The effects of ecology and evolutionary history on robust capuchin morphological diversity

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ABSTRACT

Recent molecular work has confirmed the long-standing morphological hypothesis that capuchins are comprised of two distinct clades, the gracile (untufted) capuchins (genus *Cebus*, Erxleben, 1777) and the robust (tufted) capuchins (genus *Sapajus* Kerr, 1792). In the past, the robust group was treated as a single, undifferentiated and cosmopolitan species, with data from all populations lumped together in morphological and ecological studies, obscuring morphological differences that might exist across this radiation. Genetic evidence suggests that the modern radiation of robust capuchins began diversifying ~2.5 Ma, with significant subsequent geographic expansion into new habitat types. In this study we use a morphological sample of gracile and robust capuchin craniofacial and postcranial characters to examine how ecology and evolutionary history have contributed to morphological diversity within the robust capuchins. We predicted that if ecology is driving robust capuchin variation, three distinct robust morphotypes would be identified: (1) the Atlantic Forest species (*Sapajus xanthosternos*, *S. robustus*, and *S. nigritus*), (2) the Amazonian rainforest species (*S. apella*, *S. cay* and *S. macrocephalus*), and (3) the Cerrado–Caatinga species (*S. libidinosus*). Alternatively, if diversification time between species pairs predicts degree of morphological difference, we predicted that the recently diverged *S. apella*, *S. macrocephalus*, *S. libidinosus*, and *S. cay* would be morphologically comparable, with greater variation among the more ancient lineages of *S. nigritus*, *S. xanthosternos*, and *S. robustus*. Our analyses suggest that *S. libidinosus* has the most derived craniofacial and postcranial features, indicative of inhabiting a more terrestrial niche that includes a dependence on tool use for the extraction of imbedded foods. We also suggest that the cranial robusticity of *S. macrocephalus* and *S. apella* are indicative of recent competition with sympatric gracile capuchin species, resulting in character displacement.

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1. Introduction

Morphological evidence has long supported the division of capuchin monkeys into two types: the gracile or untufted capuchins (here and throughout referred to as genus *Cebus*, Erxleben, 1777), and the robust or tufted capuchins (referred to throughout as genus *Sapajus*, Kerr, 1792). While species diversity has always been recognized in the gracile capuchins, until recently the widespread robust capuchins were treated as a single species. The lumping of all robust capuchins into one species for data analyses has obscured any patterns of geographical or phylogenetic variation in this group (Lynch Alfaro et al., 2014). Here we review the history of morphological studies of the robust capuchins, as well as recent molecular and biogeographic evidence for the evolutionary history of this clade. Then we provide hypotheses about expected trends in morphological

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variation within robust capuchins on the basis of ecology and phylogeny, and test these hypotheses using phylogenetic principal components analysis on craniofacial character variation across robust capuchin species. We also offer preliminary data analyses of robust capuchin postcranial material in a comparative biogeographic context using ancestral state reconstructions (ASR) of postcranial indices.

1.1. Morphological studies establishing differences between gracile and robust capuchins

In 1913, Elliot first proposed a deep separation between what was then referred to as the "untufted" (gracile) and "tufted" (robust) capuchins. In 1939, Tate identified a number of cranial characteristics specific to tufted capuchins, and Hershkovitz (1949, 1955) confirmed the tufted and untufted forms as distinct, with some modification to which species had tufts or not. Subsequent craniodental work by Kinzey (1974) further distinguished the tufted capuchins from the untufted forms by describing, for the first time, the tufted forms as "robust" and the untufted forms as "gracile". Following this morphologically relevant distinction offered by Kinzey, for the remainder of the text, we will continue to use the synonyms "gracile" for *Cebus* and "robust" for *Sapajus*.

To date all studies of the craniodental morphology of capuchins have identified significant differences between robust and gracile species in mandibular robusticity (Kinzey, 1974; Hershkovitz, 1977; Bouvier, 1986; Cole, 1992; Daegling, 1992), craniofacial shape (Masterson, 1996), masticatory muscle leverage (Wright, 2005), canine robusticity (Plavcan and van Schaik, 1992), tooth root size (Spencer, 2003), enamel thickness (Wright, 2005) and occlusal surface area (Anapol and Lee, 1994; Wright, 2005). In every case these analyses have found that robust capuchins differ from the gracile species in exhibiting wider and deeper mandibular corpora and symphyses (both externally and internally), anteroposteriorly shorter and mediolaterally broader faces, increased leverage for the masseter and temporalis muscles, shorter and thicker canines, larger canine roots, thicker dental enamel, and greater molar surface area. In addition, dental microwear texture analyses found *Sapajus* (previously lumped in *Cebus apella*, sensu lato) to exhibit complex wear surfaces indicative of hard food feeding (Scott et al., 2005).

Few studies have compared postcranial morphology between or within the robust and gracile capuchins, and in common with previous studies of craniodental traits, the robust capuchins have always been lumped into a single species (*Cebus apella*, sensu lato). Although one study found that the robust group shares some similarities in postcrania with some of the gracile forms, including brachial index (robust capuchins are similar to *C. capucinus*) and some features of the calcaneus and astragalus (robust capuchins are similar to *C. olivaceus*) (Ford and Hobbs, 1996), other data suggest that for a number of postcranial features, robust capuchins are postcranially distinct from gracile capuchins, exhibiting a greater degree of postcranial robusticity as well as relatively shorter fore- and hind limbs (Ford and Hobbs, 1996; K. Wright, 2005, 2007). This divergent pattern appears early in development (Jungers and Fleagle, 1980).

In summary, there is long-standing evidence of morphological differences between gracile and robust capuchin monkeys, but there has been much less attention paid to diversity among the robust capuchins.

1.2. Morphological studies of geographic variation within robust capuchins

Elliot (1913) initially recognized several distinct species of robust capuchins, but ever since studies by Cabrera (1957) and Hill (1960) placed all of the robust forms into one species, *Cebus*

apella, morphological variation within the robust group has largely been ignored, with subsequent research tending to lump robust capuchins together irrespective of place of origin (e.g. Cole, 1992; Daegling, 1992; Ford and Hobbs, 1996; Masterson, 1996; Scott et al., 2005; Wright, 2005; K. Wright, 2005, 2007). A watershed moment for understanding robust capuchin diversity came with Torres de Assumpção's (1983) recognition of significant morphological variation based on geography. Subsequent analyses of pelage patterns and skeletal characters strongly supported multiple distinct species among the robust capuchins (Groves, 2001; Silva Jr., 2001, 2002a, 2002b; Rylands et al., 2005, 2012; Rylands and Mittermeier, 2009). The robust capuchin group is now considered by most taxonomists to be comprised of several species (Silva Jr., 2001; Groves, 2001; Rylands and Mittermeier, 2009; Rylands et al., 2005, 2012). The IUCN recognizes eight species of robust capuchins (which they currently still designate as belonging to the genus *Cebus*) (IUCN, 2012). These species include those largely restricted to the Atlantic Forest: *Sapajus flavius*, the blonde capuchin; *S. nigritus*, the black-horned capuchin; *S. robustus*, the robust tufted capuchin; *S. xanthosternos*, the yellow-breasted capuchin; those found in rainforests in Amazonia and the Guianas: *Sapajus apella*, the brown capuchin; *S. macrocephalus*, the large-headed capuchin; *S. cay*, Azara's capuchin; and *S. libidinosus*, the bearded capuchin, found in the drier habitats of Cerrado and Caatinga (Fig. 1). These species differ in ecogeographic niches (IUCN; Fig. 2). If ecology is driving morphological diversity in robust capuchin monkeys, we expect that the Atlantic Forest species will cluster together, those from the Amazon will form another cluster, and *S. libidinosus*, from much drier open habitats, will be the most morphologically distinct.

1.3. Molecular and biogeographic analyses of robust capuchin diversity

Recent molecular work (Perelman et al., 2011; Lynch Alfaro et al., 2012a,b; Ruiz-García et al., 2012; Springer et al., 2012) has confirmed the long-standing morphological hypothesis that capuchins are comprised of two distinct clades. Molecular data has provided support for a split during the Miocene, both from nuclear markers (6 Ma, 3.13–9.35 Ma 95% HPD: Perelman et al., 2011) and mitochondrial markers (6.15 Ma, 4.21–7.86 Ma 95% HPD: Lynch Alfaro et al., 2012a,b). A statistical phylogeographic analysis by Lynch Alfaro et al. (2012a,b) recovered the last common ancestor (LCA) of modern capuchins as most likely to have occurred in north-west Amazonia. Lynch Alfaro et al. (2012a,b) argue that the ancestral robust capuchin stock subsequently became isolated in the Atlantic Forest. At 2.65 Ma (1.57–3.8 Ma 95% HPD), the capuchin lineage leading to all modern robust species began to diversify along the Atlantic Coast of Brazil near the present-day range of *S. robustus*. Robust capuchins were restricted to the Atlantic Forest until about 0.40 Ma (0.21–0.67 Ma 95% HPD) when they "exploded," radiating north and west through Amazonia, into the Guianas as well as into the Cerrado–Caatinga (Lynch Alfaro et al., 2012a,b). The recent expansion of robust capuchins into the Amazon and Guianas led to broad sympatry with gracile capuchins (Lynch Alfaro et al., 2012a,b). Recently Cáceres et al. (2013) used geometric morphometric analysis of seven *Sapajus* and two *Cebus* species to assess the influence of climate and cranial size on craniofacial diversity among capuchins. They argued that capuchin species in drier southern habitats had narrower anteroposteriorly longer faces and that more recently diversified northern dwelling *Sapajus* species were more craniofacially similar to northern dwelling *Cebus* species. While latitude may play a role in selecting for particular craniofacial characteristics we have opted to develop our hypotheses based on differences in habitat and ecology and on the most recent molecular phylogenetic evidence.
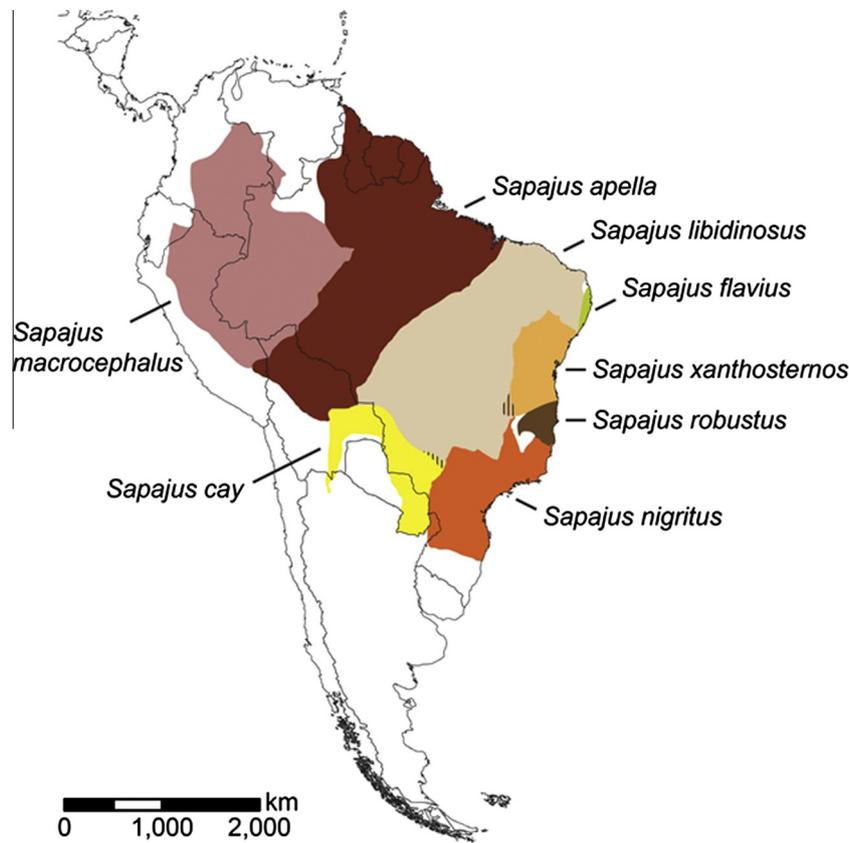
Fig. 1. Distribution map of the eight robust capuchin species currently recognized by the IUCN (IUCN, 2012). Borrowed from Lynch Alfaro et al. (2012a,b). Used with permission © 2011 Blackwell Publishing Ltd.

1.4. Comparative analysis of robust capuchin geographic diversity

Here we perform an analysis of morphological variation in cranial traits and mandibular traits across robust capuchin species, using phylogenetic principal components analysis (phyloPCA) (Revell, 2009). Principal components analysis is not a statistical test; however the distribution of taxa within the morphospace may suggest that ecological or phylogenetic effects underlie patterns of similarity. In addition, we perform an analysis of body dimension variation across robust capuchin species by comparing four postcranial indices. For this analysis we use ancestral state reconstruction (ASR) to interpret the results of nonparametric one-way analyses of variance (Kruskal–Wallis) among the robust species. If phylogeny largely determines morphology we expect closely related species to overlap strongly in morphospace. If there has been convergence in morphology due to shared ecological pressures, we expect overlap in morphospace among species with similar niches. For example, if ecological pressure is leading to character convergence among *Sapajus* species, we would predict three morphologically distinct groups: (1) an Atlantic Forest group, (2) an Amazonian–Guianan group, and (3) a Cerrado–Caatinga group, given that the species in these proposed groups share similar ecological conditions.

2. Materials and methods

2.1. Materials

We analyzed data sets compiled from specimens housed at museums throughout the United States for the cranial data, and throughout the United States and Europe for the mandibular and postcranial data. Cranial, mandibular, and postcranial data from specimens of seven of the eight robust capuchin species currently recognized by the IUCN (IUCN, 2012), based on the pelage analyses of Silva Jr. (2001, 2002a,b) are included. Due to limitations in available materials, we currently have no data for *S. flavius*. We also compare three gracile capuchin species, the weeper capuchin (*C. olivaceus*), white fronted capuchin (*C. albifrons* senso lato[1]), and white-faced capuchin (*C. capucinus*), to robust capuchin monkey variation.

Robust capuchin museum specimens are labeled in ways that may or may not have any relevance to our current understanding of species diversity and often are simply labeled *C. apella*. For this reason we only used wild-caught specimens with detailed locality data. Specific localities for each specimen were located on maps using Googlemaps (http://www.googlemaps.com) and gazetteers and then each specimen was assigned to one of the eight allopatric *Sapajus* species on the basis of locality. Although Hershkovitz (1977 and elsewhere) questioned the accuracy of some collectors' locality information, the late Prof. Vanzolini (long-term Director of the Museu de São Paulo) has adamantly stated that the collectors with whom he dealt gave dependable and accurate data on collection localities (personal communication, 1989, to SMF). In addition, three postcranial specimens assigned to *S. libidinosus* and two assigned to *S. nigritus* were collected by two of the coauthors (PI and KW) and measured on site by KW. A full list of specimens included in this study is available from the corresponding author (KW).

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[1] While paraphyly has been detected within the currently recognized species *C. albifrons* in recent molecular studies (Boubli et al., 2012; Lynch Alfaro et al., 2012a,b), for this analysis we pool the data for *C. albifrons* senso lato. Future studies are needed to understand morphological diversity within this group (Lynch Alfaro et al., 2014).
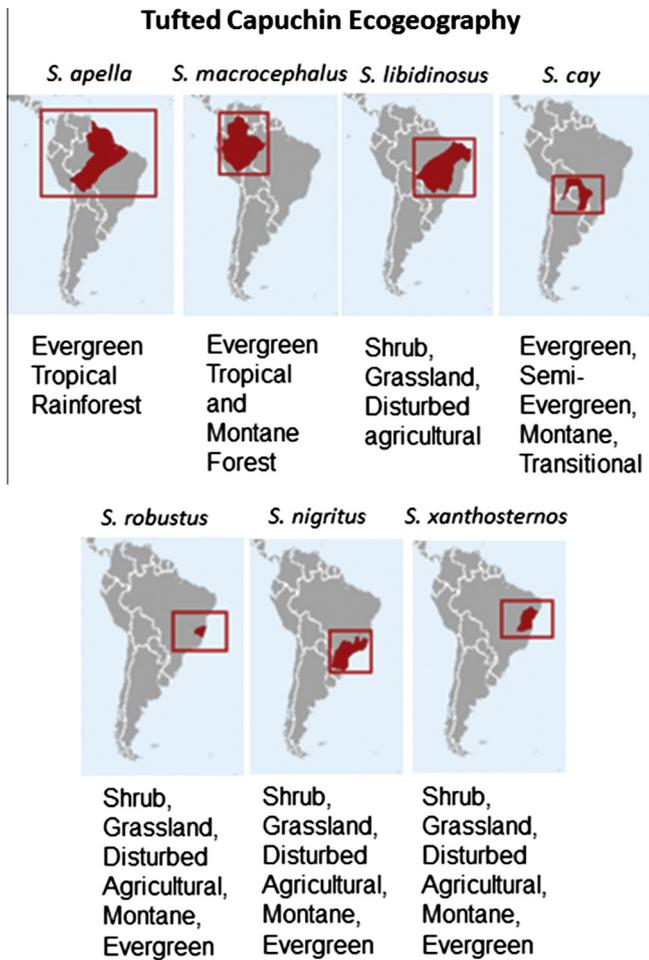
Tufted Capuchin Ecogeography

S. apella	S. macrocephalus	S. libidinosus	S. cay
Evergreen Tropical Rainforest	Evergreen Tropical and Montane Forest	Shrub, Grassland, Disturbed agricultural	Evergreen, Semi-Evergreen, Montane, Transitional

S. robustus	S. nigritus	S. xanthosternos
Shrub, Grassland, Disturbed Agricultural, Montane, Evergreen	Shrub, Grassland, Disturbed Agricultural, Montane, Evergreen	Shrub, Grassland, Disturbed Agricultural, Montane, Evergreen

Fig. 2. Geographical distribution and habitat types occupied by the seven robust capuchin species included in the current study. Range maps used with permission (IUCN: http://www.iucnredlist.org).

Table 1 presents the numbers of specimens, by data set, species, and sex. No data were available for *S. flavius*, and data for *S. xanthosternos* were absent for all but the cranial data set. The cranial data set, compiled by TM (see also Masterson, 1996), consists of twenty-three craniofacial variables measured on a pooled sex sample of 1124 individuals (118 *C. olivaceus*, 254 *C. albifrons*, 191 *C. capucinus*, 112 *S. apella*, 72 *S. cay*, 74 *S. libidinosus*, 145 *S. macrocephalus*, 110 *S. nigritus*, 29 *S. robustus*, and 19 *S. xanthosternos*). The mandibular data set, compiled by DGH (previously unpublished), includes nine mandibular measurements on a mixed sex sample of 578 individuals (58

C. olivaceus, 79 *C. capucinus*, 137 *C. albifrons*, 104 *S. apella*, 27 *S. cay*, 16 *S. libidinosus*, 77 *S. macrocephalus*, and 80 *S. nigritus*).

The postcranial dataset was compiled by DH and KW, and includes up to 6 of the robust species, along with specimens of all three gracile capuchin species. Linear measurements of the limb elements from 48 individuals (13 *S. apella*, 14 *S. macrocephalus*, 4 *S. nigritus*, 3 *S. libidinosus*, 3 *C. olivaceus*, 5 *C. albifrons*, and 6 *C. capucinus*) were used to create ratios representing the brachial (BI – radial length/humeral length), crural (CI – tibial length/femoral length), and intermembral (IM – [radial + tibial lengths]/[humeral + femoral lengths]) indices. Measurements of head-body and tail length taken at the time of capture and recorded on museum tags for 228 individuals (80 *S. apella*, 53 *S. macrocephalus*, 11 *S. nigritus*, 12 *S. libidinosus*, 5 *S. cay*, 2 *S. robustus*, 8 *C. olivaceus*, 57 *C. albifrons*, and 14 *C. capucinus*) were used to construct ratios of relative tail length (RTL - tail length/ [head + body lengths]). Male and female specimens were pooled and this was deemed appropriate given that all postcranial analyses involve ratios (see Section 2.2). Postcrania are rare in museum collections for all mammals, including primates; as such, for this study the postcranial data set is also the smallest.

2.2. Sexual dimorphism and size

Capuchins are known to exhibit sexual dimorphism in body weight and canine size (Plavcan and Kay, 1988; Ford, 1994; Plavcan, 2001). Given our relatively large samples for the cranial and mandibular data we present the results for the sexes separately.

As noted previously, all interpretations of postcranial variation are based on ratios, and should therefore be less affected by the potentially confounding effects of sexual size dimorphism. In order to assess any possible influence of sexual size dimorphism on the postcranial data set, for each species included in the study, we performed Wilcoxon Mann–Whitney tests with Bonferroni corrections to compare male and female means for each of the four postcranial ratios (BI, CI, IM, and RTL) included in the study. Bonferroni corrections on the level of significance were calculated based on the number of comparisons (species) for each index. In our postcranial sample, no taxa with available index data show any significant differences between males and females for BI, CI or IM. For the RTL index, there are no significant differences between males and females in any of the *Sapajus* species or any *Cebus* species, with the single exception of *C. albifrons* males and females (RTL significantly different at $p < .001$). The difference in RTL between *C. albifrons* males and females is peripheral to the central focus of this study and does not change the interpretation of our results regarding *Sapajus*, the focus of this study. We do not currently have a compelling explanation for why such a difference in relative tail

Table 1

Numbers of specimens by species and sex for cranial, mandibular, and postcranial analyses. A complete list of specimens is available upon request from the corresponding author (KW).

Species	Cranial data			Mandibular data			Postcranial data			Tag (tail) data		
	M	F	Total	M	F	Total	M	F	Total	M	F	Total
C. capucinus	111	80	191	32	47	79	2	4	6	5	9	14
C. olivaceus	75	43	118	36	22	58	1	2	3	5	3	8
C. albifrons	138	116	254	87	50	137	3	2	5	33	24	57
S. xanthosternos	11	8	19	nd	nd	nd	nd	nd	nd	nd	nd	nd
S. nigritus	63	47	110	47	33	80	3	1	4	6	5	11
S. robustus	12	17	29	nd	nd	nd	nd	nd	nd	1	1	2
S. apella	69	43	112	59	45	104	8	5	13	45	35	80
S. cay	36	36	72	17	10	27	nd	nd	nd	2	3	5
S. macrocephalus	91	54	145	49	28	77	10	4	14	30	23	53
S. libidinosus	42	32	74	11	5	16	1	2	3	8	4	12
Total	648	476	1124	338	240	578	28	20	48	135	107	228

length, as measured in this study, apparently exists for this one gracile capuchin species. In light of these results, males and females were pooled for all subsequent comparisons among *Sapajus* and *Cebus* species.

2.3. Capuchin phylogeny

In order to control for robust capuchin phylogenetic relationships in our analyses of morphological variation, and to be able to reconstruct ancestral character states, we used BEAST 1.7.5 (Drummond and Rambaut, 2007) to construct a chronogram for all capuchin species used in the study (Fig. 3). We inferred phylogeny and divergence times based on mitochondrial DNA sequences available on GenBank for 916bp of cytochrome *b* (*C. capucinus* JN409288; *C. albifrons* FJ529109; *C. olivaceus* FJ529106; *S. xanthosternos* FJ460174; *S. nigritus* JN409334; *S. cay* FJ529100; *S. macrocephalus* FJ529104; *S. libidinosus* JN409299; *S. apella*, unpublished). We used a *Saimiri macrodon* (LACM814, Lynch Alfaro et al., 2015) sequence as the outgroup (not pictured in tree) and the tree was calibrated with the fossil *Neosaimiri* at 12.5 Ma (Rosenberger et al., 1991; Takai, 1994; Hartwig and Meldrum, 2002) to constrain the minimum age on crown Cebinae. Our analysis employed a random starting tree, an uncorrelated lognormal relaxed clock, HKY substitution model, model of unique codon positions (1, 2, 3), and a Yule speciation process prior on diversification rate. We kept program default prior distributions on other model parameters. We ran the Markov chain Monte Carlo (MCMC) chain for 100 million steps and sampled states at every 50,000 generations. We visually assessed convergence of the data in Tracer v1.5, requiring an Effective Sample Size (ESS) > 200 for all model parameters, and discarded the first 10% as burnin in TreeAnnotator v1.6.1. We used this species phylogeny in our phyloPCA analyses for cranial and mandibular data (see Section 2.4) and in our ancestral state reconstructions for body dimensions (see Section 2.5).

2.4. Cranial and mandibular analyses

Our first analysis focuses on linear measurements of the cranium and upper face. This data set was compiled by Masterson
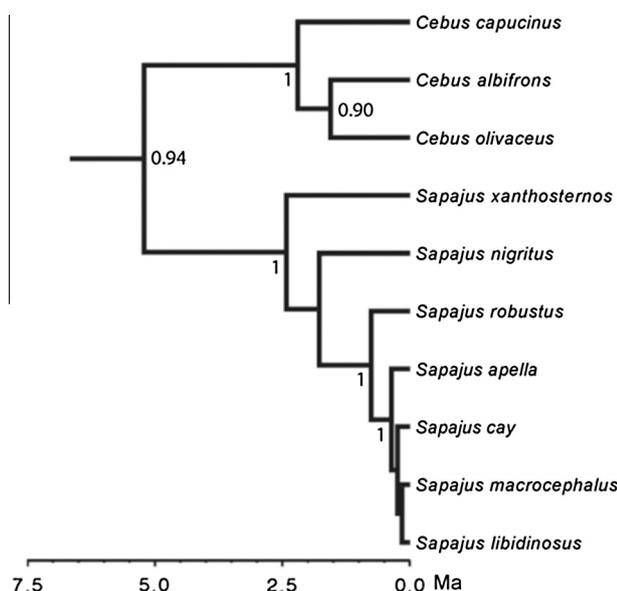

Fig. 3. Chronogram for all capuchin species included in study; three gracile species, *C. capucinus*, *C. albifrons*, and *C. olivaceus*, and seven robust species, *S. xanthosternos*, *S. nigritus*, *S. robustus*, *S, apella*, *S. cay*, *S. macrocephalus*, and *S. libidinosus*. Chronogram was constructed using BEAST 1.7.5 (Drummond and Rambaut, 2007).

(1996) in his study of dimorphic differences among *S. apella* (sensu lato) and gracile capuchins. Twenty craniofacial variables were measured (Table 2). As noted *S. flavius* was not available for cranial analyses. Aspects of the skull related to the cranial vault and the cranial base are primarily included as indicators of cranial size. Facial measures such as bizygomatic breadth, lower facial length, and facial height are primarily included given identified relationships between these measurements and diet. In a separate analysis, we compared nine mandibular measurements for the species available in a data set measured by DH (Table 3). Neither *S. xanthosternos* nor *S. flavius* were available within the mandibular data set. As with facial measures, differences among species in the collected mandibular measurements have been generally associated with patterns of food ingestion and particular food types and materials (Bouvier, 1986; Cole, 1992; Daegling, 1992; Wright et al., 2009).

Our reanalysis of cranial data measurements by Masterson (1996) and analysis of mandibular data measurements collected by DH each used the current species designations for the robust capuchin samples. We used phyloPCA implemented in R with phytools, as updated from Revell (2009). The phyloPCA is a data reduction technique that asks what the major axes of variation are in the data taking into account the shared evolutionary history and non-independence among the different capuchin monkey species due to their phylogenetic relationships. We log-transformed the raw cranial and mandibular data prior to analysis, and we ran the analyses on female means, male means, and pooled means per species. The raw averages for each variable and species, separated by sex are presented in Tables 2 and 3. These values are again addressed in the results and discussion sections. PC1, PC2 and PC3 of each phyloPCA analysis were visualized using the phylomorphospace package in phytools in R.

2.5. Postcranial analyses

Our postcranial analyses focused on general body dimension characteristics of the postcranial skeleton, as indicated by four ratios; relative tail length (RTL), brachial index, crural index, and intermembral index. Most of these data were originally compiled by DH (Table 3). Additional data, as well as ratio and index calculations, were contributed by KW. The relative tail length (RTL) was calculated from museum specimen tag data recorded at the time each specimen was collected in the field. Although museum tags provided records of field measurements for several individuals in six of the eight currently recognized robust capuchin species, most of these same specimens did not have postcranial elements preserved, thus our postcranial sample is relatively small and includes only four robust capuchin species. We used nonparametric one-way analyses of variance (Kruskal–Wallis) to test whether species differences are reflected in body and limb proportions.

In addition, ancestral state reconstructions (ASR) were performed for each postcranial ratio, using the capuchin phylogeny presented in Fig. 3 and described in Section 2.3. Ancestral state reconstructions were performed in R and accessed through the function "ace" in the package "ape" using the "geiger" library. We implemented the phylogenetic independent contrasts (pic) reconstruction for continuous variables, based on Felsenstein's (1985) method, and plotted the results using plot.phylo. The ratio values were binned by 2% intervals for each analysis, so the reconstructions are directly comparable. The visualization of the ancestral state reconstructions of character states across each tree displays the most likely character state at each internal node, representing the most likely morphology for each ancestral population in the tree.

Table 2
Average values per cranial variable for all capuchin species in the study. Variable definitions provided below variable code.

Sex/ species	PWAC Palate width canine	PWPC Palate width postcanine	PL Palate length	LFL Lower facial length	BMXW Bimaxillary width	BOW Biorbital width	OW Orbital width	OH Orbital height	POC Postorbital constriction	BZYB Bizygomatic breadth	ABCW Anterior basicranial width	BOL Basioccipital length	BAW Biauricular width	BMAW Bimastoid width	VH Vault height	MXCL Maximum cranial length	MNCL Minimum cranial length	BCL Basicranial length	BP Basion-prosthion	NP Nasion-prosthion	NBC Neurocranial breadth
Female																					
S. apella	24.45	29.33	29.02	46.06	47.82	41.01	19.5	20.89	38.49	58.96	43.03	12.94	41.54	49.79	48.19	87.71	68.94	52.28	57.89	34.43	51.31
S. cay	23.39	28.02	28.61	44.2	46.75	39.35	18.4	19.12	37.1	56.98	41.01	12.8	40.15	48.68	47.84	85.6	68.53	51.12	56.14	31.59	50.92
S. libidinosus	22.6	26.95	26.54	41.27	43.57	37.17	17.93	18.9	36.53	54.02	40.17	12.24	38.63	47.07	46.52	82.95	66.64	48.43	52.22	30.28	49.96
S. macrocephalus	25.02	29.52	29.54	44.88	49.32	40.95	19.53	20.63	38.52	60.13	43.12	13.58	41.73	49.82	48.57	86.47	70.14	53.83	60.05	34.6	51.67
S. nigritus	24.05	28.61	28.82	46.37	46.24	38.32	18.38	19.42	37.19	57.3	41.47	12.28	40.54	49.14	47.36	88.8	68.39	50.9	56.1	32.77	50.59
S. robustus	24.19	29.62	30.07	47.16	47.62	38.95	18.6	19.69	38.2	58.85	42.68	12.77	41.13	49.44	48.36	89.9	69.63	51.97	58.13	33.81	50.04
S. xanthosternos	23.95	29.38	30.5	46.65	47.76	39.71	19.17	19.8	39.22	58.2	41.71	12.93	42.93	51.69	47.6	90.37	68.47	50.75	58.87	34.63	50.51
C. olivaceus	24.06	28.57	29	43.34	43.86	42.23	19.81	20.34	39.43	57.83	42.67	12.9	40.71	48.77	47.91	86.05	71.82	52.68	58.14	31.92	53.54
C. albifrons	22.67	27.42	27.96	46.01	42.38	40.14	18.97	19.79	39.18	55.54	41.3	12.68	42.66	50.35	46.73	86.05	68.7	50.71	54.92	29.91	50.71
C. capucinus	23.74	28.31	29.79	47.3	42.88	41.54	19.53	19.83	39.9	57.84	43.09	12.96	42.66	50.35	47.62	90.02	70.52	52.86	58.02	31.61	52.01
Male																					
S. apella	27.74	30.71	31.32	50.58	53.63	43.57	20.22	20.69	39.87	67.27	45.53	14.41	43.84	53.14	50.11	93.26	72.31	57.33	64.29	36.51	53.09
S. cay	26.62	29.33	30.86	48.4	51.82	42.38	19.46	19.36	38.5	64.09	44.23	13.72	42.65	51.91	48.7	89.93	71.07	55.21	61.56	33.57	52.33
S. libidinosus	24.51	27.64	28.13	44.25	46.63	37.99	18.04	18.84	37.3	58.11	42.08	12.53	40.25	48.55	46.53	85.75	68.4	50.69	55.74	31.56	50.86
S. macrocephalus	28.09	30.82	31.44	51.06	53.9	42.83	20.21	20.47	39.55	66.61	45.28	14.41	43.58	52.61	50.04	94.48	72.68	57.05	60.58	35.49	52.8
S. nigritus	26.39	29.87	30.97	48.19	50.15	39.95	18.92	19.42	38.12	62.78	43.46	13.19	42.37	50.61	48.97	90.99	71.67	54.03	60.8	34.31	52.16
S. robustus	26.72	31.07	31.39	47.3	50.86	39.6	18.59	19.61	39.26	62.21	44.03	13.29	42.52	50.71	48.68	90.6	71.47	53.43	61.11	33.88	51.96
S. xanthosternos	24.94	29.92	31.32	48.58	50.22	39.25	18.75	19.69	39.37	60.91	42.47	13.56	41.55	49.94	47.82	91.6	69.85	52.53	62.35	35.89	51.58
C. olivaceus	26.13	29.71	30.49	49.48	46.93	44.33	20.67	20.68	40.48	62.17	44.45	13.75	44.54	53.77	48.4	93.83	73.56	55.55	62.35	33.4	54.46
C. albifrons	25.56	28.95	30.14	47.62	46.93	42.45	19.93	20.26	39.85	61.7	44	13.95	43.09	51.84	47.99	91.44	71.84	54.93	60.7	32.21	51.97
C. capucinus	25.37	28.86	30.2	47.3	43.64	41.87	19.7	19.72	40.2	59.96	44.56	13.47	43.93	52.16	47.84	91.73	71.87	54.38	59.8	32.34	53.62

3. Results

3.1. Cranial and mandibular results

3.1.1. Phylogenetic principal components analysis for cranial variation

PC1, which accounts for 92% of the variance in both the male and female samples, is defined by anterior snout (PWAC) and mid-facial breadth (BMXW & BXYB) as well as lower facial length (LFL) and basicranial length (BP) (Table 4 and Fig. 4). This holds for both males and females with a slight emphasis among females on variation in midfacial height. Along PC1 we see a separation into three groups: the Amazonian *S. apella* and *S. macrocephalus* are at one extreme, the Atlantic Forest species plus *S. cay* and all the gracile species grouped centrally, and *S. libidinosus* from the Cerrado and Caatinga at the other extreme.

PC 2 (female 3.6%, male 5.0%) is defined primarily by snout breadth unrelated to the canines (PWPC), orbital shape (BOW, OW, OH), and midfacial heights (NP). It exhibits three groups: Atlantic coastal species at one extreme (less *S. nigritus* in the case of males), and *C. olivaceus* (females) or *S. cay* (males) at the other extreme. All other species group centrally (Table 4 and Fig. 5). PC3 (female 2.7%, male 2.7%), which is defined by orbital shapes and palate length (PL), markedly separates out *S. cay* (females) or *C. olivaceus* (males) (Table 4 and Fig. 5). There is an additional notable shift between females and males in the position of *S. apella* where females group with *C. olivaceus* and males group with *S. macrocephalus*.

3.1.2. Phylogenetic PCA for mandibular variation

For all three of the first principal components, the most significant pattern is the separation of the *Cebus* and *Sapajus* species (Table 5, Figs. 6 and 7). Among *Sapajus* species *S. libidinosus* is the furthest removed from the other robust species. These patterns hold for both males and females. For both PC2 (female 22.0%, male 11.8%) and PC3 (female 6.8%, male 4.7%) the *Cebus* species remain separated from the *Sapajus* species, while the latter exhibit subtle shifts among one another (Table 5, Fig. 7). PC 1 (female 68.0%, male 79.1%), which accounts for the majority of the variation is defined by corpus (MCDP, MCTP) and symphyseal dimensions (MSYMD, MSYMT), PC2 is defined by mandibular ramus shape (MRH, MRL), and PC3 again by symphyseal and corpus shape differences as well as differences in condylar height (MCH) (Table 5 and Fig. 7).

3.2. Postcranial results

Species means and standard deviations for tail length to head + body length ratios, brachial indices, crural indices, and intermembral indices are presented in Table 6. A comparison of relative tail length (RTL) reveals significant differences among the three gracile and six robust capuchin species ($p < .01$), with the more terrestrial *S. libidinosus* exhibiting the shortest average tail length relative to head + body length. *S. nigritus*, an Atlantic Forest species, exhibits the longest average relative tail length, similar to the gracile *C. olivaceus*. The Amazon species, *S. apella* and *S. macrocephalus* fall on the shorter end of the spectrum, showing similar relative tail lengths, while *S. cay* appears to be intermediate with respect to relative tail length (Fig. 8B). The ancestral state reconstruction for the RTL index suggests that a longer tail is most likely the primitive condition for capuchins in general, and that over time tails have gotten shorter in both *Cebus* and *Sapajus*. Within *Sapajus*, *S. nigritus* appears to have retained a more primitive condition for tail length, while *S. libidinosus* is the most derived (Fig. 8A).

A significant difference was found for intermembral index ($p < 0.01$), with the robust *S. libidinosus* and gracile *C. albifrons* exhibiting the lowest IM, and the Amazon species *S. apella* and

Table 3
Average values per mandibular variable for all capuchin species in the study. Variable definitions provided below variable code.

Female									
S. apella	34.73	29.85	13.75	6.5	56.27	21.19	22.48	19.33	8.19
S. cay	34.23	29.53	14.51	6.36	56	20.97	22.48	19.92	8.62
S. libidinosus	34.88	30.69	15.77	6.56	56.49	21.6	23.16	20.5	8.85
S. macrocephalus	35.03	30.32	14.36	6.39	58.05	22.05	23.11	20.3	8.24
S. nigritus	35.76	30.75	14.32	6.63	57.14	21.54	22.57	20.17	8.54
S. robustus	37.06	30.83	14.75	7.65	60.93	23.08	24.26	22.37	9.24
C. olivaceus	27.99	23.37	11.74	5.52	54.75	19.79	22.29	18.09	7.52
C. albifrons	29.24	24.67	12.34	5.8	53.39	20.38	21.45	18.52	7.3
C. capucinus	30.06	25.4	12.72	5.78	56.28	21.4	22.48	19.27	7.31
Male									
S. apella	39.52	34.24	15.76	7.17	63.8	24.93	26.68	22.36	9.57
S. cay	40.24	35.11	16.99	7.14	64.77	24.86	26.76	22.79	9.75
S. libidinosus	41.82	35.83	17.07	8.55	65.84	25.51	27.57	24.03	10.24
S. macrocephalus	41.22	35.56	16.67	7.42	66.27	25.7	27.87	23.55	9.9
S. nigritus	40.42	35.52	16.07	7.3	64.68	25.11	26.38	22.87	9.91
S. robustus	42.5	36.44	17.56	7.55	67.52	26.1	27.67	24.68	10.03
C. olivaceus	32.25	27.65	13.95	5.91	62.64	23.49	26.44	20.73	9.04
C. albifrons	32.67	27.45	13.5	5.82	59.57	23.11	25.01	20.36	8.2
C. capucinus	33.47	29.37	14.58	6.35	63.71	25.37	26.88	22.1	8.47

Table 4
Phylogenetic PCA factor loadings by cranial variable for male and female capuchins in this study (see Table 2 for variable definitions).

	Female			Male		
	PC1	PC2	PC3	PC1	PC2	PC3
PWAC	0.234	−0.095	−0.039	0.267	0.088	−0.151
PWPC	0.215	−0.029	−0.317	0.212	0.458	−0.206
PL	0.244	0.412	−0.27	0.218	0.091	−0.519
LFL	0.319	0.141	−0.084	0.283	0.025	0.059
BMXW	0.276	0.245	−0.037	0.288	0.051	−0.388
BOW	0.225	−0.091	0.464	0.252	−0.574	0.055
OW	0.204	−0.324	0.207	0.23	−0.252	0.258
OH	0.215	−0.605	0.026	0.17	0.25	0.489
POC	0.127	−0.153	−0.071	0.119	0.157	0.131
BZYB	0.244	0.08	−0.023	0.278	−0.128	−0.026
ABCW	0.17	−0.19	0.107	0.149	−0.05	0.015
BOL	0.225	0.136	0.359	0.28	−0.063	0.104
BAW	0.182	−0.028	0.064	0.161	−0.074	0.004
BMAW	0.135	−0.003	0.15	0.167	−0.227	0.014
VH	0.098	0.108	0.032	0.145	0.047	−0.019
MXCL	0.175	0.056	−0.094	0.187	0.196	0.096
MNCL	0.115	0.12	0.103	0.119	0.025	−0.051
BCL	0.235	0.129	0.216	0.24	−0.196	0.026
BP	0.315	0.215	0.044	0.298	0.041	−0.079
NP	0.32	−0.288	−0.443	0.245	0.349	0.384
NBC	0.077	−0.021	0.347	0.078	−0.087	0.088

S. macrocephalus exhibiting the largest IM (Fig. 9B). Ancestral state reconstruction of the IM for capuchins suggests that a lower IM is derived for the entire group, although neither *Cebus* nor *Sapajus* appear to have changed very much from the ancestral condition in relative forelimb to hind limb length (Fig. 9A).

Both the brachial index (BI) and crural index (CI) appear to differ significantly among all capuchin species (BI; *p* = 0.03, Fig. 10B, CI; *p* = 0.01, Fig. 11B). The ancestral state reconstruction for BI suggests that for *Cebus*, distal forelimb elements have elongated, while *Sapajus* has retained a shorter distal forelimb element. Similar to relative tail length, *S. libidinosus* appears to be the most derived within *Sapajus*, exhibiting the relatively shortest distal forelimb among the individuals measured for this study (Fig. 10A). As with the intermembral index (IM), the ancestral state reconstruction for the crural index (CI) indicates that all capuchins retain relative distal hindlimb element lengths that are similar to the ancestral form. There does, however, appear to be some shortening of the tibia relative to the femur in the two robust Amazonian species, *S. apella* and *S. macrocephalus* (Fig. 11A).

4. Discussion

Our phylogenetically controlled principal component analysis for cranial variables suggests relatively little difference among *Sapajus* species in the Atlantic Forest. These species also appear to have the most similar crania to the gracile *Cebus*. Most interestingly, those *Sapajus* species that most recently diversified (*S. apella*, *S. macrocephalus*, *S. cay* and *S. libidinosus*) exhibit the greatest morphological differences among each other and relative to the Atlantic Forest species. In particular, the Amazonian *S. apella* and *S. macrocephalus* exhibit a distinctive and tight grouping, and *S. libidinosus* from the Cerrado–Caatinga exhibits a unique craniofacial pattern. In the phylogenetic PCA analyses, the pattern for the mandibles differs from that of the crania in that there is a clear distinction between all *Cebus* and all *Sapajus* species. This suggests that the two lineages diversified in jaw morphology prior to the modern radiations of *Sapajus* and *Cebus* species.

One discrepancy between the cranial and mandibular data required further investigation. We found from simple comparison of the raw means that *S. libidinosus* exhibits the smallest cranial measurements while exhibiting the largest mandibular measurements. We compared measurements taken by DH on mandibles of *S. libidinosus* with the same measurements taken by BW for the identical specimens and they were directly comparable. The same was done for cranial measurements taken by TM and BW. Hence the difference does not appear to be a consequence of differences in measuring technique. We were not able to compare the mandibles and crania of the same specimens since they were not collected by TM and DH on the same specimens of *S. libidinosus*. Ultimately, this discrepancy does not change our interpretation that the Cerrado–Caatinga environments have selected for unique craniofacial anatomy in *S. libidinosus*, as both the mandibular and particularly the cranial findings demonstrate, but our results suggest the need for additional investigation of *S. libidinosus* feeding behavior and morphology in the future.

Overall our cranial and mandibular results support the hypothesis that ecological selection is the primary engine driving craniofacial diversity among *Sapajus* species. For example, these results suggest a unique selective milieu in the Cerrado–Caatinga, given the distinct position of *S. libidinosus* in both cranial and mandibular morphospaces. In turn, not only do the short-and-broad faced *S. apella* and *S. macrocephalus* inhabit wet evergreen tropical rainforest, but in much of their range they are also found in sympatry with *C. olivaceus* and *C. albifrons* respectively, suggesting an important
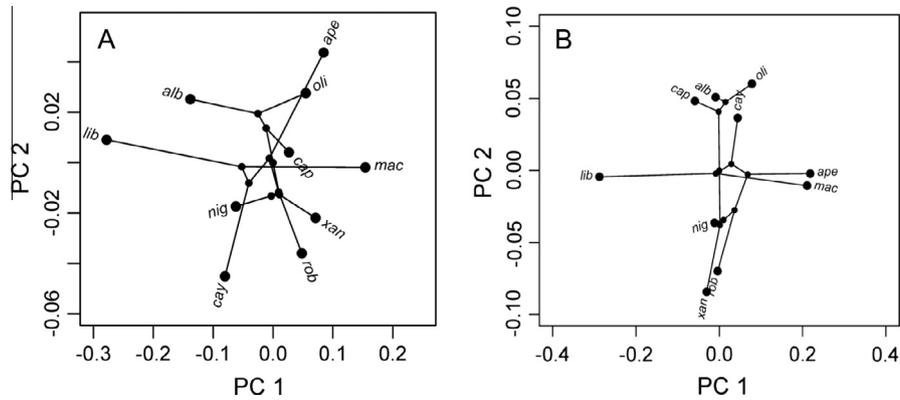
Fig. 4. Female (A) and Male (B) cranial phylogenetic PCA results for PC1 and PC2. alb = *C. albifrons*, ape = *S. apella*, cap = *C. capucinus*, cay = *S. cay*, lib = *S. libidinosus*, mac = *S. macrocephalus*, nig = *S. nigritus*, oli = *C. olivaceus*, rob = *S. robustus*, xan = *S. xanthosternos*.
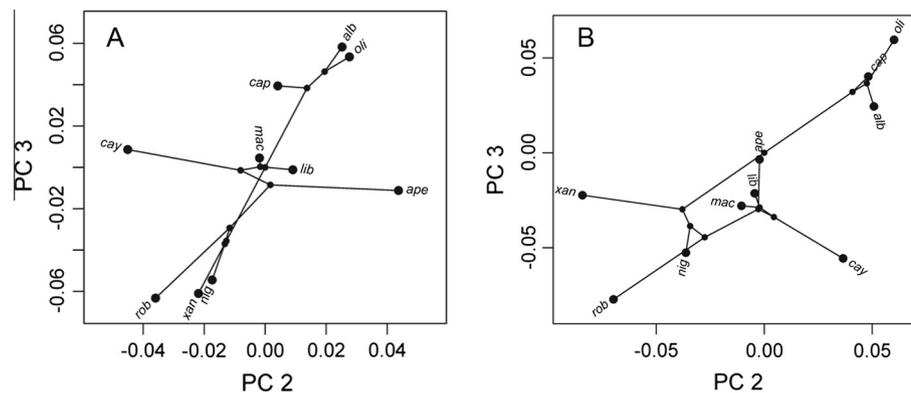

Fig. 5. Female (A) and Male (B) cranial phylogenetic PCA results for PC2 and PC3. (See Fig. 4 for species key.)

Table 5
Phylogenetic PCA factor loadings by mandibular variable for male and female capuchins in this study (see Table 3 for variable definitions).

Female				Male			
	PC1	PC2	PC3		PC1	PC2	PC3
MCH	0.117	0.416	0.398	MCH	0.225	0.299	−0.094
MRH	0.25	0.428	0.352	MRH	0.184	0.411	−0.197
MCDP	0.76	−0.077	−0.243	MCDP	0.214	0.403	−0.625
MCTP	0.216	0.145	0.513	MCTP	0.84	−0.485	0.06
MMAXL	−0.066	0.357	−0.27	MMAXL	0.084	0.308	0.226
MRL	0.021	0.502	−0.272	MRL	0.093	0.276	0.431
MJADD	0.093	0.188	−0.354	MJADD	0.096	0.315	0.505
MSYMD	0.22	0.237	−0.344	MSYMD	0.255	0.235	0.236
MSYMT	0.487	−0.381	0.074	MSYMT	0.273	0.134	−0.1

role for competition and possible character displacement in shaping the craniofacial anatomy of certain capuchin species. Our results for *S. apella* and *S. macrocephalus* are particularly relevant given the findings of Cáceres et al. (2013), who identified craniofacial similarities among northern dwelling *Sapajus* and *Cebus* species. Where they argue habitat has led to such similarities we argue that competition and character displacement has trumped ecological similarity and lead to marked differences among Amazon and Guianan dwelling *Sapajus* and *Cebus*. This discrepancy between our results and those of Cáceres et al. (2013) requires additional behavioral and morphological research.

Although far fewer postcranial Specimens were included in our analyses, the results indicate significant differences in relative limb and body dimensions that may reflect functionally significant feeding and foraging adaptations in each robust species, and thus also

support our ecological hypothesis. From our postcranial results, a pattern emerges in which the Guianan and Upper Amazonian robust species *S. apella* and *S. macrocephalus* are intermediate in relative tail length (RTL), but have very short distal hindlimb segments.

The Atlantic Forest species, *S. nigritus*, is similar in relative tail length (RTL) to the Pantanal species, *S. cay*, with both of these robust species appearing to be more similar to the gracile *Cebus* species for this feature. For the limb element indices, *S. nigritus* appears to have a longer tibia relative to femur than the other robust species, and groups with *Cebus* for this feature. The significantly longer tail and slightly longer hind limb could support higher frequencies of leaping in this Atlantic Forest species, which is known in some populations to move in the upper parts of the canopy where they forage on bromeliads year-round (K. Wright, 2005; Izar et al., 2012), and we predict that a study of positional behavior in *S. nigritus* would confirm this. Unfortunately, we were unable to include any specimens of *S. cay* in the limb element analyses, so the question remains as to how this species would group within such an analysis. Compared to the other robust species, relatively little is known about the behavior of *S. cay*, which is found primarily in riparian and flooded habitats in southern Brazil (Milano and Monteiro-Filho, 2009; Aguiar et al., 2011; De Lazari et al., 2013). More information on the behavior of this relatively understudied robust capuchin species is needed.

The Cerrado–Caatinga species *S. libidinosus* appears to have diverged from its robust congeners in having a particularly short tail, even relative to the overall trend towards shortened tails in *Sapajus*. In addition, the bearded capuchins included in this part of the analyses show a marked reduction in forelimb such that
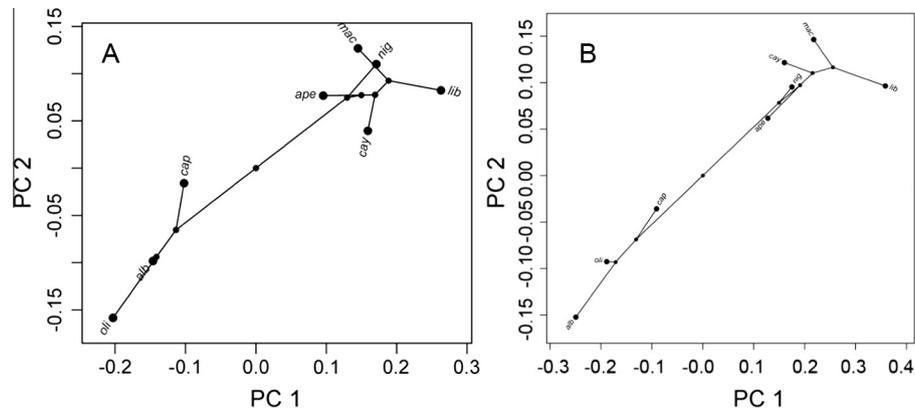
Fig. 6. Female (A) and Male (B) mandibular phylogenetic PCA results for PC1 and PC2. alb = *C. albifrons*, ape = *S. apella*, cap = *C. capucinus*, cay = *S. cay*, lib = *S. libidinosus*, mac = *S. macrocephalus*, nig = *S. nigritus*, oli = *C. olivaceus*.
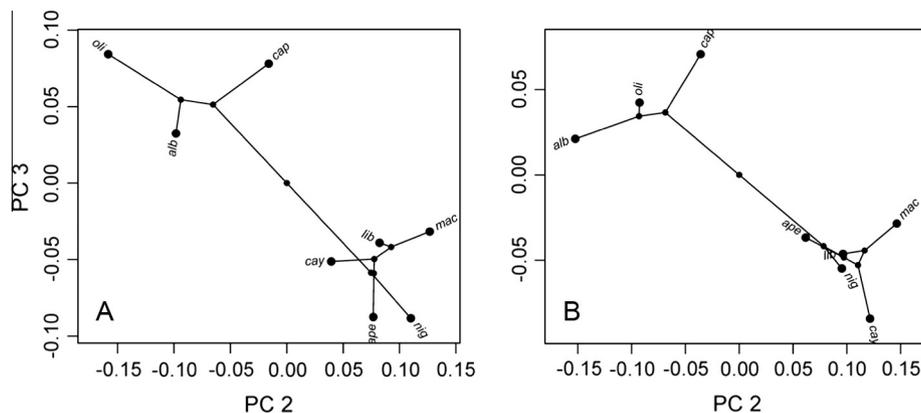

Fig. 7. Female (A) and Male (B) mandibular phylogenetic PCA results for PC2 and PC3. (See Fig. 6 for species key.)

the distal forelimb elements are the shortest, possibly accounting for their lower intermembral index. Our postcranial findings for *S. libidinosus* support the idea that the Cerrado–Caatinga environment presents a suite of unique selective factors that have shaped the behavior and morphology of bearded capuchins.

Previously published data comparing limb segment lengths and intermembral indices among *S. apella*, *S. libidinosus*, and the gracile *C. olivaceus* revealed that *C. olivaceus* has longer fore- and hind limbs than the robust capuchins and a lower intermembral index (Wright et al., 2009). It has been suggested that longer limbs, and particularly relatively longer distal limb segments, afford greater mechanical advantage during quicker-paced quadrupedal behaviors, and higher frequencies of leaping, such as that found in *C. olivaceus* (Wright, 2007). On the other hand, relatively short limbs would be beneficial in a slower paced, clambering form, such as *S. apella*. The shorter limbed *S. apella* is known to exhibit slower, more deliberate locomotion than sympatic *C. olivaceus* (K. Wright, 2005, 2007; Fleagle and Mittermeier, 1980). The trend (though weak) in our data is consistent with some previous accounts of distinctive patterns of locomotor behavior in *S. apella* as well as behavioral accounts suggesting this species may frequently move and forage in areas within their habitats that require negotiating complex arrangements of relatively smaller or more densely tangled substrates (Fleagle and Mittermeier, 1980; Terborgh, 1983; K. Wright 2005, 2007) Although the robust capuchins are similar in terms of limb robusticity, the *S. libidinosus* included in the present study appear to have slightly shorter fore- and hind limbs compared to *S. apella*, with an intermembral index that indicates a relatively shorter forelimb than the other robust capuchin species.

Table 6
Species means and standard deviations for relative tail length (RTL), brachial indices (BI), crural indices (CI), and intermembral indices (IMI).

Species	N[*]	MEAN	SD	SE
Relative tail length (RTL)				
S. apella	83	1.06	0.124	0.014
S. cay	5	1.12	0.069	0.013
S. libidinosus	12	0.96	0.078	0.022
S. macrocephalus	55	1.05	0.113	0.015
S. robustus	2	1.00	0.066	0.047
S. nigritus	11	1.20	0.153	0.046
S. flavius	1	1.24	.	.
C. olivaceus	8	1.17	0.142	0.050
C. albifrons	57	1.10	0.117	0.015
C. capucinus	15	1.07	0.114	0.029

Species		BI	CI	IMI
Brachial index (BI), crural index (CI), and intermembral index (IMI)				
S. apella	13	94	92	83
S. macrocephalus	14	94	92	83
S. nigriuts	4	93	95	82
S. libidinosus	3	89	93	80
C. olivaceus	3	94	93	83
C. albifrons	5	96	94	80
C. capucinus	6	97	96	81

[*] Sexes are pooled (see Methods).

This is in contrast to previously reported data (B. Wright et al., 2009) that suggested that *S. libidinosus* has a relatively longer fore-limb. This contrast may be the result of differences in sampling and/or accuracy of assigned provenance. The B. Wright et al.
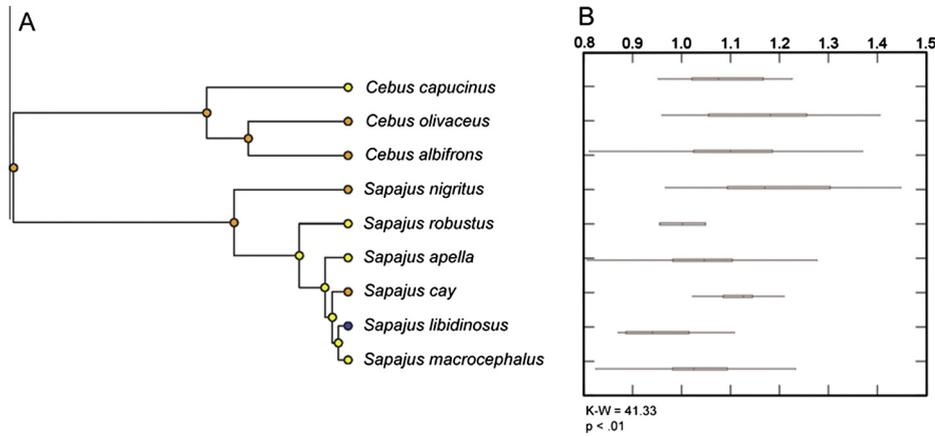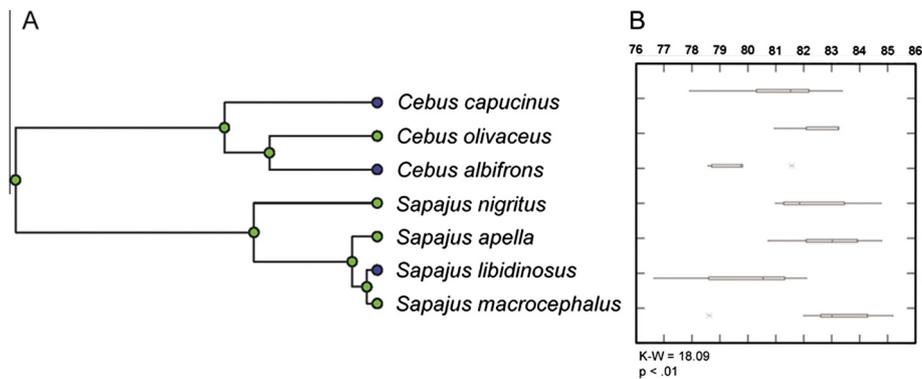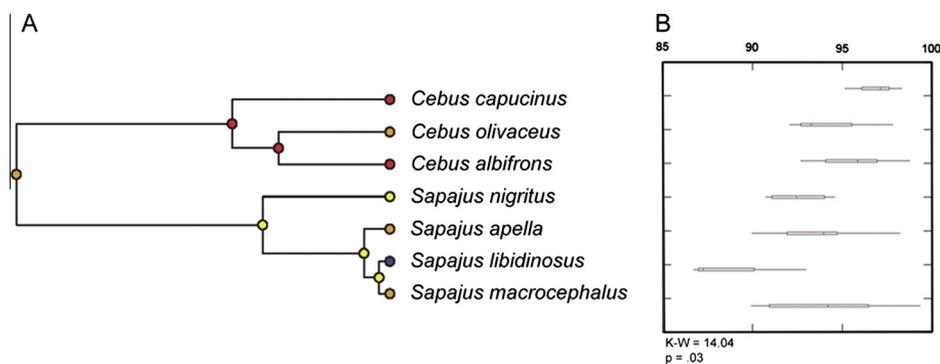
Fig. 8. (A) Ancestral state reconstruction (ASR) for relative tail length (RTL). Ratios are binned on a scale of 0.02 points (2% intervals) per bin where blue is 0.95–0.97, green is 0.97–0.99, yellow is 0.99–1.1, and orange is 1.1–1.3. (B) Comparison of relative tail length (ratio of tail length to head + body length) for five robust species (*S. libidinosus*, *S. macrocephalus*, *S. apella*, *S. cay*, and *S. nigritus*) and three gracile species (*C. capucinus*, *C. olivaceus*, and *C. albifrons*). $p < .01$, K–W = 41.33. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 9. (A) Ancestral state reconstruction (ASR) for intermembral index (IM). Ratios are binned on a scale of 0.02 points (2% intervals) per bin where blue: $\leqslant 0.81$; green: >0.81 and $\leqslant 0.83$. (B) Comparison of intermembral index (forelimb length/hind limb length) for four robust species (*S. libidinosus*, *S. macrocephalus*, *S. apella*, and *S. nigritus*) and three gracile species (*C. capucinus*, *C. olivaceus*, and *C. albifrons*). $p < .01$, K–W = 18.09. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 10. (A) Ancestral state reconstruction (ASR) for brachial index (BI). Ratios are binned on a scale of 0.02 points (2% intervals) per bin. Blue: $\leqslant 0.89$; green: >0.89 and $\leqslant 0.91$; yellow: $>$ than 0.91 and $\leqslant 0.93$; orange: >0.93 and $\leqslant 0.95$; red: >0.95 and $\leqslant 0.97$. (B) Comparison of brachial index (maximum radius length/maximum humerus length) for four robust species (*S. libidinosus*, *S. macrocephalus*, *S. apella*, and *S. nigritus*) and three gracile species (*C. capucinus*, *C. olivaceus*, and *C. albifrons*). $p = .03$, K–W = 14.04. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(2009) sample was comprised of museum specimens assigned to subspecific categories of *Cebus apella* (sensu lato), which were then reassigned to *C. libidinosus* based on published accounts of subspecific assignments (Groves, 2001). As noted in the Methods section, the current study uses three individuals that were collected and measured by one of the coauthors (KW) from a well-studied wild population known to be *S. libidinosus*. It is of note that the

population from which the three individuals in the current study are drawn regularly uses terrestrial substrates and engages routinely in stone tool use, as well as relatively frequent terrestrial bipedal behaviors associated with hammer stone tool transport and nut cracking (Fragaszy et al., 2004; Duarte et al., 2012; Massaro et al., 2012). This may hint at the possibility of population differences within a given robust capuchin species, related to
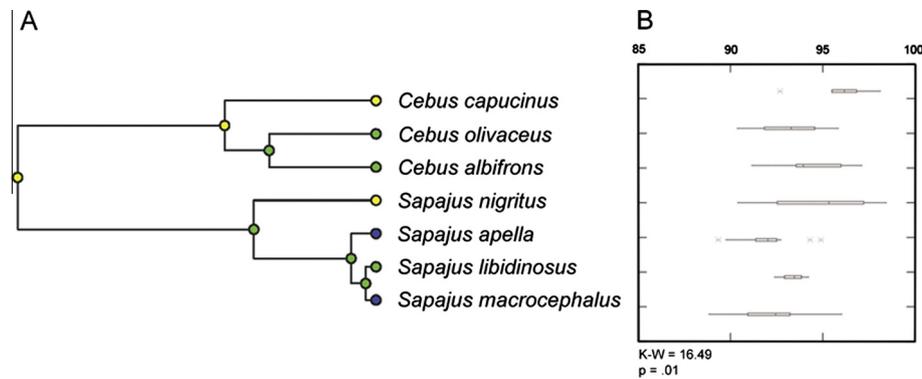
Fig. 11. (A) Ancestral state reconstruction (ASR) for crural index (CI). Ratios are binned on a scale of 0.02 points (2% intervals) per bin where blue: ⩽0.92; green: >0.92 and ⩽0.94, yellow: >0.94 and ⩽0.96. (B) Comparison of crural index (maximum tibia length/maximum femur length) for 4 tufted species (*S. libidinosus*, *S. macrocephalus*, *S. apella*, and *S. nigritus*) and three untufted species (*C. capucinus*, *C. olivaceus*, and *C. albifrons*). $p = .01$, K–W = 16.49. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

variation in foraging or other population-specific patterns of positional behavior related to habitat use.

5. Conclusions

Our results support the prediction that ecological factors have driven morphological diversification within *Sapajus*, and from our study we offer the following conclusions:

(1) Our morphological data strongly support the generic distinction between *Cebus* and *Sapajus*.
(2) Despite relatively long divergence times, the Atlantic Forest species *S. nigritus*, *S. robustus*, *and S. xanthosternos*, and the Southern species *S. cay* are still quite similar to one another in craniofacial morphology.
(3) *Sapajus libidinosus* from the Cerrado–Caatinga habitat is the most distinct among all *Sapajus* species both craniofacially and postcranially. We suggest that this is due to inhabiting an environment that has selected for greater reliance on terrestriality and the use of tools to access imbedded food items.
(4) The Amazonian–Guianan rainforest species *S. apella* and *S. macrocephalus* are highly similar to one another in cranial, mandibular and postcranial morphology. These species have diverged relatively recently from Atlantic coastal species, exhibiting a derived craniofacial morphology that is markedly distinct from *Cebus*. We suggest that competition with sympatric gracile species has led to accelerated rates of character change and greater craniofacial morphological specialization in these two robust species.

Additional insights into the evolutionary mechanisms driving morphological differentiation among *Sapajus* species can be gained through collection of more detailed, morphological, behavioral and ecological data for each of the eight species currently recognized by the IUCN. We suggest that this can be achieved through fostering better communication and collaboration among ecologists, morphologists, and phylogeneticists interested in understanding Neotropical primate biodiversity (Lynch Alfaro et al., 2014).

Acknowledgments

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