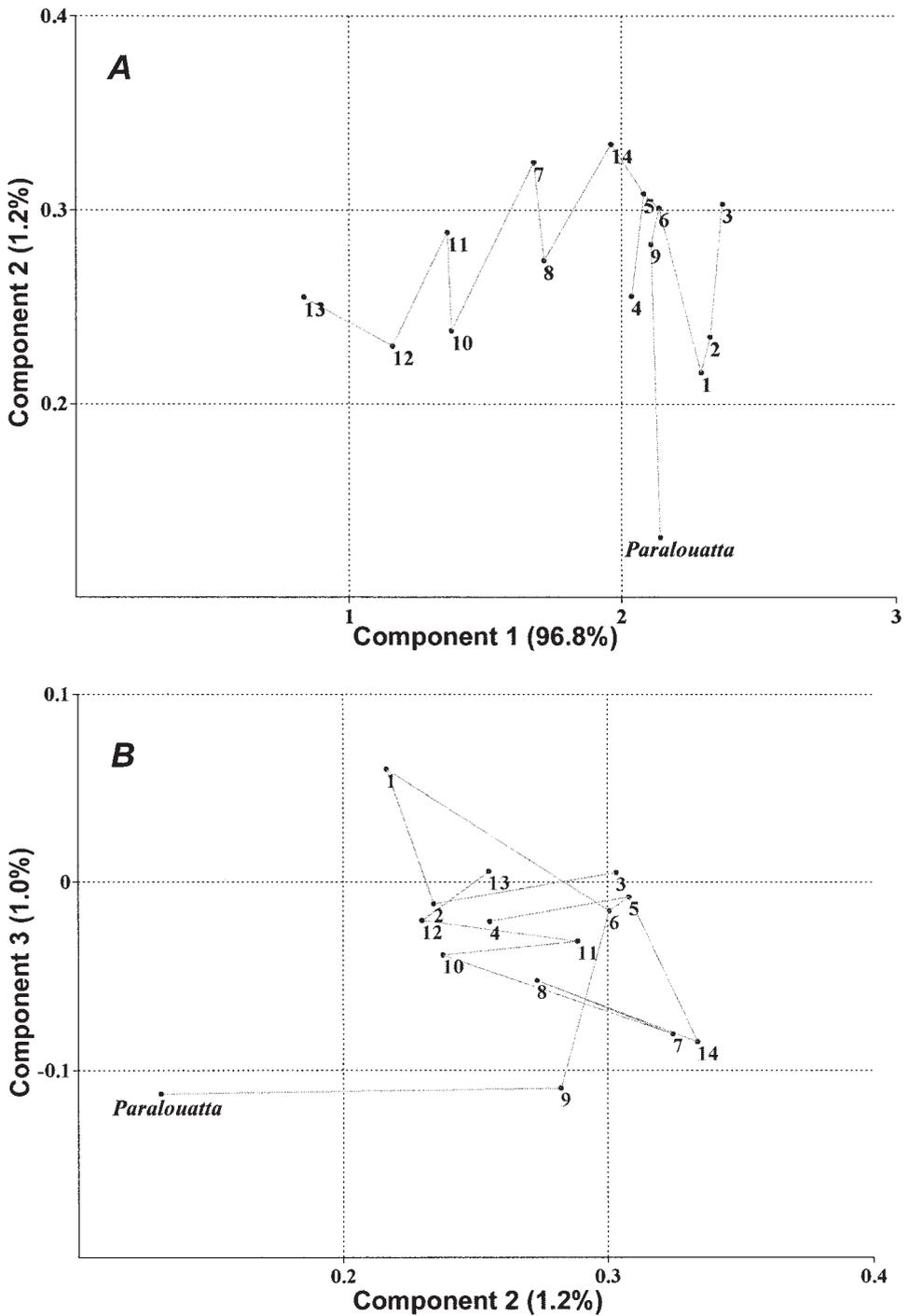
Fig. 29.   Principal components analyses (**A**, **B**) of 12 measurements of tali in a sample of extant platyrrhine genera plus *Paralouatta*. Key: **1**, *Ateles*; **2**, *Lagothrix*; **3**, *Alouatta*; **4**, *Pithecia*; **5**, *Chiropotes*; **6**, *Cacajao*; **7**, *Aotus*; **8**, *Callicebus*; **9**, *Cebus*; **10**, *Leontopithecus*; **11**, *Saguinus*; **12**, *Callithrix*; **13**, *Cebuella*; **14**, *Saimiri*. See text for discussion.

TABLE 13
Talus: Principal Component Loadings

Variable[a]	1	2	3
L	0.5235	0.6305	0.6305
HDW	0.2173	−0.2427	−0.2427
HDH	−0.2175	0.2412	0.2412
ACF	0.2765	0.1628	0.1628
IO	0.06522	−0.1388	−0.1388
PCL	0.2833	0.087	0.087
PCW	0.09695	−0.1509	−0.1509
TW	0.3153	0.04539	0.04539
TH	0.2189	0.05175	0.05175
ATW	0.2927	−0.2607	−0.2607
PTW	0.2101	−0.5192	−0.5192
W	0.4289	−0.2591	−0.2591

[a] See figure 27.

mitis. Previously, it was assumed (e.g., MacPhee, 1994) that the cotylar fossa was limited to cercopithecoids, in which it is normally well defined. Very deep cotylar fossae, not to be compared with the modest versions in primates under discussion here, occur in graviportal terrestrial mammals as disparate as the bear *Ursus*, the giant rodent *Amblyrhiza*, and the bibymalagasy *Plesiorycteropus* (MacPhee, 1994; see also Zack et al., 2005).

To better characterize the distinctions of the *Paralouatta* talus, we took 12 morphometric measurements on MNHNCu 76.3059 and the tali of 14 other platyrrhine genera (fig. 27; see tabulated data presented by Meldrum [1990]). Size-adjusted variates were created by scaling
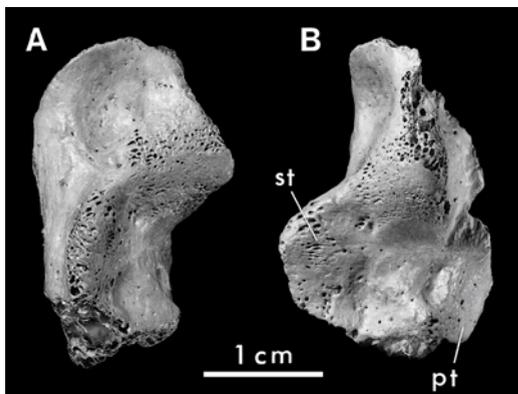

Fig. 30. *Paralouatta varonai*, partial calcaneus: MNHNCu 76.1020 (L) in medial (**A**) and dorsal (**B**) aspects.

to the sum of talar head width and height. *Paralouatta* stands somewhat apart from the main trend linking talar size to m1 mesiodistal length in platyrrhines (although it is closest to uakaris and woolly monkeys), suggesting that it has a relatively large m1 for its talar length (fig. 28).

Principal components analysis was carried out on both the individual specimens and the genus-level means, with comparable results. For brevity, the plots of the analysis of the means are presented along with the loadings of each variable on the first three axes, accounting for 99% of the variance (fig. 29, table 13). The scatter produced a pattern that arranged the tali in a series of clusters corresponding to atelines, pitheciines-cebines, and callitrichines, with modest intergroup overlap; these results are comparable to those previously reported by Meldrum (1990). The talus of *Paralouatta* is notably distinct from the tali of other platyrrhines. In particular, the lack of trochlear ''wedging'' sets *Paralouatta* off from all other large-bodied platyrrhines along the second component in the principal components analysis, and is reflected in the high negative loading of posterior trochlear width (PTW) in table 13.

Paralouatta MNHNCu 76.1020 (Calcaneus) and MNHNCu 76.1021 (Middle Cuneiform)

The single calcaneus ascribed to *Paralouatta* is highly incomplete and badly preserved (fig. 30). Among the few features that can be readily discriminated is the indication of a very wide peroneal shelf on the lateral side of the specimen, also seen (but not uniquely) in *Callicebus*.

Only a fraction of the plantar surface is preserved. The area still present is relatively flat as in *Lophocebus* rather than sharply ridged as in *Alouatta*. However, *Lophocebus* is not markedly different from *Brachyteles* in this regard, indicating that this feature is not correlated with a single locomotor category. Unfortunately, the plantar tuberosity for the origin of quadratus plantae m. (flexor accessorius m.), which is very pronounced and projecting in *Alouatta* and *Brachyteles* but not as developed in *Lophocebus* and *Theropithecus*, is not preserved in this specimen.

Among the more unlikely fossils recovered from Cueva Alta is the perfectly preserved middle cuneiform illustrated in figure 31. The facet for the head of the navicular is narrow but markedly rounded for reception of the navicular. This suggests that midfoot dorso-ventral mobility was well developed, as is true of most anthropoids other than humans.

Paralouatta MNHNCu 76.1022, 76.1023, and 76.1025–76.1028 (Metapodials)

Examples of both MC1 and MT1 are available, permitting them to be clearly discriminated morphologically and metrically. The single specimen of MC1 (MNHNCu 76.1022) is about three-quarters the length of the only MC2 (MNHNCu 76.1023) in the collection (table 14). Compared to that of *Alouatta seniculus* and other large-bodied extant platyrrhines, the MC1 of *Paralouatta* (fig. 32) has a relatively less bulbous head, a straighter shaft, and a less projecting ulnar border. In addition, there are two prominent crests on the distal end not seen in the howler monkey. The one on the radial side is presumably for insertion of abductor pollicis longus m.; the one on the ulnar side, if not for the attachment of ligamentous tissue, is dubiously for the origin of an unusually developed first palmar interosseous m. A similar morphology is seen in the thumbs of some Old World monkeys (e.g., *Trachypithecus pileatus*). The joint surface for the trapezoid is uniaxial and semicylindrical, as is normally the case in platyrrhines. There are obvious facets for distal sesamoids.

Of the two MT1s in the collection, MNHNCu 76.1025 (fig. 34) is relatively complete; MNHNCu 76.1026 lacks its proximal end and has not been illustrated. The MT1 resembles the equivalent element of *Alouatta*, with the difference that the process for peroneus longus m. is better developed in the former. There is torsion of the head, but *Alouatta* exhibits about the same degree of twisting as *Paralouatta*. There are several additional metapodials in the hypodigm (table 2), the best preserved of which are MC2 MNHNCu 76.1023 (fig. 33) and MT3 MNHNCu 76.1028 (fig. 35). As discussed below, in relation to the estimated BM of
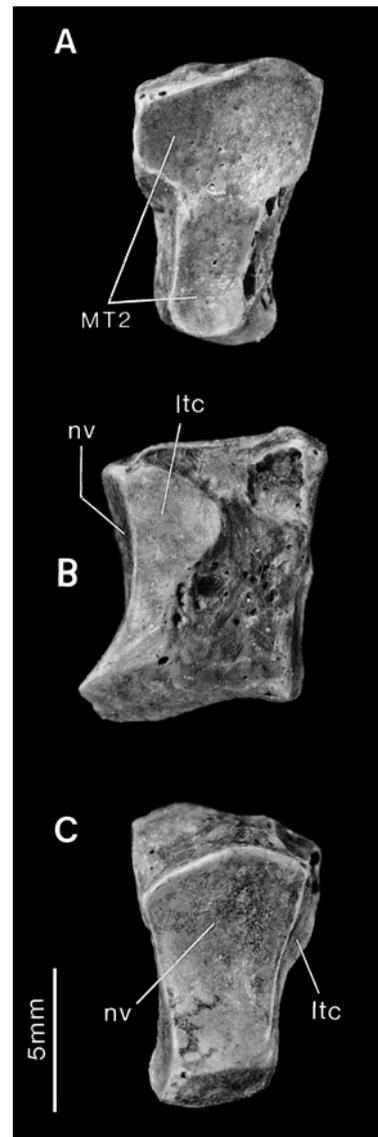

Fig. 31. *Paralouatta varonai*, middle cuneiform: MNHNCu 76.1021 (R) in distal (**A**), medial (**B**), and proximal (**C**) aspects. Articulations with other foot bones are indicated.

Paralouatta, all metapodials are robust and relatively short (cf. table 14).

Paralouatta MNHNCu 76.1029–76.1033 (Phalanges)

As already noted, some of the phalangeal elements described in this section assigned to the *Paralouatta* hypodigm have unusual fea-
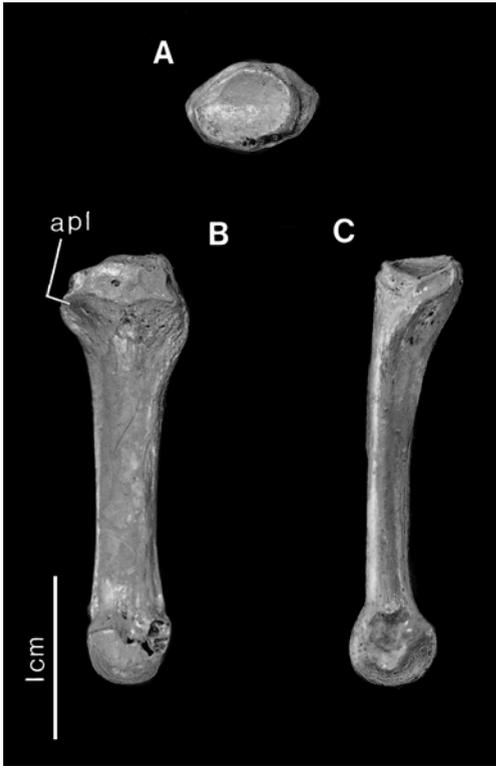
Fig. 32.   *Paralouatta varonai*, first metacarpal: MNHNCu 76.1022 (R), in proximal (**A**), palmar (**B**), and medial (**C**) aspects.

Fig 33.   *Paralouatta varonai*, second metacarpal: MNHNCu 76.1023 (R), in proximal (**A**), palmar (**B**), and oblique medial (**C**) aspects.

tures. However, there does not appear to be any other vertebrate taxon to which they could be justifiably assigned, and they are therefore accepted here as belonging to the Cuban monkey.

There are four proximal phalanges assignable to *Paralouatta*. The first of these (MNHNCu 76.1029, fig. 36A) is distinct morphologically, and judging from the asymmetry of its proximal articular surface, it must be part of a DR1. Its size and robusticity suggest that it belongs to the DR1 of the pes (cf. Hamrick et al., 1995), which means that the condition of the thumb in the Cuban monkey is still unknown. However, given the large size of MC1, there is no reason to suspect that the thumb was reduced as in atelines.

The remaining proximal phalanges (MNHNCu 76.1030a–c) can be placed only in a general sense, as representatives of one or another of DR2–5; only one (MNHNCu

76.1030a) is complete (fig. 36B). Its proximal end is notably expanded, with a single concave facet for reception of a large metapodial head. The shaft is marked by ridges for the flexor sheath, and the head presents the usual pulley-shaped articular surface for the middle phalanx. Although this specimen is utilized in the reconstruction of DR2 (manus) in figure 37, there is no morphological basis for regarding it as manual rather than pedal.

A group of 12 distinctive middle phalanges from the monkey caves were compared to, and found to be unlike, those of any known megalonychid, capromyid, echimyid, or solenodontid (i.e., the other terrestrial mammalian taxa represented in the Quaternary fauna of Cuba). All are extremely short, averaging 9.6 mm in length (cf. table 14, footnote b),

Fig. 34. *Paralouatta varonai*, first metatarsal: MNHNCu 76.1025 (L), in proximal (**A**), volar (**B**), and oblique medial (**C**) aspects.

and are robust for their length. Apart from size, however, they otherwise resemble typical platyrrhine middle phalanges and may reasonably be considered to represent *Paralouatta* (fig. 36C). Their proximal ends are dimpled by two small, concave facets separated by an indistinct ridge, to articulate with the pulleys of the proximal phalanges. Their distal ends are likewise pulley-shaped to receive the unguals. Each bears well-defined medial and lateral ridges for insertion of flexor digitorum superficialis m. and associated flexor sheath.

The five distal phalanges in the hypodigm are notably unlike their counterparts in other Cuban mammals. Four are similar to one another and display expanded or "cauliflower"

Fig. 35. *Paralouatta varonai*, third metatarsal: MNHNCu 76.1028 (R), in proximal (**A**), volar (**B**), and oblique medial (**C**) aspects.

distal ends (tuberosities or apical tuffs), to which connective tissues of the finger-tip pulp would have attached (MNHNCu 76.1032a–d, fig. 36D). One would normally conclude without hesitation that unguals having this morphology must represent DR1, because in known platyrrhines the unguals of digits other than the thumb and big toe are conical or only slightly expanded. In the existing *Paralouatta* hypodigm there is only one specimen (MNHNCu 76.1033, fig. 36E) an-
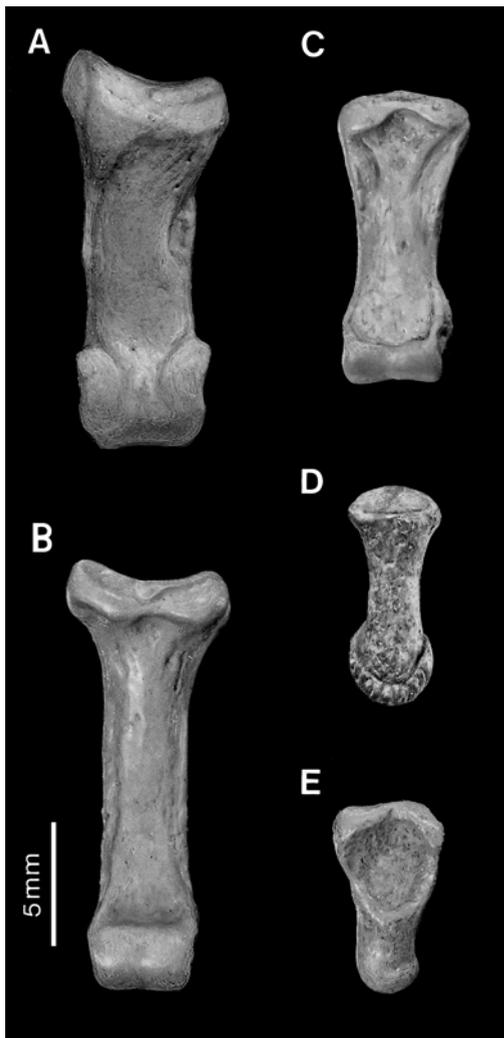
Fig. 36. *Paralouatta varonai*, phalanges: **A**, proximal phalanx MNHNCu 76.1029, DR1 (probably from pes), ventral aspect; **B**, proximal phalanx MNHNCu 76.1030a, DR2–5 (position uncertain), ventral aspect; **C**, middle phalanx MNHNCu 76.1031a, DR2–5 (position uncertain), ventral aspect; **D**, distal phalanx MNHNCu 76.1032a, DR?, dorsal aspect, showing expanded terminus; **E**, distal phalanx MNHNCu 76.1033, DR2–5 (position uncertain), ventral aspect, showing conical terminus and damaged area on shaft. To same scale.

Fig. 37. Digital ray length (manual DR2) in *Paralouatta varonai* (**A**) and *Alouatta seniculus* (**B**) AMNHM 70087. In the case of *P. varonai*, the depicted ''DR2'' is a composite of unassociated specimens (cf. figs. 33, 36), scaled to proximodistal lengths as given in the text. The DR2 of *A. seniculus* (AMNHM 70087) is a ligamentous preparation. Rays are lined up on a plane that passes through the metacarpophalangeal joints (arrows) to emphasize short finger length in *Paralouatta*.

swering to this latter description, although because the specimen in question is somewhat damaged it is difficult to be sure of its original condition. It might be argued that

the odds are against recovering four unguals of DR1 but only one representative from all of the other digital rays combined, but the alternative interpretation is that distal expansion was present on many or most distal phalanges in *Paralouatta*. Were that the case, distal phalanx morphology in the Cuban monkey would be unlike that of any other New World monkey, large or small—or, for that matter, any Old World monkeys except the large ground-adapted species like *Theropithecus gelada* and *Macaca nemestrina* in which the unguals are distally expanded. *Erythrocebus patas* displays a different pattern which may be relevant to note: the distal phalanges of most fingers and toes other than the thumb and big toe are only slightly expanded, but the axial digits (DR3) have larger and wider elements not unlike MNHNCu 76.1032a (fig. 36D).

It is unfortunate that the issue of distal phalanx placement has to be left unresolved, as the condition of DR2–5 unguals would appear to have some diagnostic value regarding preferred substrate. However, there is an additional source of inference, digital ray length, that provides some further functional insight into the Cuban monkey's cheiridial morphology (see next section).

Functional Considerations

DIGITAL RAY LENGTH: As a group, the phalangeal specimens discussed in the pre-ceding section are chiefly remarkable for their short length and sturdy build. If properly assigned, and if phalanges scaled in *Paralouatta* as they typically do in other platyrrhines, for its projected BM the Cuban monkey must have had relatively short fingers and toes. Obviously, this notion is difficult to explore in detail given the material available: With the exception of DR1, the units of which are morphologically distinctive, there is no way of allocating specific phalanges to their proper DRs with any certainty. The best that can be done is to assemble a ''typical'' DR by piecing together appropriate specimens to achieve a first approximation of ray length.

The digital ray chosen for illustrative purposes is DR2 of the manus, which we reconstruct in figure 37 using MC2 MNHNCu 76.1023 (33.9 mm) + proximal phalanx MNHNCu 76.1030a (17.0 mm) + an ''average'' middle phalanx (9.6 mm) + distal phalanx MNHNCu 76.1033 (7.6 mm) (table 14; fig. 37A). The middle phalanx depicted in figure 37A, MNHNCu 76.1031a, is actually the longest in the available sample at 11.2 mm, but it is scaled to the average. As noted in the preceding section, MNHNCu 76.1033 is the only distal phalanx in the collection with the conical extremity typical of DR2–5 unguals in other platyrrhines. The ''cauliflower'' unguals are only a millimeter or two longer, however, so for this purpose it matters little which kind is chosen.

TABLE 14
Selected Digital Ray Elements: *Paralouatta varonai*, Dimensions (in mm)[a]

MNHNCu	Element	MaxL	Proximal MLW	Distal MLW	Distal DVW
76.1022	1MC	26.1	5.0	7.4	5.2
76.1023	2MC	33.9	5.6	6.1	6.1
76.1025	1MT	32.5	6.9	8.0	9.9
76.1027	3MT	42.5	5.7	6.5	*7.1e*
76.1028	3MT	44.4	6.1	7.2	9.2
76.1029	PP DR1, ?pes	15.6	6.6	5.2	3.4
76.1030a	PP DR2–5, ?manus	17.0	6.3	4.2	2.7
76.1031a	MP	11.2[b]	5.1	3.9	3.6
76.1032b	DP ?DR1, ?manus	8.6	3.7	3.4	2.1
76.1032c	DP ?DR1, ?manus	9.4	3.4	3.7	3.2
76.1033	DP ?DR2–5	7.6	4.3	2.1	1.4

[a] Measurements in italics are not precise (*e* = estimate, due to damage or breakage).
[b] Average is 9.6 mm for all 12 MPs in the hypodigm (MNHNCu 76.1031a–l).

TABLE 15
Manual DR2: *Xenothrix*, *Paralouatta*, and Selected Living Primates, Metacarpal and Middle Phalanx Contribution Ratios (MCCR, MPCR)

Taxon	MC2L (I)[a]	DR2L (II)[b]	MCCR (I/II)[c]	MPL (III)[d]	MPCR (III/TPL)[e]
Theropithecus gelada AMNHM 238034	35.0	61.9	0.57	4.8	0.18
Erythrocebus patas AMNHM 14020[f]	32.1	62.5	0.51	9.7	0.32
Paralouatta varona[g]	33.9	68.1	0.50	9.6	0.28
Chiropotes satanus AMNHM 96123	33.5	71.7	0.47	11.7	0.31
Lophocebus albigena AMNHM 52609	30.1	70.9	0.42	12.0	0.29
Presbytis johnii AMNHM 41498	46.3	112.7	0.41	20.5	0.31
Ateles belzebuth AMNHM 30192	52.7	127.1	0.41	23.6	0.32
Cebus olivaceous AMNHM 30198	23.5	59.4	0.40	12.3	0.34
Brachyteles arachnoides AMNHM 260	52.3	132.5	0.39	25.3	0.32
Callicebus sp. AMNHM 201270	15.4	39.9	0.39	8.5	0.35
Saguinus sp. AMNHM 14438	11.3	29.1	0.39	7.2	0.40
Aotus infulatus AMNHM 94992	16.5	43.6	0.38	9.5	0.35
Lagothrix lagotricha AMNHM 238487	34.8	94.6	0.37	18.3	0.31
Alouatta seniculus AMNH 70088	31.0	87.3	0.35	17.5	0.31

[a] MC2L, maximum length of second metacarpal, in mm.

[b] DR2L, total length of second manual DR (including MC2), in mm. For disarticulated specimens, DR2L was measured by summing lengths of disarticulated individual elements; for ligamentous preparations, entire ray was measured, then MC2 separately. First method leads (usually) to slightly longer total length measurements than does second method, but differences are not consequential.

[c] MCCR, ratio of MC2L/DR2L.

[d] MPL, maximum length of middle phalanx of DR2, in mm. Mean value in case of *P. varonai* (see table 13).

[e] MPCR, ratio of MPL/Total Phalangeal Length (DR2L – MC2L).

[f] Unfortunately, none of the adult *E. patas* in the AMNHM collections have complete hands, so measurements had to be taken on AMNHM14020, an immature specimen in which some epiphyses were unfused.

[g] Composite; see text.

Adding these values together provides the basis for computing a "metacarpal contribution" ratio (MPCR); in table 15 values for this ratio in a variety of anthropoids are set out in descending order of magnitude. The range is fairly substantial, 0.35 to 0.57, although most values lie within the range 0.38–0.41 regardless of BM. The ratio for the composite DR2 of *Paralouatta* (0.50) is notably high in comparison to other platyrrhines in the table, and is consistent with the interpretation that the fingers would have been rather short in relation to the palmar skeleton. In the comparative set the Cuban monkey's value is exceeded only by that of the highly terrestrial cercopithecids *Theropithecus gelada* and *Erythrocebus patas*. (Estimates using the longest and shortest middle phalanges in the available *Paralouatta* sample yield ratios of 0.49–0.51. Using a short metapodial like MC2 actually favors a lower metapodial contribution ratio; utilization of the same phalangeal elements with the other complete metapodials would result in higher ratios.)

Although among measured platyrrhines *Chiropotes satanus* (BM, 2.6–2.9 kg; Fleagle, 1999) makes the closest approach to *Paralouatta* for this ratio, comparison needs to be made to a species of comparable BM. In figure 37B (see also table 15), a ligamentous preparation of the DR2 of a relatively small male *Alouatta seniculus* (AMNHM 70087) is depicted at the same scale as the *Paralouatta* reconstruction and positioned so that their metacarpophalangeal joints are in tandem (arrows). Morphologically, the elements making up the howler DR2 appear to be slightly more gracile than their counterparts in *Paralouatta*, but actual differences are minor. However, the blunt appearance of the fingertip in the *Paralouatta* reconstruction would have been even more pronounced if one of the distal phalanges with an expanded distal end had been used instead. Although MC length is similar in the howler specimen and the

Paralouatta reconstruction, there is a sharp contrast in ray length because *A. seniculus* possesses relatively much longer PPs and MPs. Indeed, the red howler's index finger is about a third longer, its PP alone being as long as the combined length of the Cuban monkey's PP and MP (cf. fig. 37).

Having fingers and toes that were short relative to metapodial length need not mean that the former were short in an absolute sense. However, in the case of *Paralouatta* this appears to be true, as can be appreciated by examining the "middle phalanx contribution" ratio in various taxa (table 15). Once again there is a considerable spread in values (0.18–0.40), although most species cluster in the range 0.31–0.35, which indicates that middle phalanges do not vary much in proportion to total finger length. The outstanding contrast in this column is between *Theropithecus*, which has an extremely short MP (ratio, 0.18), and all other taxa. This is similar to Schultz' (1963) finding that ground-living monkeys like *Theropithecus* and *Erythrocebus* (and humans) have dramatically shorter toes relative to MT length than do other anthropoids. *Paralouatta* is next, with 28% of total phalangeal length being contributed by the MP (mean length, 9.6 mm). However, the Cuban monkey cannot be sharply separated from the mass of other taxa in the table unless the absolute size of DR units is also taken into account. Thus in the case of the measured specimen of *A. seniculus*, the ratio is 0.31, which is only a little higher than that of *Paralouatta*. However, in absolute terms the howler's middle phalanx is almost twice as long as that of *Paralouatta*. In the case of *Brachyteles*, the MPCR is also about the same, but the woolly monkey's MP is more than two and a half times longer than the mean value for *Paralouatta*.

We will not repeat this exercise for the DR skeleton of the foot, as it is obvious that results would be similar because the same made-up set of phalanges would have to be used for *Paralouatta*. Nevertheless, it seems reasonable to conclude that, just as with many other parts of the skeleton of *Paralouatta*, cheiridial metrics point strongly away from the Cuban monkey's having had a locomotor repertoire like those of living atelines.

DISCUSSION

CALLICEBINAE AND XENOTRICHINI AS PHYLETIC ARRAYS

Although this paper is not concerned with platyrrhine systematics as such, it is worth noting that the known part of the xenotrichin postcranium displays few obvious candidate synapomorphies that might be used either to better define this tribe or to buttress its cladistic association with *Callicebus*. On the other hand, no platyrrhine subfamily other than Callicebinae, as we define it, displays a 10-fold difference in BM in its current membership, or such apparent diversity in locomotor and postural adaptations. If, as seems likely from the perspective of the GAARlandia hypothesis (Iturralde-Vinent and MacPhee, 1999; MacPhee and Iturralde-Vinent, 2005), mainland and insular callicebines have not shared a common ancestor since the Oligocene, perhaps the amount of morphological variation seen within the group is not implausible. This is, after all, the same temporal distance that separates *Carlocebus* and other hard-to-place Patagonian platyrrhines from their putative extant pitheciine relatives. Among xenotrichins, both *Xenothrix* and *Paralouatta* are spectacularly autapomorphic. This of course makes them morphologically quite different from *Callicebus*, but they differ just as markedly from other suggested relatives (e.g., *Aotus*, sister group of *Xenothrix* according to Rosenberger, 2002; *Alouatta*, sister group of *Paralouatta* according to Rivero and Arredondo, 1991).

SIZE VARIATION IN *PARALOUATTA*

The nature of sexual dimorphism in New World primates is a topic of current interest (Kay et al., 1988; Anapol et al., 2005). That size differences existed among *Paralouatta* individuals is obvious (cf. ulnae, fig. 13), but whether these were due to sex or something else is difficult to decide empirically. For example, the jaw MNHNCu 76.1213 is considerably smaller than the type skull MNHNCu 76.2565, yet the jaw possesses the largest m1 in the admittedly small sample used for BM estimation (table 3). Both specimens exhibit relatively tiny canines (Horovitz and MacPhee, 1999). If these speci-

mens were to be interpreted as male and female, respectively, then the only conclusion currently supported by the facts is that *Paralouatta* was dimorphic for BM but not for dental features—a combination not unknown, but highly unusual, in terrestrial primates. The postcranials are of little help in refining this notion because so few elements are intact or represented by more than one specimen. In view of how little is known about the Cuban monkey, and pending much better samples to work with, we prefer to leave open the question of the presence or absence of significant dimorphism in *Paralouatta*.

LOCOMOTOR ADAPTATIONS OF *XENOTHRIX*

The new material of *Xenothrix* adds somewhat to previous knowledge, but it is not especially helpful in further refining MacPhee and Fleagle's (1991) conclusion that the Jamaican monkey was "probably a heavy, slow-moving quadruped or climber", morphologically quite distinct from any mainland species. Now that there is a complete humerus that can be definitely ascribed to *Xenothrix*, it is easier to see that the arm and shoulder joints resemble those of arboreal quadrupedalists more than they do any other functional grouping. These resemblances include the bone's relatively short length, broad and distolaterally extensive capitulum, and moderately prominent trochlear lips. The posteriorly directed medial epicondyle and relatively deep olecranon fossa are less typical for New World quadrupedal monkeys, although present in *Cebus*. On the ulna, the short olecranon, wide saddle-shaped surface on the upper trochlear notch, and "inset" radial facet are also consistent with arboreal quadrupedalism.

By contrast, as noted in detail by MacPhee and Fleagle (1991), the hind limb of *Xenothrix* departs noticeably from the typical quadrupedalist model. The os coxae and the femur do not closely resemble those of other platyrrhines and are reminiscent in a general way of those of mammalian slow climbers. The fact that the more derived features of the postcranium of the Jamaican primate reside in the hindlimb is not unexpected, given that the locomotor systems of many primate species are dominated by the hindlimb (Fleagle, 1999). Although it would of course be useful to have a complete limb bone picture for this monkey, improvement in our understanding of the locomotor behavior of *Xenothrix* will depend on the discovery of potentially informative elements that are still unknown, such as the talus and calcaneus.

SEMITERRESTRIALITY IN *PARALOUATTA*

Although it is obviously a worthwhile endeavor to try to infer aspects of behavior from fossil remains through the medium of comparative biology, one's possibilities are limited in several respects by the nature of the remains being investigated. In reconstructing locomotor behaviors, the strongest inferential cases are usually based on correlated series of numerous, specific resemblances between the extinct form and one or more well-studied extant species (Meldrum and Kay, 1997)—in other words, an exercise in the constructive use of homoplasy (Lockwood, 1999). But even in these instances, it is not the entire repertoire of locomotory and postural behaviors that one tries to reconstruct, but only the apparently dominant modes. "Apparent" is the correct term here, because as numerous behavioral studies show, anatomy is certainly not always destiny. For example, just because a living primate species is classified for some purposes as an arboreal quadruped does not mean that it is therefore incapable of leaping, running, climbing, suspension, clambering, or galloping along on the ground some of the time. Rather, what we may reasonably expect to infer from the use of such terms as "arboreal quadruped" is that gaits that do not involve a regular alternation of all four feet on an arboreal substrate are infrequently utilized by the species in question. For extinct species, the problem of defining dominant mode is exacerbated when the fossil evidence appears to point in behavioral directions that are not normally associated with any of the taxon's living relatives. When the remains are highly incomplete, then one is no longer relying on a correlated series of numerous, specific resemblances as a basis for making inferences, but instead on a grab bag of hints that may or may not add up to very much. It is within this far from ideal context that we wish to raise, in order to invite critical comment,

the possibility that *Paralouatta* was predominantly semiterrestrial.

Anapol et al. (2005) made the interesting point, in connection with their analyses of certain cercopithecine species, that "semiterrestriality" may comprise a distinct suite of locomotor adaptations, i.e., it is not just a description of the behavior of a species that engages in both arboreal and terrestrial activities. It would be presumptuous to assert that such a suite can be identified in the material currently available for *Paralouatta*. What we have instead is an unexpected medley of features that together distinguish *Paralouatta* from all other known taxa in the platyrrhine record. Some of these features make sense as adaptations for ground living, but others do not. Whether items in the first category are truly indicative of semiterrestriality or point toward another form of arboreal adaptation likewise not seen in extant platyrrhines will have to remain an open matter until a better fossil record is available. For the present, it will have to be sufficient to catalog such distinctions as there are and place a reasoned functional interpretation upon them.

To make this exercise worthwhile, some limitations on speculation are required. First, functional interpretation of the known postcranium of *Paralouatta* is complicated by the fact that a number of pertinent features appear to be unique, or at least seldom seen, in large-bodied platyrrhines (e.g., combination of narrow trochlea/deep olecranon fossa/retroflexed medial epicondyle). Some of these features occur in catarrhine monkeys, but care is needed when developing functional interpretations based on platyrrhine/catarrhine similarities because the morphologies in question are not simply interchangeable or interpretable in a linear manner. For example, in comparing the width and degree of proximal flattening of the humeral head in Old and New World monkeys, it would be clearly incorrect to reach the conclusion that cercopithecines are less arboreal than platyrrhines because their humeral heads are characteristically flatter and narrower (cf. Fleagle and Simons, 1982; Gebo and Sargis, 1994). Relying on single indicators is obviously dangerous.

Secondly, unlike the catarrhine fossil record (cf. Gebo and Sargis, 1994), the platyrrhine

record offers virtually no empirical evidence of experimentation with terrestriality in any lineage. Some extant large-bodied platyrrhines (e.g., *Alouatta caraya*; Fleagle, 1999) will descend to the ground to forage briefly or cover short distances between forest patches, but no species is behaviorally committed to the ground in the way that many Old World monkey species are—an important distinction. Although Kay and Williams (1995) cited some intriguing dental similarities between late Oligocene *Branisella boliviana* (the earliest known fossil platyrrhine) and terrestrial Old World monkeys, because there are no limb bones recognized for *Branisella* the significance of this insight cannot be tested with postcranial data. Where the evidence is better, as it is for several Miocene Patagonian and Colombian taxa (Meldrum, 1993; Meldrum and Kay, 1997), no features diagnostic of terrestrial adaptation have been identified.

Finally, there is an underlying skeletal "stamp" of primitive arboreal quadrupedalism on the anthropoid skeleton which is obvious even in species whose lineage adaptations radically depart from the ancestral activity pattern (cf. Ford, 1994; Lockwood, 1999). Accordingly, given poor or otherwise limited material, as is often the case with fossil taxa, it is a challenge to establish whether there is enough evidence to overturn what might be called the "presumption of arboreality" when interpreting the locomotor behavior of a fossil primate. In the case of *Paralouatta*, such evidence as there is appears to support the following points:

Excludable Patterns: Other than leaping, for which there is no evidence whatsoever, the only major locomotor pattern that can be definitely excluded for *Paralouatta* on the basis of the available skeletal evidence is the kind of suspensory, arm-over-arm locomotion epitomized among platyrrhines by *Ateles*. Absence of arm swinging capabilities in the Cuban monkey is indicated primarily by the comparatively short and robust humerus, retroflexed medial epicondyle, and short, straight fingers and toes. In platyrrhine arm swingers, the humerus is elongated, the medial epicondyle juts directly medially, and the recurved digits are long relative to metapodial length. The tail, which is in effect a fifth limb in atelines and

Alouatta, is not known for *Paralouatta*. The appendicular skeleton of arm swingers is built for high mobility at the major joints of the limbs; this emphasis is not apparent in known parts of the skeleton of *Paralouatta*.

Elbow: The elbow is the only major post-cranial articular area that is well represented by relatively intact joint surfaces in the *Paralouatta* material. In *Paralouatta*, the olecranon fossa is narrow and deep, articular surfaces are mediolaterally compressed, and the ulnar trochlear notch extends onto the triceps process to articulate with the large, continuous lip formed by the lateral margins of the trochlea and the olecranon fossa. Although the howler monkey humerus is comparable in several ways to that of *Paralouatta* (e.g., comparative length, robusticity, low head height), the distal end is notably different. In *Alouatta*, the medial epicondyle is large and medially projecting, the olecranon fossa is broad and shallow, and the trochlea/capitulum complex is relatively wide, just as in the more active arm swingers. Narrow trochleae and deep olecranon fossae are features seen in highly terrestrial cercopithecines, as is the extension of the trochlear notch's articular surface.

Among the few traits that might be cited as evidence favoring high mobility at the elbow is the radial facet, which is "inset" and in lengthy contact with the trochlear notch in both *Xenothrix* and *Paralouatta*, as in platyrrhines generally. This feature does not seem to be exclusively correlated with acrobatic arm swinging, however. Gebo and Sargis (1994) distinguished a reduced radial facet in *Cercopithecus lhoesti*, the predominantly terrestrial "mountain" guenon, from the broader version seen in the highly arboreal species *C. mitis*. However, in cercopithecines (including *C. lhoesti*) the facet is always jutting, unlike the case in New World brachiators. Like the condition of the humeral head, the size and orientation of the radial facet may be constrained in a lineage-specific way in Old and New World monkeys.

Knee: It is unfortunate that the femur is poorly represented in the *Paralouatta* hypodigm. With only an incomplete distal epiphysis to comment on there is little that can be said in functional terms. Nevertheless, it is

clear that *Paralouatta* lacked certain specializations prominently seen in *Theropithecus*, such as the great development of the lateral side of the patellar surface. Arboreal quadrupeds, and to a greater degree terrestrial quadrupeds, have rather tall femoral condyles and narrow patellar grooves (MacPhee and Fleagle, 1991; Meldrum, 1993). Although as noted the intact portions of the condyles of *Paralouatta* are taller than those of *Xenothrix*, and the patellar groove has greater relief, the Cuban monkey actually diverges very little from arboreal quadrupeds such as *Chiropotes* in these features.

Proximal Tarsus: The outstanding features of the tibiotalar joint of *Paralouatta* are its massivity and stability, as expressed in the size and robusticity of the medial malleolus (and inferred for the unknown lateral malleolus), the moderately developed malleolar semicondylar/cotylar articulation with the neck of the talus, and the high, parallel-sided dorsal talar surface. Some of these features can be seen in other large-bodied platyrrhines, such as substantial malleolar development in *Ateles*, but in these cases it is associated with a quite different dorsal articular surface of the talus ("wedged" appearance, low relief). Greater shape similarity is found with ankle bones of *Cacajao* and *Chiropotes*, but as our morphometric treatment shows, the talus of *Paralouatta* lies outside the main platyrrhine cluster and is not therefore "like" any of them. At the same time, it would not be correct to say that it morphologically or metrically groups with the tali of the gelada or patas monkey. The talar trochlea is tall in all three, but beyond that the resemblances are not strong. *Paralouatta marianae*, on which these comments are based, has the relatively long and gracile neck and head seen in most platyrrhines. The tibia of *Antillothrix* may also have articulated with a relatively high talar trochlea, although this is simply an inference from the size of the malleolus.

Digits: Some of the most distinctive aspects of the skeleton of *Paralouatta* are found in the skeleton of the hand and foot. Although intact elements are few, digital rays were evidently robustly built and quite short—at least for an animal of the projected size of *Paralouatta*. In

both New and Old World anthropoids, hand and foot lengths scale positively with body size, such that large-bodied arboreal species always have comparatively very long fingers and toes (Schultz, 1963). Conversely, taxa that are short-fingered are never acrobatically arboreal, even though they may spend varying amounts of time in the trees during their daily activities. In this regard, as in all others considered above, *Paralouatta* never matches the most ground adapted of the Old World monkeys, but skeletally it is arguably the most cercopithecinelike of any of the New World monkeys. Although cercopithecine species differ widely in the amount of time they spend on the ground, the point is that many of them do, in fact, spend a considerable proportion of the time out of the trees—raising the question whether semiterrestriality may actually be primitive for this radiation (e.g., Strasser, 1988; Harrison, 1989; Meldrum, 1991; Gebo and Sargis, 1994). Large-bodied *Paralouatta* was surely not highly suspensory on the model of *Ateles*, nor is it very much like *Alouatta*, the only large arboreal quadruped in the extant platyrrhine radiation. Other modes of primate locomotion, such as leaping and slow climbing, can also be ruled out. Although it is true that the evidence for its being semiterrestrial is hardly decisive, there is no other way obvious to us to explain its strange amalgam of postcranial features.

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APPENDIX 1

**Specimens of Extant Primates Utilized for Morphological Comparisons
and Measurements**

Genus	Species	AMNHM	Locality	Gender/Age[a]
Callicebus	*moloch*	201270	no data	?
Callicebus	*moloch*	211487	Camiaco: Bolivia	male
Callicebus	*moloch*	210393	Bolivia	?
Chiropotes	*satanus*	95760	R. Tapajoz: Brazil	male
Chiropotes	*satanus*	96123	R. Xingu: Brazil	male
Ateles	*belzebuth*	30192	Rio Mato: Venezuela	male
Ateles	*fusciceps*	188140	Rio Samiria: Peru	male
Ateles	*fusciceps*	188135	Rio Samiria: Peru	female
Brachyteles	*arachnoides*	260	Brazil	?
Lagothrix	*lagotricha*	70404	no data	male
Lagothrix	*lagotricha*	238487	no data	male
Lagothrix	*lagotricha*	201554	no data	?
Alouatta	*seniculus*	23377	Guaiaroco: Colombia	female
Alouatta	*seniculus*	132790	Palenque: Venezuela	male
Alouatta	*seniculus*	70088	no data	male
Cebus	*apella*	209927	Rondônia: Brazil	female
Cebus	*apella*	133637	Matto Grosso: Brazil	male
Cebus	*apella*	133622	Matto Grosso: Brazil	?
Cebus	*olivaceous*	30198	Rio Macho: Venezuela	male
Aotus	sp.	201647	no data	?
Aotus	*infulatus*	94992	Rio Tapajoz: Brazil	female
Saguinus	sp.	14438	no data	?
Saguinus	*midas*	266481	Paracau: French Guiana	female
Colobus	*guereza*	99468	Aberdare Range: Kenya	female
Presbytis	*johnii*	41498	no data (mounted specimen)	?
Trachypithecus	*pileatus*	43072	Yunnan: China	male (late immature)
Trachypithecus	*pileatus*	43078	Yunnan: China	male
Trachypithecus	*pileatus*	43071	Yunnan: China	female
Macaca	*nemestrina*	28256	Borneo	male
Macaca	*nemestrina*	106564	Boekit, Sanggoel: Sumatra	male
Macaca	*nemestrina*	106563	Boekit, Sanggoel: Sumatra	male
Lophocebus	*albigena*	52609	Niapu: Zaire	male
Lophocebus	*albigena*	52627	Niapu: Zaire	male
Lophocebus	*albigena*	52598	Akenge: Zaire	male
Lophocebus	*albigena*	52596	Akenge: Zaire	female
Theropithecus	*gelada*	254572[b]	Ethiopia	male
Theropithecus	*gelada*	238034	Ethiopia	female
Theropithecus	*gelada*	60568	no data	male
Theropithecus	*gelada*	201008	"Abyssinia"	? (late immature)
Erythrocebus	*patas*	14020	no data	male (late immature)
Erythrocebus	*patas*	34709	Nasin Gishu dist.: Kenya	female (late immature)
Erythrocebus	*patas*	34712	Nasin Gishu dist.: Kenya	male

[a]Unless otherwise indicated, specimens are mature (i.e., metaphyses obliterated). "Late immature" implies that some long bone metaphyseal lines were found to be still open.

[b]This *Theropithecus* specimen is a cast of Cleveland Natural History Museum B1207, humerus only.

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