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A closer look at the “Protopithecus” fossil assemblages: new genus and species from Bahia, Brazil

Lauren B. Halenar [a,c,*], Alfred L. Rosenberger [b,c,d]

[a] City University of New York and NYCEP, Division of Vertebrate Paleontology, American Museum of Natural History, 79th Street at Central Park West, New York, NY 10024, USA
[b] Department of Anthropology and Archaeology, Brooklyn College, City University of New York, 2900 Bedford Avenue, Brooklyn, NY 11210, USA
[c] New York Consortium in Evolutionary Primatology (NYCEP), The Graduate Center, City University of New York, 365 Fifth Avenue, New York, NY 10016, USA
[d] Department of Mammalogy, American Museum of Natural History, 79th Street at Central Park West, New York, NY 10024, USA

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ABSTRACT

The recently extinct large-bodied New World monkey *Protopithecus brasiliensis* Lund 1836 was named based on a distal humerus and proximal femur found in the Lagoa Santa cave system in the southeastern Brazilian state of Minas Gerais. These bones are from an animal about twice the size of the largest extant platyrrhines. One hundred and seventy-five years later, a nearly complete skeleton was discovered in the Toca da Boa Vista caves in the neighboring state of Bahia and was allocated to the same taxon as it was the first platyrrhine fossil of comparable size found since the originals. Our detailed study of the equivalent elements, however, reveals important morphological differences that do not correspond to intraspecific variation as we know it in related platyrrhine taxa. The presence of both an expanded brachioradialis flange on the humerus and gluteal tuberosity on the femur of the Bahian skeleton distinguishes it from the Lagoa Santa fossil as well as from all other platyrrhines. Further cranial and postcranial evidence suggests a closer relationship of the former with the alouattine *Alouatta*, while the limited Lund material fits more comfortably with the ateline clade. Therefore, we propose to limit *P. brasiliensis* Lund to the distal humerus and proximal femur from Lagoa Santa and erect a new genus and species for the skeleton from Toca da Boa Vista. *Cartelles coimbrafilhoi* was a large-bodied frugivore with a relatively small brain and diverse locomotor repertoire including both suspension and climbing that expands the range of platyrrhine biodiversity beyond the dimensions of the living neotropical primates.

Introduction

Remains of *Protopithecus brasiliensis* were first discovered in 1836 by the Danish naturalist Peter Wilhelm Lund. A left proximal femur, UZM (Universitets Zoologisk Museum) 3530, and right distal humerus, UZM 1623, were found in the Lagoa Santa (LS) cave system in Minas Gerais, Brazil, and despite their robusticity and large size, twice that of the largest living platyrrhine, Lund understood that the bones belonged to a New World monkey (Lund, 1838). These fossils were the first to be correctly recognized as a primate at the time of their discovery (Hartwig, 1995b) and were mentioned in passing by Darwin (1859) along with several other early monkey fossil discoveries in *On the Origin of Species*. Lund's writings concerning *Protopithecus* were neither extensive nor detailed, but a later monograph by Winge (1895) describing Lund's Brazilian excavations included a brief comparative analysis and an expanded hypodigm that included several more postcranial elements but no teeth or cranial material (Fig. 1). Winge noted that the distal humerus and proximal femur were each found in the same cavern, but not at the exact same site. He concluded that they are ‘probably’ from the same individual and, using an outmoded taxonomic name (*Eriodes*), allocated the material to the genus we now know as *Brachyteles*, distinguished at the species level from *Brachyteles arachnoides* based on the fossil's larger size. As a consequence, the LS fossils were relegated to scientific obscurity for over 100 years (Hartwig, 1995a,b).

Then, in 1992, the matter was reopened when two nearly complete skeletons of comparably large platyrrhines were discovered in the Toca da Boa Vista (TBV) caves in the neighboring state of Bahia, approximately 1200 km northeast of Lagoa Santa (Fig. 2). In a brief preliminary announcement (Cartelle, 1993), both were identified as conspecific with Lund's material and called *Brachyteles*.

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* Corresponding author.
E-mail address: lauren.halenar@gmail.com (L.B. Halenar).

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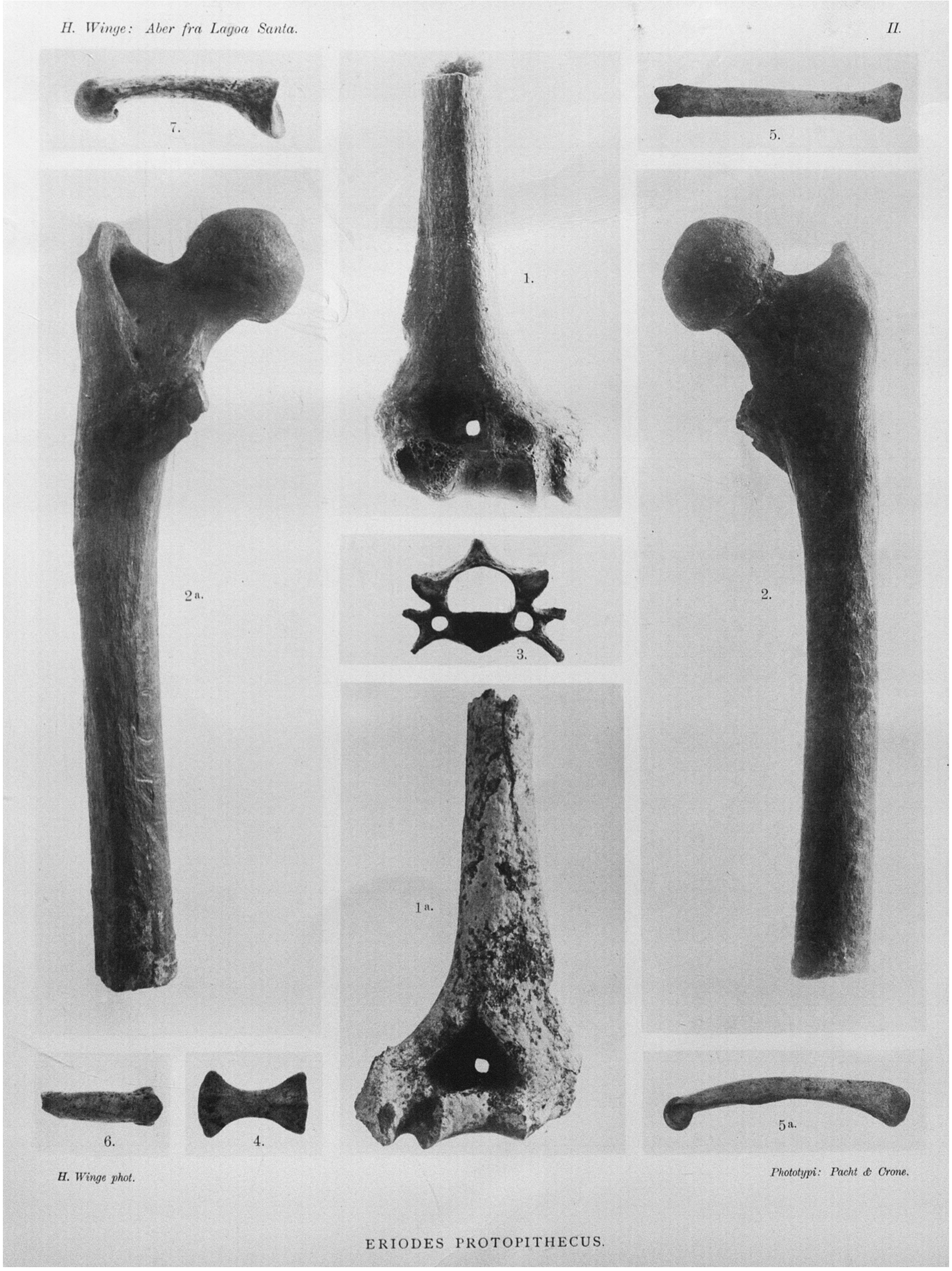

Figure 1. Fossil material collected by Lund from the Lagoa Santa Caves. This plate appeared in the Winge (1895) monograph describing Lund's excavations across Brazil in the early 1800s. The *Protopithecus brasiliensis* (here still referred to as *Eriodes protopithecus*) humerus (UZM 1623; 1, 1a) and femur (UZM 3530; 2, 2a) described in detail here are figured along with a cervical vertebra (UZM 12480; 3), caudal vertebra (UZM 12481; 4), proximal phalanx (UZM 12484; 5, 5a), middle phalanx (UZM 12486; 6), and metatarsal (UZM 12483; 7), which have not been studied in detail since their discovery. Their attribution to *Protopithecus* needs to be confirmed as they are from a different cavern than the humerus and femur and Winge describes them as being from a similar, but slightly smaller animal and not all from the same individual.

One, a subadult, would eventually be named a new genus and species, *Caipora bambuiorum*, and described as a giant spider monkey (MCL [Museu de Ciências Naturais PUC Minas Gerais] 05; Cartelle and Hartwig, 1996). And soon after Cartelle's published note, Hartwig (1995a) showed that Lund's large limbs from Lagoa Santa were misinterpreted as being muriqui-sized (see Hill, 1962), and he argued that generic status was, in fact, warranted.

Hartwig's (1995a) analysis, which was the first modern consideration of the original LS material, concluded that the Lund fossils were "grossly indistinguishable" from *Brachyteles* and *Ateles*, except for their larger size. A regression equation for estimating body mass based on femoral head volume in catarrhine primates (Ruff, 1990) returned an estimate of 23–24 kg (Hartwig, 1995a); the largest body mass reported for any extant atelid is 12–15 kg (Di Fiore and Campbell, 2007). A closer phylogenetic relationship to *Brachyteles* was suggested because of Lagoa Santa's location within the region of pre-Columbian Atlantic Coastal Forest where the woolly spider monkeys currently live in a very restricted distribution. Hartwig's (1995a) analysis led to the resurrection of the genus *Protopithecus* and the eventual transferral of the MCL 06 skeleton to the hypodigm of *P. brasiliensis*, based largely on similarities in long bone dimensions and estimated body mass (Hartwig and Cartelle,

Figure 2. Brazilian fossil mammal localities. The labeled black starbursts show the location of the Lagoa Santa caves in the state of Minas Gerais and the Toca da Boa Vista caves in the state of Bahia. Black dots indicate other caves in the area where Quaternary non-primate mammals have been found. Modified from Auler et al. (2006).

1996; Table 1; Fig. 3). However, while their body mass may have been similar, the morphology of the distal humeri and proximal femora of the two individuals now referred to *P. brasiliensis* presents several anatomical and inferred behavioral differences that we contend are of systematic importance.

In suggesting that the LS and TBV samples constitute a mosaic wherein *Protopithecus* is *Alouatta*-like cranially and *Brachyteles*-like postcranially, a pattern not seen in any other extant or extinct platyrrhine, Hartwig and Cartelle's phylogenetic hypothesis (Hartwig, 1995a; Hartwig and Cartelle, 1996) is internally inconsistent, for these patterns are each derived among platyrrhines and indicative of separate atelid clades. While a subsequent, more detailed biometric analysis of the LS and TBV material found complimentary support in several traits of the forelimb and vertebral column that suggested a functional link between the fossils from both localities and the highly suspensory locomotion of extant atelines (Jones, 2008), more recent work (Halenar, 2012; Rosenberger et al., in press) raises additional questions by extending the range of cranio-skeletal similarities shared by only the TBV material and *Alouatta*, which includes such features as a relatively small brain and extended cranial base.

In the context of a broad analysis of atelid postcranial and cranial morphology, diversity, and evolution (Halenar, 2011a,b, 2012), we have reexamined all of the original material pertaining to these fossils and find both qualitative and quantitative indications suggesting the presence of two distinct morphologies and clades within the current '*Protopithecus*' sample. Differences between the two specimens include the larger dimensions of the TBV material, the presence of a large brachioradialis flange on the TBV distal humerus, and the different shape and size of both the gluteal tuberosity and lesser trochanter between the two proximal femora. These femoral characters involve likely synapomorphies linking the TBV specimen with *Alouatta*. Their absence in the LS femur, as well as the taxonomic expression of brachioradialis flange expansion amongst extant platyrrhines, suggests that the LS fragments and TBV complete skeleton are taxonomically distinct at the genus level. As a consequence, we propose a new genus and species to accommodate the TBV material from Bahia. Data presented here support Hartwig's original observations of the ateline affinities of the LS material (Hartwig, 1995a), while the TBV material shares likely derived resemblances with *Alouatta* in the cranium, innominate, and proximal femur, suggesting that it is more closely related to alouattines. Without any other skeletal elements represented, we are in a similar position to Winge and other earlier authors in

Table 1
Linear measurements (in mm) collated from Hartwig (1995a) and Hartwig and Cartelle (1996).

Genus	*n*	Femoral head diameter	Femoral neck diameter	Femoral length	Femoral midshaft width	Proximal femur max breadth	Femoral bicondylar breadth	Humeral head diameter	Humerus biepicondylar breadth	Humerus shaft thickness	Intermembral index
'*Protopithecus*' MCL 06	TBV	25	16.2	237	20.4[a]		45.5	28.4	48	18.5	1.04
Protopithecus UZM 3530, 1623	LS	26.02		n/a	18.65	48.01	n/a		46.54	13.75	n/a
Brachyteles	4	18.75			13.5	33.5			32.54	10.65	
	3	18.2 (16.9–19.8)	10.3 (9.5–11.2)	202.0 (186.5–212.0)			29.0 (28.0–30.9)	19.8 (18.2–21.6)	30.0 (26.7–33.0)	10.4 (9.4–11.6)	1.07 (1.05–1.08)
Ateles	16	17.51			13.68	33.32			30.63	8.08	
	31	17.9 (15.8–20.2)	9.9 (8.0–11.8)	205.6 (190.5–226.0)			31.8 (29.2–34.9)	20.5 (17.8–24.1)	30.9 (28.5–33.2)	11.0 (10.0–12.4)	1.05 (1.01–1.07)
Lagothrix	6	14.99			13.21	30.56			29.84	8.72	
	17	15.0 (14.0–15.7)	8.3 (7.4–9.6)	166.4 (157.5–176.5)			27.1 (24.2–29.3)	20.1 (18.6–22.2)	28.0 (25.6–30.0)	10.2 (9.2–11.4)	0.98 (0.96–1.00)
Alouatta	17	14.47			11	28.24			29.02	7.68	
	25	13.4 (11.8–15.9)	7.9 (6.4–10.8)	154.2 (139.0–171.0)			23.9 (21.4–26.7)	19.8 (16.9–23.1)	26.6 (22.5–30.8)	9.5 (7.3–12.1)	0.95 (0.92–0.98)
Cacajao	2	12.48			9.54	26.2			24.01	7.49	
Chiropotes	2	11.52			7.18	22.68			20.05	6.52	
Pithecia	3	10.33			6.92	21.5			18.21	5.64	
Cebus	7	10.57			8.75	22.98			21.58	6.75	

[a] Measurement taken by LBH.

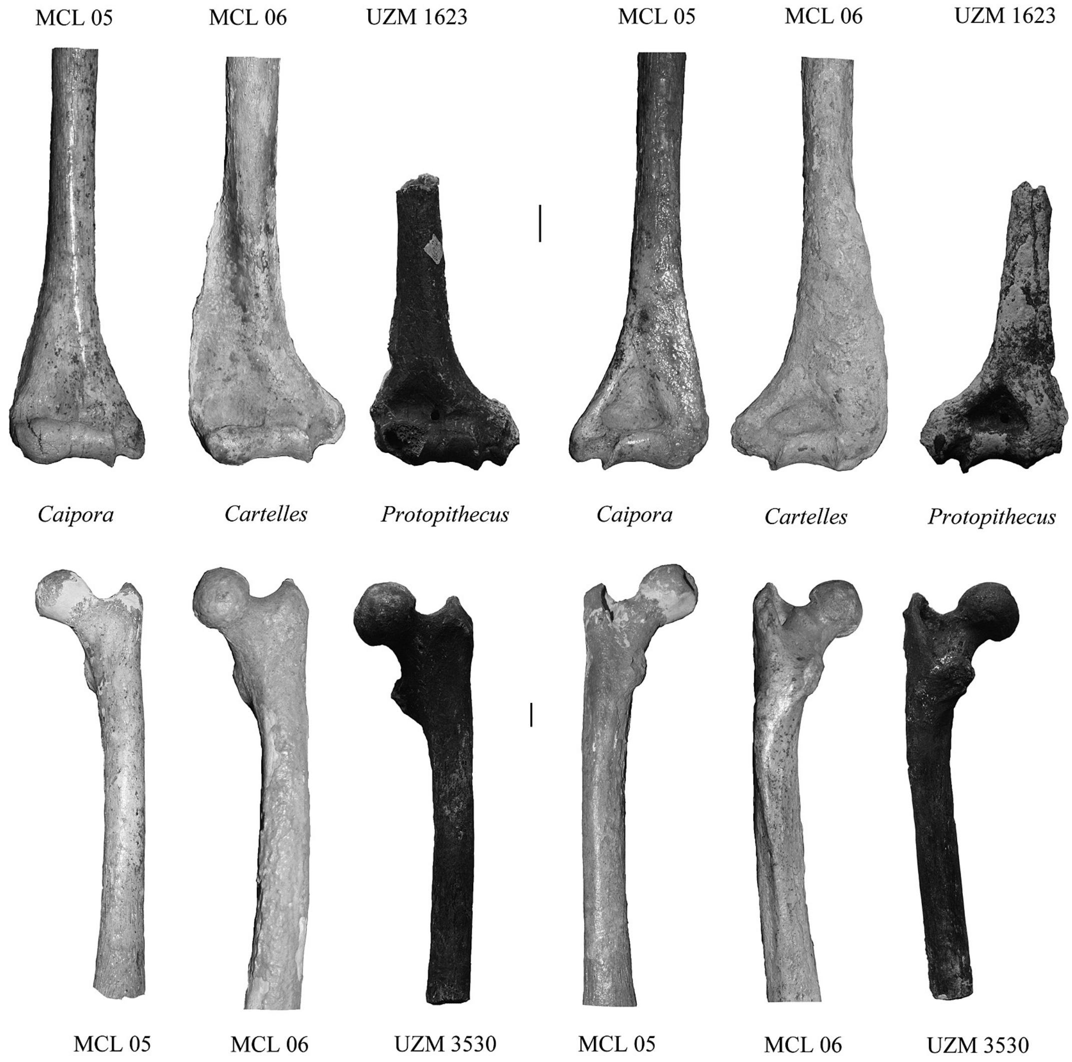

Figure 3. Fossil material. Distal humerus (top) and proximal femur (bottom) of *Caipora* (MCL 05), *Cartelles* (MCL 06), and *Protopithecus* (UZM 1623, 3530) (left to right anterior view and posterior view). Despite the mislabeling in Hartwig (1995a), UZM 1623 is the proper number for the Lagoa Santa humerus specimen as it is written on the yellow tag affixed to the shaft, visible here. UZM 3530 is the Lagoa Santa femur. For both the humerus and femur, the LS specimens are broken around midshaft while the TBV bones are digitally shortened to a similar length. Scale bars = 1 cm.

suggesting that the LS material is best interpreted as a large-bodied relative of *Brachyteles*.

Materials and methods

As noted, all of the original pertinent fossils have been examined by both authors. The samples, measurements and statistics employed to estimate body size in the fossils have been described elsewhere (Halenar, 2011a). Centroid size of various joint surfaces, based on three-dimensional landmark measurements, was used as the independent variable in both ordinary least squares as well as reduced major axis regression models with an atelid-only, platyrrhine-only, and primate-wide comparative sample. In addition to the commonly referenced correlation coefficient, the standard error of the estimate, mean prediction error, and a correction factor for bias introduced by log transforming the data were also calculated to assess the strength of the parameters of the equations produced.

Additionally, to assess the variability of a feature specific to this project, the morphology of the brachioradialis flange, the distal humeri of 111 individuals representing 12 extant platyrrhine species plus *Propithecus verreauxi* from the collections at the American Museum of Natural History in New York were measured with digital calipers (Table 2). The length of the flange (represented by the length of the supracondylar ridge and associated muscle scar from the brachioradialis muscle; BRFL), the maximum width of the flange in anterior view (BRFW), the width across the distal epiphysis excluding the medial epicondyle (DHW), and the maximum length of the humerus (HL) were measured and used to calculate two indices of flange development (flange width/epiphysis width [BRFW/DHW] and flange length/humerus length [BRFL/HL]; Fig. 4). While the shaft of the LS specimen is incomplete and the brachioradialis flange is broken, both BRFL and BRFW could still be measured accurately; the superior end of the muscle scar is visible on the preserved shaft and maximum width of the flange occurs just superior to the break (Fig. 5).

How many primate taxa are represented in the TBV and LS caves?

Distal humerus

The distal humeri from Lagoa Santa and Toca da Boa Vista differ from one another in their size and robusticity, especially in the

Table 2
Measurements (in mm) and indices describing the size and of the distal humerus and prominence of the brachioradialis flange across selected primate species.

Taxon		*n*	BRFL			BRFW			DHW			HL			BRFW/DHW			BRFL/HL		
			Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
'*Protopithecus*' MCL 06	TBV	1	70			9			42			252			0.21			0.28		
Protopithecus UZM 1623	LS	1	45			3			36						0.08					
Alouatta seniculus	M	5	27.2	22.1–34.8	4.9	1.8	1.0–2.4	0.6	22.6	19.8–26.3	2.3	163.5	148.3–175.2	9.7	0.08	0.05–0.11	0.02	0.17	0.13–0.21	0.03
	F	5	30.2	26.0–35.0	3.6	1.1	0.7–1.2	0.2	19.2	16.8–22.6	2.1	146.9	137.7–168.9	10.1	0.06	0.03–0.07	0.01	0.20	0.17–0.23	0.02
Alouatta belzebul	M	3	26.9	23.1–31.2	4.1	1.1	0.9–1.2	0.1	21.9	20.0–23.3	1.7	160.4	152.5–170.2	9.0	0.05	0.04–0.06	0.01	0.17	0.15–0.19	0.02
	F	1	30.7			1.3			20.6			156.3			0.06			0.19		
Alouatta caraya	M	9	33.2	26.6–38.8	3.5	1.6	0.9–2.9	0.6	21.6	18.5–23.9	1.7	159.6	137.7–172.0	10.4	0.07	0.04–0.14	0.03	0.21	0.16–0.25	0.03
	F	10	34.9	32.5–37.3	1.4	1.1	0.7–1.5	0.3	20.2	18.7–21.5	1.0	145.2	138.3–150.9	3.4	0.06	0.04–0.08	0.02	0.24	0.23–0.26	0.01
Ateles belzebuth	M	1	39.3			2.4			30.2			200.2			0.08			0.19		
	F	1	33.7			1.9			23.8			207.1			0.08			0.16		
Ateles fusciceps	M	1	41.7			1.1			23.4			204.4			0.05			0.20		
Ateles geoffroyi	F	1	43.8			1.8			28.7			210.0			0.06			0.21		
Brachyteles arachnoides	?	1	38.1			2.5			27.7			221.0			0.09			0.17		
Lagothrix lagotricha	F	2	36.5	36.2–36.8	0.5	1.4	1.1–1.7	0.4	22.7	21.0–24.4	2.4	163.8	162.4–165.3	2.0	0.06	0.05–0.07	0.01	0.22	0.22–0.23	0.0001
Aotus azarae	M	9	20.7	15.3–23.9	2.8	1.3	0.9–1.6	0.2	12.4	10.9–13.3	0.7	79.1	71.8–82.3	3.1	0.10	0.07–0.14	0.02	0.26	0.19–0.31	0.04
	F	10	21.4	16.3–25.7	2.8	1.2	0.9–1.8	0.3	12.3	10.9–13.2	0.7	79.1	68.2–83.3	4.4	0.09	0.07–0.14	0.02	0.27	0.24–0.32	0.03
Propithecus verreauxi	M	3	31.4	30.1–32.2	1.1	3.7	3.2–4.3	0.5	18.0	17.2–18.5	0.7	89.5	88.9–90.8	1.1	0.21	0.17–0.23	0.03	0.35	0.34–0.36	0.01
	F	4	34.6	30.8–38.5	3.3	3.3	2.9–3.7	0.4	18.2	17.3–19.2	0.8	94.7	91.1–99.8	4.0	0.18	0.15–0.21	0.02	0.36	0.34–0.39	0.02
Cebus albifrons	M	10	35.1	27.9–44.7	4.9	3.1	2.8–3.6	0.3	19.3	17.5–20.6	1.0	107.2	98.9–112.8	4.9	0.16	0.14–0.19	0.01	0.33	0.28–0.39	0.04
	F	10	27.6	24.2–29.5	1.4	2.2	1.7–2.7	0.4	17.1	14.8–20.2	1.8	100.5	93.1–113.0	5.9	0.13	0.08–0.17	0.03	0.28	0.25–0.29	0.02
Cebus apella	M	10	34.8	30.8–38.8	2.2	2.6	2.1–3.1	0.3	19.9	18.4–22.2	1.2	111.6	105.3–119.2	4.4	0.13	0.11–0.16	0.02	0.31	0.29–0.33	0.01
	F	10	30.9	28.1–34.7	2.2	1.9	1.4–2.6	0.4	17.2	15.6–20.0	1.5	101.0	93.8–106.9	4.1	0.11	0.08–0.14	0.02	0.31	0.29–0.34	0.02
Cebus olivaceous	M	3	33.3	32.7–34.2	0.8	2.1	1.6–3.0	0.7	19.7	19.4–20.3	0.5	117.8	115.9–120.8	2.6	0.11	0.08–0.15	0.04	0.28	0.27–0.29	0.01
	F	2	31.9	30.7–33.2	1.8	1.9	1.7–2.1	0.3	18.5	17.9–19.2	0.9	113.4	108.3–118.4	7.2	0.10	0.09–0.12	0.02	0.28	0.26–0.31	0.03

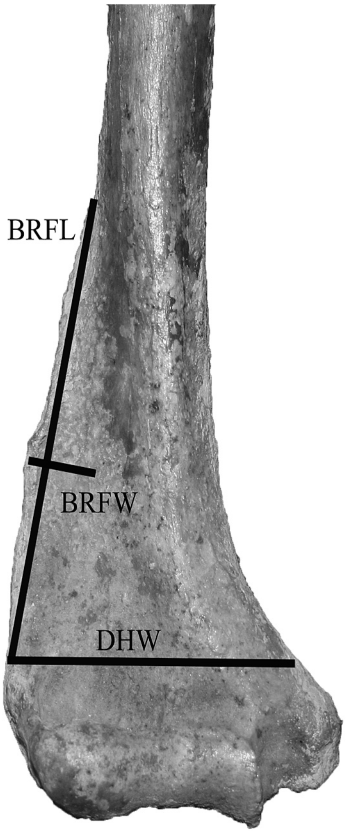

Figure 4. Brachioradialis flange measures. Measurements taken on the distal humerus, shown on the TBV specimen in anterior view. BRFL = brachioradialis flange length. BRFW = brachioradialis flange width. DHW = distal humerus width. This measurement was taken at this position to avoid including the medial epicondyle, which also varies in length and orientation across species in the comparative sample. Not shown is HL = maximum humerus length.

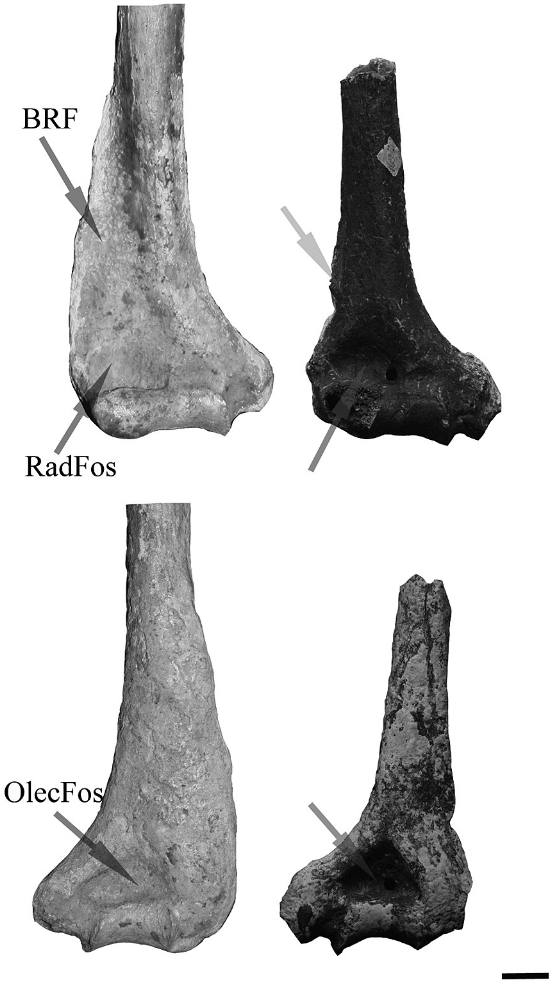

Figure 5. Fossil humeri. Anterior view (top) and posterior view (bottom) of the TBV specimen (left) and the LS specimen (right). The LS specimen is broken around mid-shaft and the TBV specimen has been cut off to show a similar amount of bone. The shaft is wider in the TBV specimen than the LS specimen. Arrows point out other features discussed in the text that differ substantially between the two individuals. BRF = brachioradialis flange. This feature is greatly expanded in the TBV specimen. While the LS flange is broken, maximum flange width could still be measured accurately just superior to the break. RadFos = radial fossa. The fossa superior to the capitulum, which articulates with the head of the radius, is deeper and narrower in the LS specimen. OlecFos = olecranon fossa. The fossa on the posterior surface of the distal humerus that articulates with the olecranon process of the ulna is taller and deeper in the LS specimen. Scale bar = 1 cm.

width of the joint and the prominent brachioradialis flange on the lateral side of the TBV specimen, which is hardly identifiable on the LS element (Fig. 5). The difference in humeral shaft thickness between the two fossils, 4.75 mm, is larger than the differences in this measurement between the means of any of the atelid genera (Table 1). Other aspects of the joint surfaces on the two distal humeri are more similar to each other, especially when compared with the distal humerus of the similarly-sized *Caipora* (Fig. 3). For example, the medial epicondyle on both '*Protopithecus*' specimens is large and projects medially. In *Caipora* it is slightly retroflexed, approaching the condition seen in extant *Cebus* (Fig. 6).

While the articular surface of the capitulum is abraded on the LS specimen, it seems to share a more flattened, elongated shape with the TBV humerus, which is unlike the more rounded globular shape seen in the most suspensory atelines and *Caipora* (Figs. 3, 5 and 6). Despite this similarity, the radial fossa in the LS specimen is narrower and deeper than that on the TBV specimen (Fig. 5). Posteriorly, the olecranon fossae are also shaped differently, with the LS specimen again showing a deeper pit that extends further superiorly as opposed to the shallow, more laterally extensive fossa in the TBV humerus (Fig. 3). This suggests that the LS individual was capable of more extreme extension at the elbow, while the TBV individual would have kept its forearms more flexed. This positional difference also agrees with the interpretations of the function of the large brachioradialis flange seen on the TBV specimen (see discussion below). Neither the LS, TBV, nor *Caipora* humeri have an entepicondylar foramen, a feature that has been lost in atelids but is frequently seen in other platyrrhines such as *Cebus*, *Aotus*, and *Pithecia* (e.g., Gebo, 1993). In many taxa, the foramen is found in combination with an expanded brachioradialis flange, which suggests that the relatively large flange in the TBV individual, in a clade where the foramen appears to be lost synapomorphically, is not a primitive holdover but an apomorphic feature.

While many of the morphological differences between the two fossil humeri described above are relatively subtle, the extreme difference in both the absolute and relative size of the brachioradialis flange between the LS and TBV specimen is anything but. We quantified aspects of the expression of flange development across platyrrhines, and one vertically clinging and leaping strepsirhine, in an attempt to distinguish differences potentially related to intraspecific sexual dimorphism from those that may be related to interspecific morphological variation.

The LS specimen is similar in some aspects of shape to the larger TBV specimen and its smaller size could be a product of

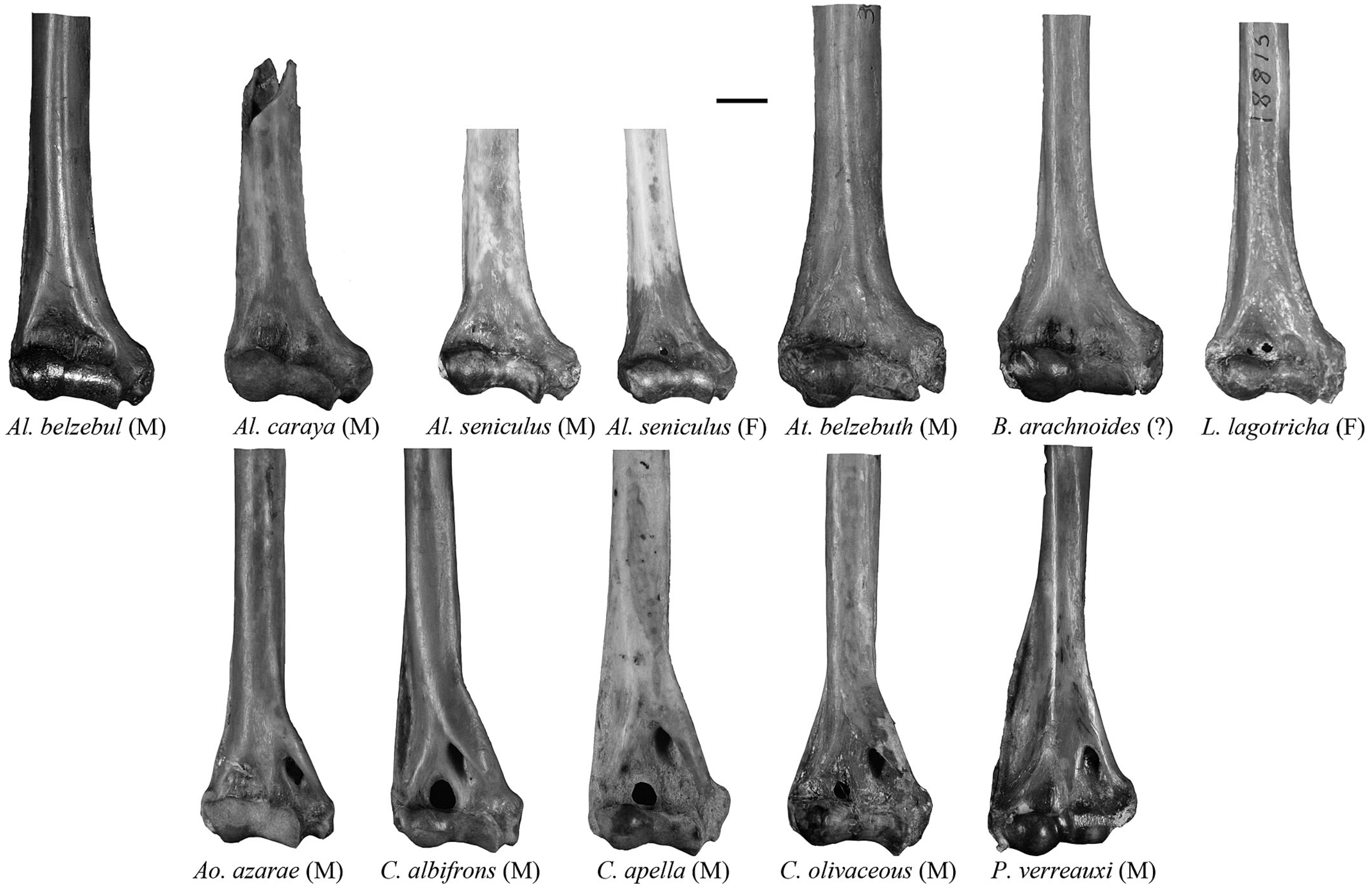

Figure 6. Distal humeri of selected species from the comparative sample. Top row (left to right) = *Alouatta belzebul* (AMNH 133544M), *Al. caraya* (AMNH 211525M), *Al. seniculus* (AMNH 211528M, 211531F), *Ateles belzebuth* (AMNH 30192M), *Brachyteles arachnoides* (AMNH 260), *Lagothrix lagotricha* (AMNH, 188153F). Bottom row (left to right) = *Aotus azarae* (AMNH 211482M), *Cebus albifrons* (AMNH 211547M), *C. apella* (AMNH 133656M), *C. olivaceous* (AMNH 30197M), *Propithecus verreauxi* (AMNH 170463M). All are shown in anterior view only to highlight the small, non-sexually dimorphic brachioradialis flange shared by the atelids in contrast to the intermediate expansion of *Cebus* and the even more flattened condition in *Propithecus*. The specimens in the bottom row have been scaled up to approximately the same size as *Ateles*, about 2.0–2.5 times their normal length, so the morphology can be seen more clearly. Scale bar for the top row = 1 cm.

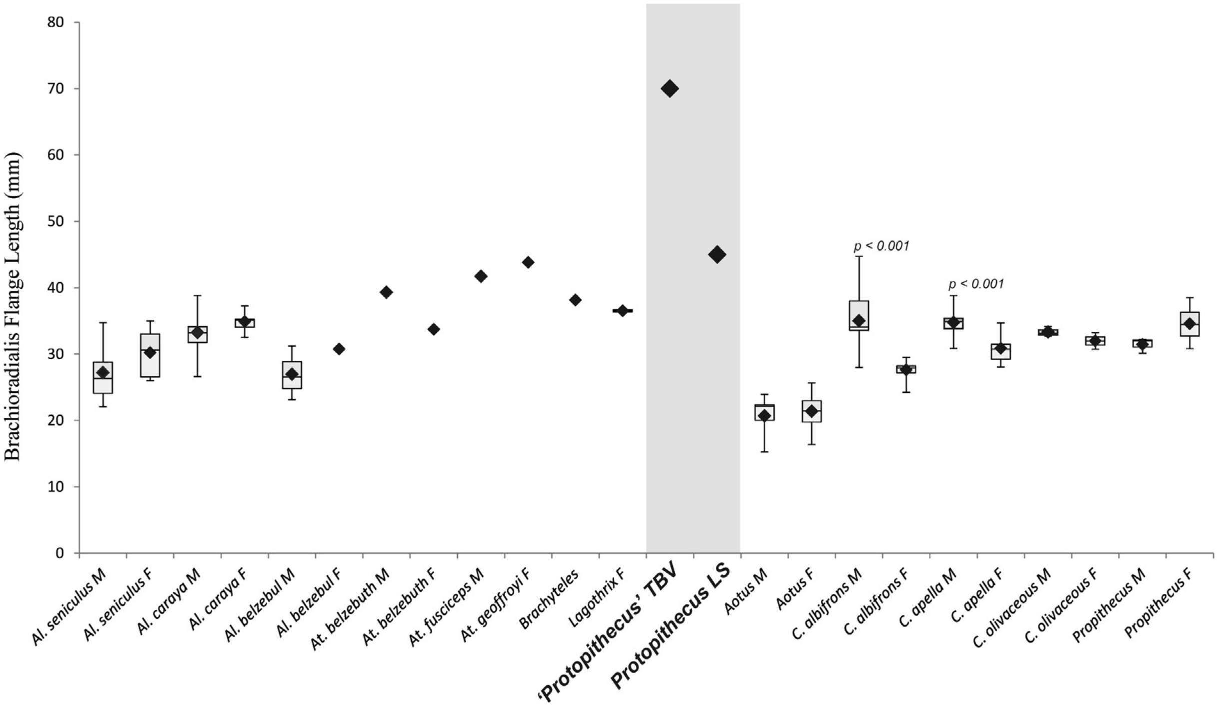

Figure 7. BRFL. Box and whisker plot of brachioradialis flange length (mm). *P*-values for *C. albifrons* and *C. apella* represent the only significant differences between males and females, based on a two-tailed *t*-test for samples with unequal variances. The difference between the values for the two fossil specimens is well outside the range of differences between males and females for any of the extant taxa.

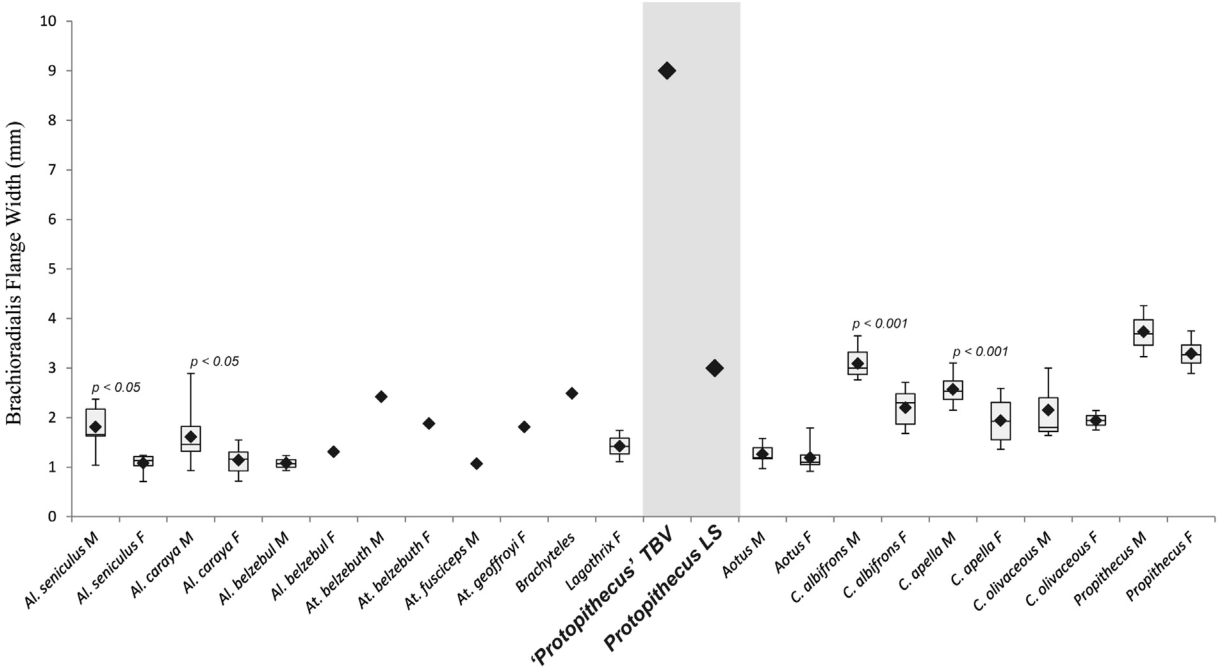

Figure 8. BRFW. Box and whisker plot of brachioradialis flange width (mm). *P*-values for *C. albifrons* and *C. apella* represent the only significant differences between males and females, based on a two-tailed *t*-test for samples with unequal variances. Differences between male and female *A. seniculus* and *A. caraya* are approaching significance. The difference between the values for the two fossil specimens is well outside the range of differences between males and females for any of the extant taxa.

sexual dimorphism. However, in the other taxa that were measured here as examples of primates with a well-developed brachioradialis flange, such as *Cebus* and *Propithecus*, its development is not consistently sexually dimorphic (Table 2). When comparing the absolute length and width of the flange in the two fossils with the differences between males and females of other platyrrhine taxa, it is clear that the differences between TBV and LS are outside of the range seen in the extant species (Figs. 7 and 8). *P*-values for *Cebus albifrons* and *Cebus apella* represent the only significant differences between males and females in BRFL and BRFW, based on a two-tailed *t*-test for samples with unequal variances (Figs. 7 and 8). Differences between male and female *Alouatta seniculus* and *Alouatta caraya*, taxa that are sexually dimorphic in body size, are only approaching significance for

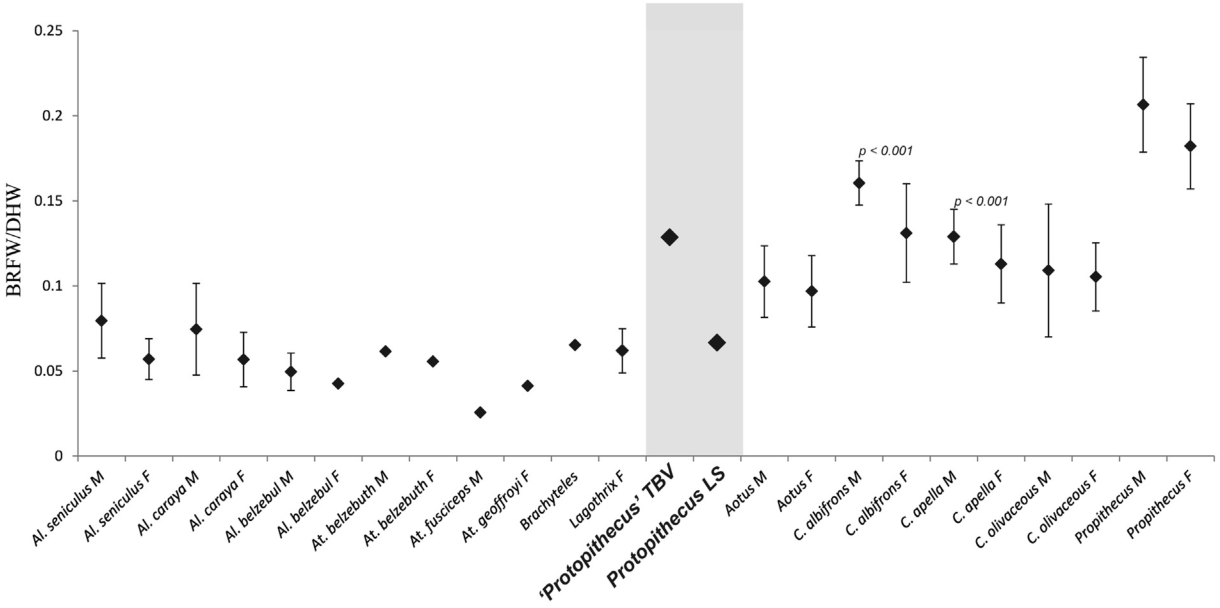

Figure 9. BRFW/DHW. Mean values for the width of the brachioradialis flange divided by the width of the distal humerus. Error bars are one standard deviation above and below the mean. The development of the flange in the LS specimen is more similar to the condition seen in the atelines while the TBV specimen is more similar to *Cebus*. *C. albifrons* and *C. apella* are again the only species showing significant levels of sexual dimorphism in this trait, based on a two-tailed *t*-test for samples with unequal variances. The difference in this index between the two fossil specimens is twice the difference in means of the taxon that is the most significantly dimorphic, suggesting that the two fossils are not a male and female of the same species.

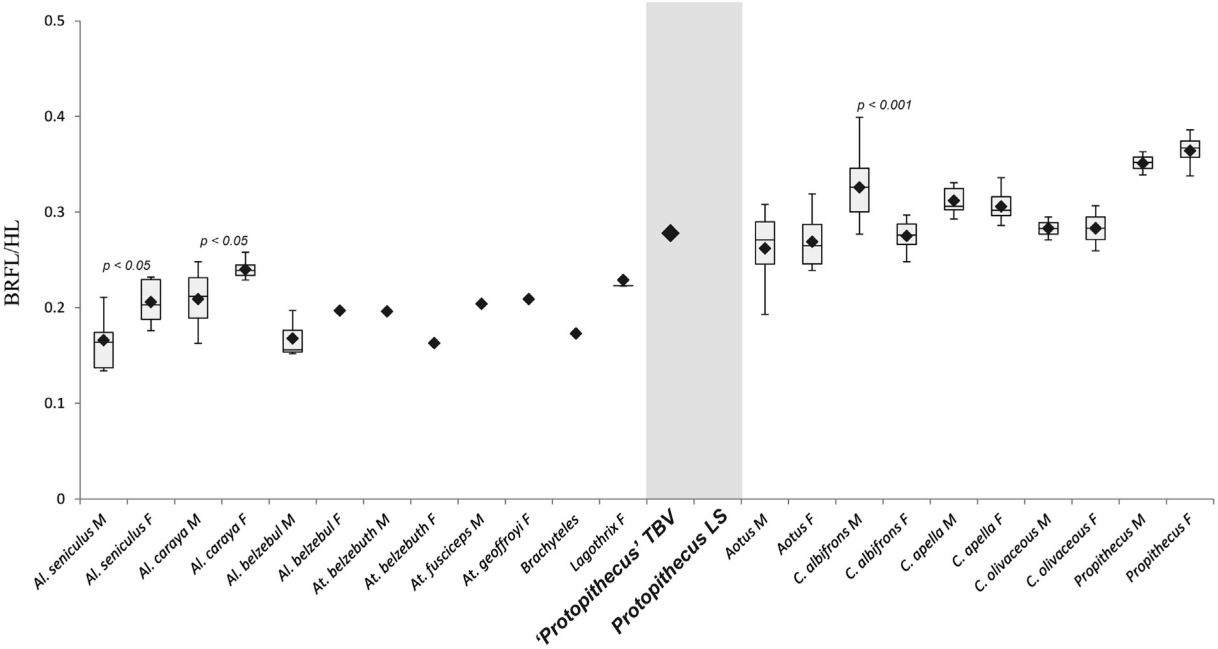

Figure 10. BRFL/HL. Box and whisker plot of the length of the brachioradialis flange divided by the length of the humerus. There is a divide between the development of the flange in atelids compared to *Aotus* and *Cebus*, with the TBV specimen falling more closely inside the range of the non-atelid species. Unfortunately the LS humerus is incomplete so this index could not be calculated and the difference between the two specimens cannot be seen. Again, *C. albifrons* shows the only significant difference between males and females while *A. seniculus* and *A. caraya* approach significance, based on a two-tailed *t*-test for samples with unequal variances.

BRFW (Fig. 8). Interestingly, despite body mass estimates for the LS specimen being approximately five times the body mass of a male *Cebus*, their brachioradialis flanges are of similar width (Fig. 8).

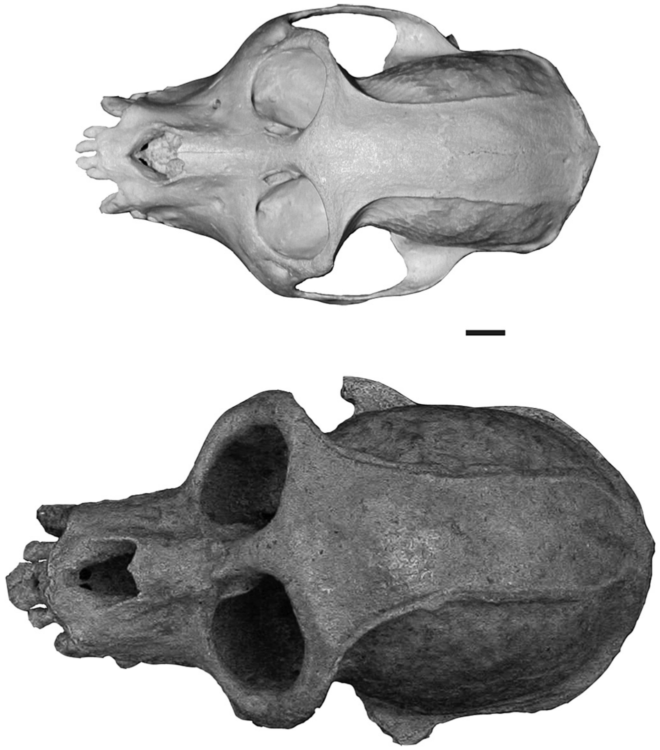

Figure 11. Cranial morphology. Superior views of the TBV skull (bottom) compared with a male *Alouatta* sp. (top) to show comparable development of the temporal lines and canines. Scale bar = 1 cm. TBV skull photo courtesy of Andrea Jones.

When the measurements are converted to indices, the proportion of distal humerus width taken up by the width of the flange in the TBV specimen is more similar to that of *Aotus* and *Cebus* while the LS specimen is more similar to the range of flange width development seen in the atelids (Fig. 9). In the LS specimen and the atelids, the flange is less than 10% of the overall epiphysis width

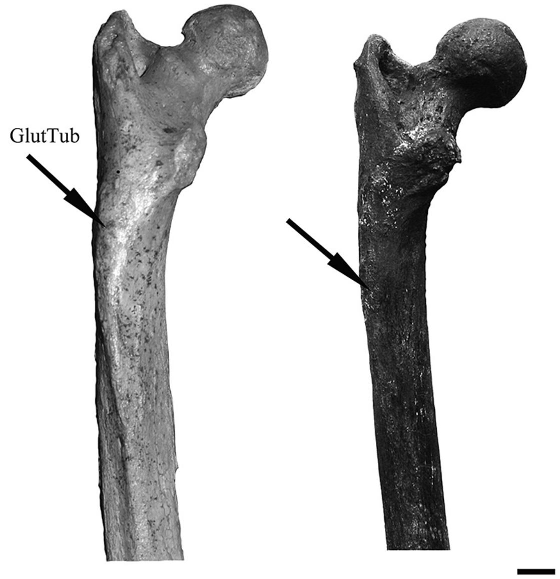

Figure 12. Fossil femora. Proximal femur from TBV (left) and LS (right) in posterior view. The shaft of both specimens has been cut off to show a similar amount of bone. As in the distal humerus, the difference in shaft diameter can be seen clearly with the TBV specimen exhibiting more robusticity. GlutTub = gluteal tuberosity. The attachment for the gluteus superficialis muscle is more prominent on the TBV specimen, beginning more proximally on the shaft, ending more distally, and extending further laterally than on the LS femur. Scale bar = 1 cm.

while the TBV specimen and *Cebus* are between 10 and 15%. *Cebus albifrons* and *C. apella* are again the only species showing significant levels of sexual dimorphism in BRFW/DHW (Fig. 9). The difference in this trait between the two fossil specimens is twice the difference in means of the taxon that is the most significantly dimorphic, continuing to suggest that the two fossils are not a male and female of the same species but instead belong to two different taxa.

The results for BRL/HL show that there is a small but noticeable divide between the development of the length of the flange in atelids compared with *Aotus* and *Cebus*, with the TBV specimen falling more closely inside the range of the non-atelid species (Fig. 10). Unfortunately the LS humerus is incomplete so this index could not be calculated and the difference between the two specimens cannot be seen. But this index also shows that the development of the brachioradialis flange is not consistently sexually dimorphic in these taxa (again, *C. albifrons* is the only species where males and females are significantly different from one another while *Al. seniculus* and *Al. caraya* approach significance), so the fossil would not necessarily be expected to follow this pattern. Where body mass is dimorphic in these taxa, the BRL/HL index actually shows reverse dimorphism as humeral length is shorter in females than males, making the length of the flange a larger percentage of overall length in the former.

Newly published regression equations for body size estimation that make use of a platyrrhine reference sample highlight the difference between the TBV and LS specimens, especially when using the distal humerus as the skeletal estimator (Halenar, 2011a). The 'best' equation from that study, i.e., the one with the combined highest R^2 (=0.98) and lowest %SEE (=11.0), MPE (=14.7), and QMLE (=1.005), used the distal humerus with a platyrrhine-only reference sample. It yields a body mass estimate of 28 kg for the TBV specimen and 24 kg for the LS specimen. This result, a 3–4 kg difference between these two individuals, was consistently estimated from measures of the distal humerus. This is slightly larger than the 1–2 kg difference recovered from the proximal femur (Halenar, 2011a).

While the TBV skeleton appears to be a male individual based on the prominence of its canines and temporal lines, for example, which are comparable in development with a male *Alouatta* (Fig. 11), these body mass estimates are not divergent enough to support the interpretation of the TBV specimen as a male and the LS specimen as a female of a species presenting a similar level of sexual dimorphism. For example, calculating the dimorphism index frequently used in surveys of platyrrhines (e.g., Ford, 1994), and assuming the TBV specimen is a male and the LS specimen is a female, gives a value of 1.17 using the estimates quoted above. This is within the range of values for *Ateles* (0.853–1.101) and *Brachyteles*

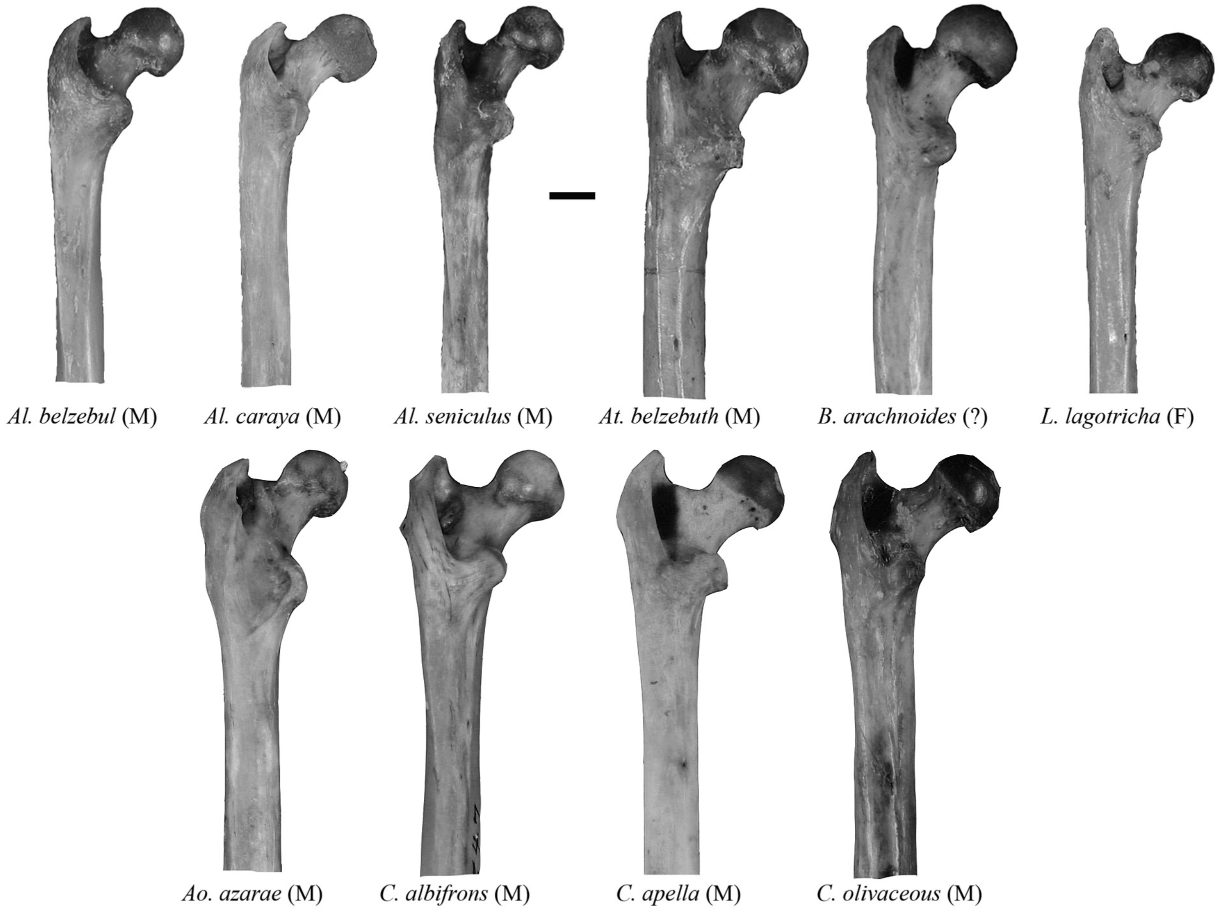

Figure 13. Proximal femora of selected species from the comparative sample. Top row (left to right) = *Alouatta belzebul* (AMNH 133544M), *Al. caraya* (AMNH 211525M), *Al. seniculus* (AMNH 211528M), *Ateles belzebuth* (AMNH 30192M), *Brachyteles arachnoides* (AMNH 260), *Lagothrix lagotricha* (AMNH, 188153F). Bottom row (left to right) = *Aotus azarae* (AMNH 211482M), *Cebus albifrons* (AMNH 211547M), *C. apella* (AMNH 133656M), *C. olivaceous* (AMNH 30197M). All are shown in posterior view only to highlight the area of gluteus superficialis insertion on the proximolateral region of the shaft. The relative proportions of the greater trochanter and femoral head can also be seen. The specimens in the bottom row have been scaled up to approximately the same size as *Ateles*, about 2.0–2.5 times their normal length, so the morphology can be seen more clearly. Scale bar for the top row = 1 cm.

(1.283), both of which are less dimorphic than *Alouatta* (1.286–1.764) and *Lagothrix* (1.450) (Ford, 1994).

The interpretation of the size differences between various aspects of the LS and TBV individuals as indicating the presence of a male and female of the same sexually dimorphic species would also require that the two specimens, separated by 1200 km of space and an indeterminate amount of time, have randomly sampled a single population. This is highly unlikely. Without a skull from LS with its own canines and temporal lines, there is no way to rule out that these are both male individuals based on body mass differences alone. A difference of 3–4 kg can be seen between male individuals of *A. caraya*, for example (see Table 4 in Halenar, 2011a). These male individuals of the same species, however, do not show the same degree of morphological variation described here for the TBV and LS fossil individuals.

Proximal femur

The femur is also represented from two individuals, the LS left proximal femoral shaft and head, and the essentially complete TBV exemplars. In both cases, the morphology is well-preserved, although the lesser trochanter of the right TBV femur is abraded. Here, comparison to the morphology seen in *Caipora* is less useful as the femoral head and greater trochanter are plastered back into place and the lesser trochanter remains unfused (Fig. 3). As described for the humerus, the differences between the specimens seem to mostly reflect the larger size and greater robusticity of the TBV individual (Fig. 12). The LS specimen is broken about two-thirds of the way down the shaft, but the difference in shaft diameter between the two individuals is still obvious. Femoral shaft width of the TBV specimen is 20.40 mm while the same measurement for the LS specimen is 18.65 mm (Table 1). This difference of 1.75 mm between the two '*Protopithecus*' specimens is larger than the size difference between any of the means for ateline genera and is more similar to the difference between any of those three genera and *Alouatta*. The gracile nature of the LS femur and humerus shafts, despite the large body mass estimates recovered from their joint surfaces, is consistent with the acrobatic suspensory locomotion practiced by *Ateles* and *Brachyteles*, as opposed to the more robust bones of the TBV specimen and *Alouatta*, which uses a slower, more deliberate, less suspensory quadrupedal locomotion (see discussion below).

The difference in robusticity between the LS and TBV specimens is also visible in the development of various muscle attachment sites. As noted by Hartwig and Cartelle (1996), one of the unique features of the TBV proximal femur as compared with the LS specimen is an enlarged gluteal tuberosity for the insertion of the gluteus superficialis muscle (Fig. 12). While the gluteus superficialis is relatively small in the atelids compared with other platyrrhines, within atelids it is most well developed in *Alouatta*, with a broad ascending tendon inserting more proximally on the femur than *Ateles* or *Lagothrix* and a descending tendon that inserts more distally. This makes for a long muscle attachment site that can extend nearly halfway down the posterolateral surface of the shaft (Grand, 1968; Stern, 1971). In some *Alouatta* males, the muscle scar extends laterally into an enlarged gluteal tuberosity not seen in other extant taxa (see Fig. 6 in Ciochon and Corruccini, 1975; Fig. 13). The extensive attachment sites for these muscles on the TBV femur with a relatively proximal position of the gluteal tuberosity and a ridge running to nearly halfway down the shaft, are features again absent from the LS specimen but similar to the condition seen in *Alouatta* (Figs. 12 and 13).

The large, proximally placed lesser trochanter on both fossil specimens provides attachment for the iliopsoas muscles, powerful hip and thigh flexors hypothesized to be used during climbing (Schön, 1968; Ciochon and Corruccini, 1975; Anemone, 1993; Meldrum, 1993). The lesser trochanter seems to be larger in the smaller LS individual as it projects further medially in anterior view, but in the TBV individual it is longer in the proximodistal dimension. In both fossil specimens, the greater trochanter sits below the relatively large and globular femoral head and is open posteriorly with a relatively deep trochanteric fossa widely spaced from the head and neck, similar to the configuration seen in *Brachyteles* (Figs. 12 and 13). The femoral neck is especially short and robust in the TBV specimen, the condition normally seen in leaping primates (Ciochon and Corruccini, 1975), but this is most likely related to body size as this individual is much larger than any leaping platyrrhine. While the shape of the proximal femur from Lagoa Santa looks very similar to that of *Brachyteles*, the morphology of the TBV specimen that suggests well-developed musculature used during both climbing and hindlimb suspension

Table 3
Preserved elements of *Cartelles coimbrafilhoi*.

Element	Condition
Cranium	Complete except for broken zygomatic arches, pterygoids, and right postglenoid process – calcite deposition obscures some sutures and surface anatomy, especially on the posterior basicranium
Mandible	Anterior portion only (broken behind the M3 on each side, some right ramus present)
Dentition	Upper: incisors (central covered in calcite), canines (tips broken, especially the right), P4, M1–3 (left M3 plastered back in place, right M1 missing anterior portion) Lower: incisors (central and right lateral are broken at the crown tips), canines (broken more than uppers), P2–4
Vertebrae	11 caudal, 13 thoracic and lumbar (some too fragmentary to distinguish type)
Ribs	At least nine partial
Clavicle	Left: complete except for the medial epiphysis
Scapula	Left: acromion process and base of the glenoid fossa connected by partial spine, no blade Right: partial glenoid, acromion process, and spine, no blade
Humerus	Left: broken about midway down the shaft, only distal end is present – brachioradialis flange, medial and lateral epicondyles are slightly eroded Right: complete except for the head which is eroded away, especially the posterior portion – shaft is covered in calcite deposits
Radius	Proximal end only (broken just below the radial tuberosity) – head and shaft are eroded and covered in calcite deposits, obscuring morphology
Ulna	Left: nearly complete (posterior border of radial facet is slightly eroded), distal epiphysis is missing – some calcite accretions on the proximal epiphysis Right: shaft is broken in thirds with approximately 1–2 cm missing of the middle portion, epiphyses are complete except for the posterior portion of the radial facet
Phalanges	At least a full set from one cheiridium
Innominate	Right: nearly complete, missing ischiopubic ramus and superior border of the ilium
Sacrum	Superior half only (two vertebral bodies preserved with calcite deposits obscuring details of the transverse and spinous processes, left auricular surface is eroded)
Femur	Left: complete with calcite deposits on shaft (posterior and inferior surfaces of head are slightly eroded) Right: complete with thick calcite deposits on the distal portion of the shaft and patellar surface (lesser trochanter is slightly eroded and medial half of the medial condyle is missing)
Patella	Right: complete with slight erosion around the circumference
Tibia	Left: complete but the anterior surface of the tibial plateau is heavily eroded as is the anterior portion of the medial malleolus Right: complete with thick calcite deposits on the distal portion (medial portion of the medial malleolus is eroded)
Tarsals	Calcaneus (right and left), talus (right and left), and right navicular, cuneiforms, and cuboid
Metatarsals	*I–V* (right and left)

are parts of the postcranial skeleton that provide the strongest functional link between this species and *Alouatta* (see discussion below as well as Halenar, 2012).

Systematics

The evidence presented above suggests the LS and TBV specimens that have both previously been assigned to *P. brasiliensis* Lund actually represent two distinct taxa. The type specimen from Lagoa Santa is morphologically similar to *Brachyteles* and *Ateles*, but comparable elements of the TBV specimen are distinctly different. When the evidence from the entire skeleton is taken into account along with its behavioral and systematic implications, the case for a conspecific allocation becomes weak. The anatomy of the distal humerus of TBV is sui generis among platyrrhines (and crown anthropoid primates) and its proximal femur and innominate (discussed below) resemble *Alouatta*, which is also generically distinct among modern platyrrhines and believed to exhibit a derived pattern with evident locomotor consequences. Finding synapomorphic postcranial features shared exclusively with *Alouatta* is consistent with a suite of features displayed in the TBV cranium (Rosenberger et al., in press), including highly reduced relative brain size, a cylindrical braincase, posteriorly positioned foramen magnum, long basicranial axis, prominent nuchal crest, strong temporal lines, and an airorynchous prognathic face. As this adds support to the hypothesis that the TBV species is more closely related to *Alouatta* than the LS species, we herein allocate the former to a new genus and species, rather than simply a new species of *Protopithecus*.

Order Primates (Linnaeus, 1758)
Suborder Haplorhini (Pocock, 1918)
Semisuborder Simiiformes (Hoffstetter, 1977)
Hyporder Anthropoidea (Mivart, 1864)
Infraorder Platyrrhini (Geoffroy St. Hilaire, 1812)
Superfamily Ateloidea (Gray, 1825)
Family Atelidae (Gray, 1825)
Subfamily Alouattinae (Trouessart, 1897)

Cartelles coimbrafilhoi, gen. et. sp. nov.

Holotype Museu de Ciências Naturais PUC Minas Gerais (MCL) 06, a nearly complete adult skeleton consisting of a cranium and mandible with partial dentition; at least partial elements of every long bone, except the fibula; several thoracic, lumbar, and caudal vertebrae; several partial ribs; clavicular and scapular fragments; nearly complete right innominate and partial sacrum; calcanei, tali, and several other tarsals; metacarpals, metatarsals, and at least one full set of phalanges (Table 3; Figs. 14–18).

Type locality and age The Toca da Boa Vista cave entrance is located at 40° 51′ 39″ W longitude and 10° 09′ 36″ S latitude, near Campo Formosa in Bahia, Brazil, at an altitude of 600 m above sea level. Mass spectronomic U-series dating of speleothem calcite deposits suggest a late Pleistocene date for the fossils, but the skeletal elements have not been dated directly. Samples from the caves range from 359,890 ± 23,373 ya (years ago) to 10,276 ± 2001 ya with a cluster of dates around 15–20 kya (thousands of years ago) for material associated with some of the non-primate fossils (Auler et al., 2006). Unfortunately, none of those samples come from the exact *Cartelles* locality so a more precise age estimate is not possible at this time.

Etymology *Cartelles*, in honor of Dr. Castor Cartelle, for his important contributions to the paleontology of Pleistocene Brazil, and with reference to the atelids *Ateles* and *Brachyteles*. *coimbrafilhoi*, in honor of Dr. Adelmar Faria Coimbra-Filho, for his indispensable leadership in creating the Brazilian conservation movement.

Synonomy Names associated with Lund's Lagoa Santa material can be confused in synonymy with *Cartelles coimbrafilhoi*, most commonly the genus name *Brachyteles* up until 1995 (see Hartwig, 1995b). Also pertinent is *Eriodes protopithecus* Winge, 1895. The genus name *Eriodes* Geoffrey Saint-Hilaire 1829 is a junior synonym for *Brachyteles* Spix 1823, and the species epithet was an invalid nomenclatural change done to maintain continuity with Lund's original taxonomic language.

Diagnosis A large atelid, 25–28 kg in body weight, thus more than twice the body mass of any living New World monkey and the estimated mass of the atelid fossils *Stirtonia*, *Solimoea*, and

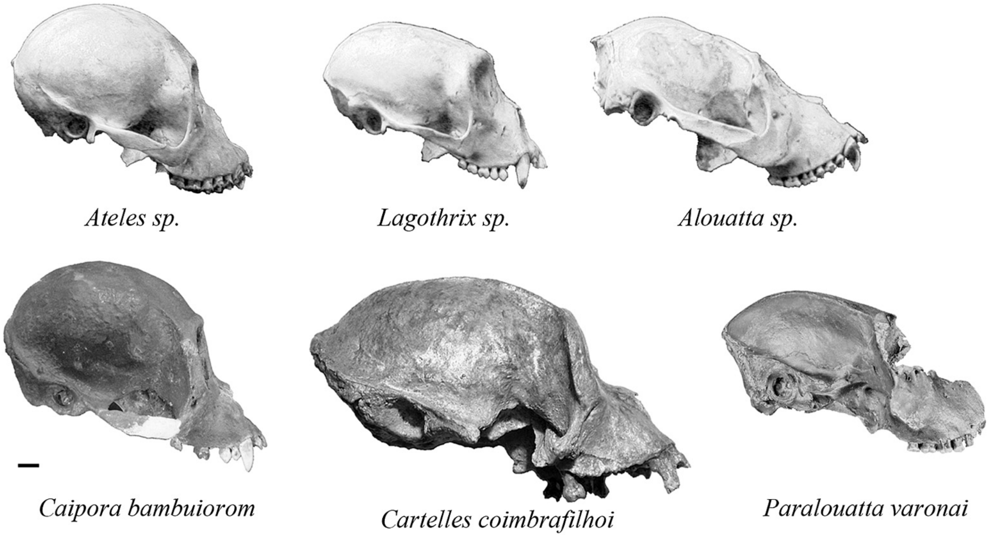

Figure 14. Comparative cranial anatomy. Top row (left to right) = *Ateles* sp., *Lagothrix* sp., *Alouatta* sp. Bottom row (left to right) = *Caipora bambuiorom*, *Cartelles coimbrafilhoi*, *Paralouatta varonai*. In lateral view many of the similarities between *Cartelles*, *Paralouatta*, and *Alouatta* are evident including their large airorynchous faces, ovoid braincases, posteriorly directed nuchal planes, and strong temporonuchal crests. These features are all absent or less well-developed in *Ateles*, *Lagothrix*, and *Caipora*. Scale bar = 1 cm.

Paralouatta. Skull with a prognathic, somewhat airorhynchous face, small endocranial capacity relative to body size, marked temporal lines, prominent compound temporo-nuchal crests, posteriorly positioned foramen magnum with moderately elongate basicranium and subvertical nuchal plane, a combination differentiating *Cartelles* from the modern atelines *Ateles*, *Brachyteles*, and *Lagothrix* and resembling the *Alouatta* pattern. Proportionally large incisors and bunodont cheek teeth differentiate *Cartelles* from *Alouatta* and *Stirtonia*, which have relatively small incisors and cristodont molars. Limb bones distinguished from *Protopithecus* and all other platyrrhines by their combined robustness, marked development of the brachioradialis flange on the humerus and very well-developed gluteal tuberosity, short neck, and distally elongate lesser trochanter on the femur. This configuration of craniodental and postcranial features distinguishes *Cartelles* from the similarly-sized Pleistocene *Caipora* from the same cave site.

Description Prior to our relegation of the TBV specimen to the new genus and species *Cartelles coimbrafilhoi*, the taxonomic uniqueness of this material was described and discussed in several, often detailed reports under its former nomen, *P. brasiliensis* (Hartwig, 1995a,b; Hartwig and Cartelle, 1996; MacPhee and Horovitz, 2002; Rosenberger et al., 2009, 2011, in press; Halenar, 2011a,b). These studies emphasized the skull, mandible, dentition, parts of the postcranium, and body mass but none, with the exception of Hartwig (1995a), incorporated the Lund material except as a passing reference. Thus the essentials of those descriptions and interpretations of *P. brasiliensis* actually apply to *C. coimbrafilhoi*.

Craniodentally, while *Cartelles* can be easily distinguished from all known atelids, including extant *Alouatta*, *Lagothrix*, *Ateles* and *Brachyteles*, and the extinct *Paralouatta* from Cuba, it most resembles *Lagothrix* and *Paralouatta* in a mixture of characteristics (Rosenberger et al., 2011, in press). Like *Paralouatta* and *Lagothrix*, the cheek teeth are bunodont, lacking the cristodont patterns seen

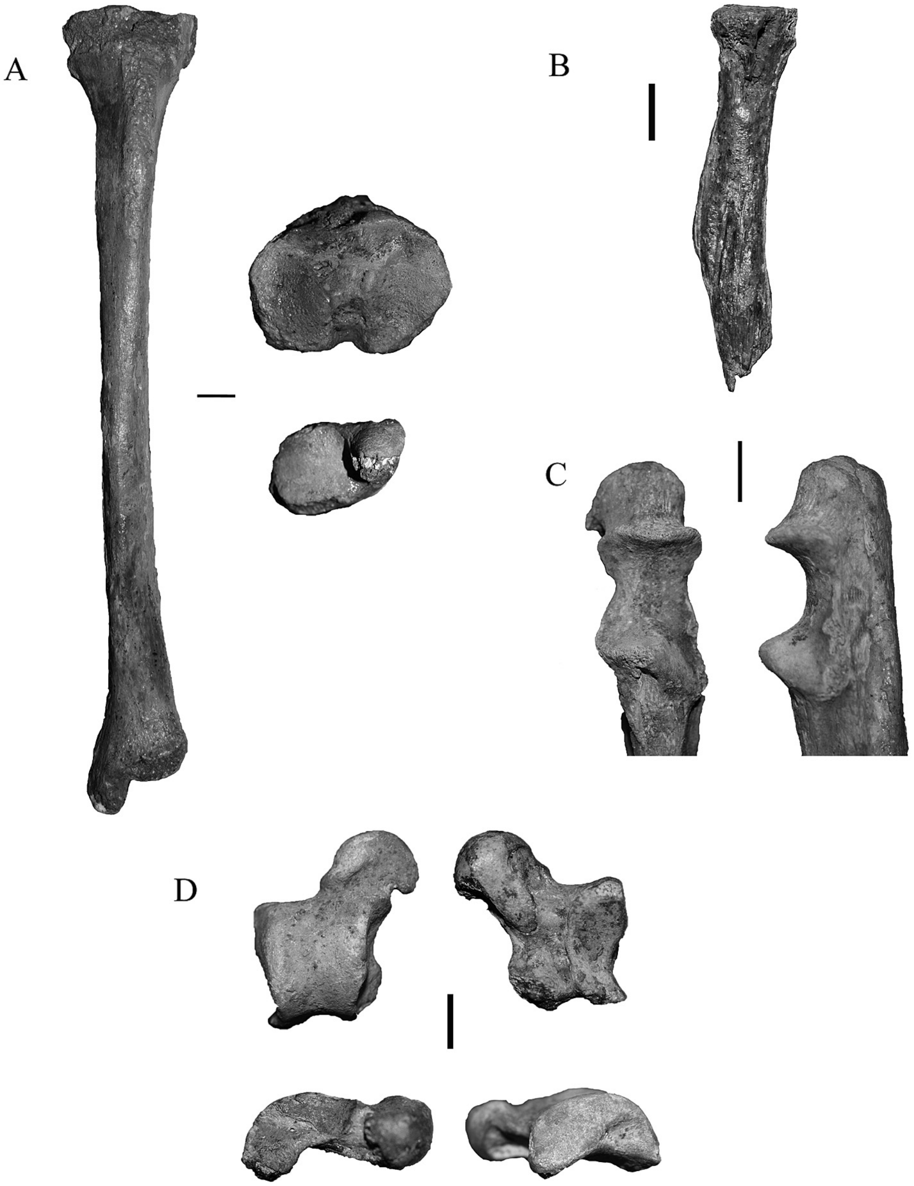

Figure 15. Holotype of *Cartelles*. A. Left tibia in anterior (left), superior (top), and inferior (bottom) view. B. Left radius in anterior view. C. Close-up of left proximal ulna in anterior (left) and lateral (right) view. D. Left talus in superior (top left), inferior (top right), medial (bottom left), and lateral view (bottom right). Scale bars = 1 cm.

in *Alouatta* and *Brachyteles* and the reduced crown size and morphology of *Ateles*. This further distinguishes *Cartelles* from two extinct, cristodont alouattines, the middle Miocene *Stirtonia* from La Venta, Colombia, and the late middle Miocene *Solimoea*, from the central-west Brazilian state of Acre. The latter is poorly known and its affinities within Atelidae are a matter of debate (see Kay and Cozzuol, 2006; Rosenberger et al., in press), but we regard it as alouattine. Among the atelids, relative to molar size, the proportions of the lower incisor crowns are largest in *Cartelles* and *Lagothrix* (Rosenberger et al., in press).

The cranium may be described similarly. It differs markedly from most atelines but resembles *Alouatta* and *Paralouatta* in a number of important features, some reported initially by Hartwig and Cartelle (1996), who emphasized the *Alouatta*-like traits. Thus, *Cartelles* exhibits a moderately large, upturned snout, an elongated basicranium and a small relative endocranial volume with a posteriorly directed foramen magnum, but in combination with an expansive, angled nuchal region framed by a marked compound temporo-nuchal crest (Fig. 14). The mandibular morphology is also unique. It does not resemble the reduced lower jaw of *Ateles* or, at the opposite end of the atelid spectrum, the massively postero-inferiorly enlarged and elevated ramus of *Alouatta*. While the *Cartelles* mandible is incomplete, the anterior portion that is preserved shows species-specific morphologies within atelids, and the two sides of the corpus in *Cartelles* are not widening away from one another or deepening posteriorly as in *Alouatta* (Halenar, 2012).

Other aspects of the *Cartelles* skeleton not considered above are also consistent with craniodental assessments. Despite the poor preservation of its scapula, *Cartelles* has been shown to share traits with the suspensory atelines *Ateles* and *Brachyteles* that suggest a very mobile glenohumeral joint (Hartwig and Cartelle, 1996; Jones, 2008). The bicipital groove on the proximal humerus is relatively narrow and deep and the tubercles sit below the level of the head, a configuration that is seen in suspensory primates (e.g., Larson, 1993). Despite a suggestion that their large body size would have rendered them predominantly terrestrial (Heymann, 1998), there are no classic indicators of a commitment to terrestrial locomotion exhibited by the *Cartelles* postcranial remains. For example, the fossil humerus does not exhibit the extreme distal projection of the medial edge of the trochlea like those in terrestrial primates (e.g., Rose, 1988, 1993). To the contrary: the evidence from the morphology of the forelimb and vertebral column in particular indicates arboreality with a relatively high degree of suspensory ability (see also Jones, 2008; Halenar, 2011b).

The radius of *Cartelles* is not complete (Fig. 15B); only the proximal end is present and the head is heavily worn. But the preserved radial tuberosity is relatively large and situated more distally on a long radial neck, increasing the length of the lever arm for the biceps toward a range seen in more suspensory atelines (Jones, 2008). The talus is also similar to *Ateles* and the suspensory atelines with a broad articular surface and a relatively short neck (Fig. 15D).

In addition to these postcranial traits indicative of suspensory locomotion in the ateline style, there are several features of the elbow and hip joints suggesting that climbing and hindlimb suspension could also be important parts of the locomotor repertoire (Hartwig and Cartelle, 1996; Halenar, 2011b). The expanded brachioradialis flange is one of the features pointed out by Hartwig and Cartelle (1996) that suggests an emphasis on forelimb flexion during climbing. Other fossil primates that have a well-developed brachioradialis flange, such as *Adapis*, *Notharctus*, *Apidium*, and *Aegyptopithecus*, have also been suggested to emphasize climbing in their locomotor repertoire (e.g., Dagosto, 1993; Gebo, 1993; Fleagle and Simons, 1995). However, it is unclear whether the size of the flange correlates with the size and power of the brachioradialis muscle and whether the size and power of that muscle correlates with a singular locomotor pattern. Extant anthropoids such as *Cebus*, *Papio*, *Pan*, and *Pongo* also have a brachioradialis flange, but none are as prominent as that seen in the *Cartelles* humerus, which is qualitatively more similar to the large, flattened condition of many strepsirhines and does not match the morphology of any other platyrrhine (Fig. 6). In fact, a 3D geometric morphometric analysis of the LS and TBV forelimb elements found that while both fell generally within a cluster of suspensory atelines, the two fossils were not their nearest neighbors in shape space (Halenar, 2011b). The TBV specimen instead showed phenetic similarities with a group of extant strepsirhines (Halenar, 2011b). For the strepsirhines, the prominent brachioradialis flange has been viewed as an indicator of flexion in an adducted posture, as seen during vertical clinging and leaping (Dagosto, 1993; Fleagle and Simons, 1995).

Non-locomotor interpretations of the size of the brachioradialis flange can also be entertained. Extant *Alouatta* also keep their elbows flexed while howling, and the inferred development of the relevant musculature in this large-bodied individual, which also presents an enlarged subbasal space in the cranium (Halenar, 2012; Rosenberger et al., in press), could indicate the importance of a

Figure 16. Partial right innominate of *Cartelles* (lateral view). Scale bar = 1 cm.

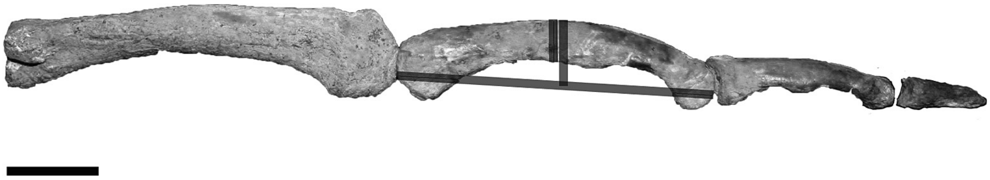

Figure 17. Composite ray of *Cartelles*. Lines on the proximal phalanx show the dimensions necessary for calculating the included angle of curvature, which on this specimen was approximately 60°. Scale bar = 1 cm.

similar positional behavior. However, it should be noted that the brachioradialis flange and associated flexor musculature are not any larger in extant *Alouatta* than the other atelids (e.g., Schön, 1968, Fig. 6; Table 2).

Other skeletal features that have been suggested to indicate climbing as an important part of the locomotor repertoire can also be noted. Like an arboreal climber that emphasizes more pronation/supination at the elbow, the radial facet on the proximal ulna is inset against the shaft of the bone and faces anterolaterally (e.g., Gebo, 1993; Rose, 1993, Fig. 15C). While the olecranon process is not retroflexed and resembles *Ateles* in orientation and size, aspects of the semilunar notch are dissimilar. For example, the distal facet of the trochlear notch is much smaller and less convex and the coronoid process is slightly more projecting and oriented at a shallower angle. As in the humerus, the ulna exhibits a combination of traits usually seen only in either suspensory taxa like the atelines or taxa that are more generalized arboreal climbers like *Alouatta*.

Hartwig and Cartelle (1996) point out the large, deeply concave iliac fossa on the *Cartelles* innominate for the attachment of the gluteus medius muscle (Fig. 16), which is also well-developed in *Alouatta* (i.e., Schön, 1968). It has been suggested by some to function as a medial rotator and stabilizer of the hip that could also be useful during hindlimb suspension and climbing (i.e., Stern, 1971; Larson and Stern, 2009). Both of these behaviors are used frequently by *Alouatta*, with hindlimb suspension, particularly during feeding, seen even more frequently than the forelimb suspension characteristic of *Ateles* (Mendel, 1976; Schön Ybarra, 1984; Cant, 1986; Schön Ybarra and Schön, 1987; Gebo, 1992; Bergeson, 1998). In the lower leg, the articular surfaces of the *Cartelles* proximal tibia are separated by a wider distance across the anterior portion of the plateau than the posterior (Fig. 15A). The tibial plateau is not tilted posteriorly, as in small-bodied primates that are well-adapted for leaping (Anemone, 1993), but they do overhang the shaft posteriorly as in climbing primates like *Alouatta* (Schön Ybarra and Schön, 1987).

Phalangeal specimens exist, but it is unclear whether they are from the hands or the feet. They are nonetheless informative (Halenar, 2011b). The included angle of curvature (Stern et al., 1995) for one proximal phalanx of *Cartelles* is approximately 60° (Fig. 17). This is in the high end of the range of values reported for *Ateles* and *Hylobates* but below the range of *Pongo* (Jungers et al., 1997). The phalanges also have relatively strong and distally placed flexor sheath ridges, indicating strong grasping abilities (Almecija et al., 2007, 2009). Several caudal vertebrae are also preserved in the *Cartelles* sample (Fig. 18). While their morphology has not been studied in detail, indices of robusticity and estimates relating tail to trunk length ratios suggest proportions comparable to that of typical atelid prehensile tails (Jones, 2008; Halenar, 2011a).

The completeness of the *Cartelles* skeleton also allows for limb proportions to be entered into the data pool. The intermembral index of the TBV skeleton is 1.04, a value within the range of the suspensory, forelimb-dominated *Ateles* and *Brachyteles* and above the range of *Alouatta* (Erikson, 1963; Hartwig and Cartelle, 1996; Heymann, 1998, Table 1). While this has been used to support the

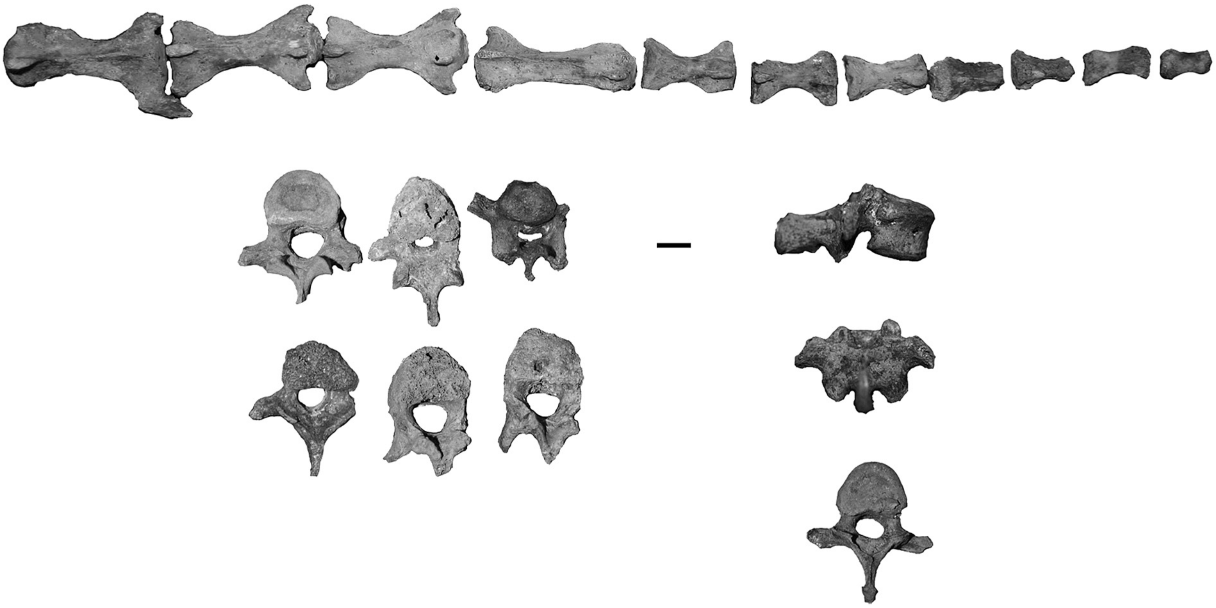

Figure 18. Assorted vertebrae of *Cartelles*. Top row are the preserved caudal vertebrae, arranged in descending size order but not meant to represent the complete tail. Bottom left are the most complete thoracic and lumbar vertebrae in inferior view. Bottom right is one of the best preserved thoracic vertebrae in lateral (top), posterior (middle), and inferior (bottom) views. Scale bar = 1 cm.

hypothesis of a more suspensory mode of locomotion for the fossil (Hartwig and Cartelle, 1996), the intermembral index should not be used in a vacuum and other aspects of the paleobiology of the fossil such as body size need to be taken into account (Heymann, 1998). A bivariate plot of log body mass against intermembral index for the extant atelids, as well as *Cartelles* and *Caipora*, shows that despite their relatively high index, the large body size of the fossils actually puts them directly on a regression line with the slower, more deliberately quadrupedal species of *Alouatta* (see Figure 1 in Heymann, 1998) and suggests an allometric component of intermembral index, which could be important to consider (i.e., Jungers, 1985). From this point of view, relative limb proportions could be seen as another postcranial trait linking the *Cartelles* skeleton with *Alouatta* as opposed to the extant atelines.

Conclusions

The new Bahian genus provides evidence that a third very large arboreal fossil atelid existed in the Pleistocene of Brazil. A fourth large-sized fossil from a different clade, a *Lagothrix*-sized cebine, is also known from the late middle Miocene of western Brazil, *Acrecebus solimoensis* (Kay and Cozzuol, 2006). This suggests we should rethink the common supposition, based on today's distribution, that New World monkeys are somehow size-constrained by their very nature, perhaps in connection with their exclusively arboreal habits. It should also enlarge our views concerning the possibility of mainland platyrrhines being arbo-terrestrial. Smaller New World monkeys, i.e., those less that 10 kg in body mass, almost all of which now live in greater Amazonia and may have been consigned to that biome since the middle Miocene, have less opportunity to engage in terrestriality under flooded forest conditions that can last half a year (Rosenberger et al., 2009). But in more marginal, dryer areas verging on open habitats, as has been suggested to be the case at various times throughout the Pleistocene at TBV (Cartelle, 1994; Auler et al., 2004; MacFadden, 2005), one might justifiably speculate that large body size could confer a sufficient aptitude to allow facultative terrestriality without involving discernible modifications of obligate ground-dwellers (Halenar, 2011a,b).

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