

REVIEW ARTICLE

How Different Are Robust and Gracile Capuchin Monkeys? An Argument for the Use of *Sapajus* and *Cebus*JESSICA W. LYNCH ALFARO^{1*}, JOSÉ DE SOUSA E SILVA JR², AND ANTHONY B. RYLANDS³¹*Institute for Society and Genetics, University of California, Los Angeles, California*²*Museu Paraense Emílio Goeldi, Belém, Pará, Brazil*³*Conservation International, Arlington, Virginia*

Capuchin monkey behavior has been the focus of increasing numbers of captive and field studies in recent years, clarifying behavioral and ecological differences between the two morphological types: the gracile and the robust capuchins (also referred to as untufted and tufted). Studies have tended to focus on the gracile species *Cebus capucinus* (fewer data are available for *C. albifrons*, *C. olivaceus*, and *C. kaapori*) and on *Cebus apella*, a name that has encompassed all of the robust capuchins since the 1960s. As a result, it is difficult to ascertain the variation within either gracile or robust types. The phylogenetic relationships between gracile and robust capuchins have also, until now, remained obscure. Recent studies have suggested two independent Pliocene radiations of capuchins stemming from a common ancestor in the Late Miocene, about 6.2 millions of years ago (Ma). The present-day gracile capuchins most likely originated in the Amazon, and the robust capuchins in the Atlantic Forest to the southeast. Sympatry between the two types is explained by a recent expansion of robust capuchins into the Amazon (ca. 400,000 years ago). Morphological data also support a division of capuchins into the same two distinct groups, and we propose the division of capuchin monkeys into two genera, *Sapajus* Kerr, 1792, for robust capuchins and *Cebus* Erxleben, 1777, for gracile capuchins, based on a review of extensive morphological, genetic, behavioral, ecological, and biogeographic evidence. *Am. J. Primatol.* 00:1–14, 2012. © 2012 Wiley Periodicals, Inc.

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INTRODUCTION

There is a long history of utter confusion regarding the systematics of the capuchin monkeys, much of which was, as pointed out by Hill [1960], resolved by the thorough review of Hershkovitz [1949]. Elliot [1913] provided a taxonomic key that divided the species into tufted (or crested) and untufted (not crested) groups. Subsequent major revisions maintained this division, but all were confounded to a greater or lesser degree by the taxonomy, confused identifications and nomenclature, and an immensely confusing variability in coat colors and color patterns. Hershkovitz [1949] provided a taxonomy of the untufted species which has withstood the test of time, although he expressed his doubts about the validity of a number of named taxa, and as he suspected, some of these have since been found to be not valid [Boubli et al., 2012; Ruiz-García et al., 2012]. Hershkovitz [1949] did not review the tufted capuchins, leaving this to Remington Kellogg, who never published his findings. Kellogg did correspond extensively, however, with W. C. Osman Hill, who published Kellogg's taxonomy with what information

he had in Volume IV, Part A of his monograph series *Primates: Comparative Anatomy and Taxonomy* [1960]. A partial insight into Hershkovitz's views on the taxonomy of the capuchin monkeys prior to his death in 1997 is provided by Aquino and Encarnación [1994], who mapped the Peruvian forms.

The taxonomy arising from Hershkovitz's [1949] review and from Hill's [1960] conclusions concerning the findings of Kellogg was as follows: Untufted group—the white-faced capuchin monkey *Cebus capucinus* [Linnaeus, 1758], the white-fronted capuchin *C. albifrons* [Humboldt,

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*Correspondence to: Jessica Lynch Alfaro, 1321 Rolfe Hall, Institute for Society and Genetics, University of California, Los Angeles, CA 90095. E-mail: jlynchalfaro@ucla.edu

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1812], and the weeper or wedge-capped capuchin *C. nigrivittatus* Wagner, 1848, today referred to as *C. olivaceus* Schomburgk, 1848 [see Rylands, 1999]; Tufted group—the brown or tufted capuchin *C. apella* [Linnaeus, 1758]. All of the capuchin monkeys consistently have been recognized as belonging to just one genus, *Cebus* [see Fragaszy et al., 2004a], and the considerable phenotypic diversity within each of the four species was described by Hershkovitz [1949] and Hill [1960] as the result of subspecific variation.

The division of the untufted and tufted capuchins was well-resolved by Hershkovitz [1949, 1955]. *Cebus xanthosternos* of the tufted group is sometimes indicated as being an exception in lacking tufts, but does in fact have two small backward pointing tufts when inspected more carefully [Silva, 2001]. With age, the untufted capuchins, especially the females, tend to develop a certain bushiness on the face and head, which in some cases includes tufts, notable, for example, in the females of *C. albifrons* [illustrated in Hill, 1960; Napier & Napier, 1967]. One evident feature that clearly separates the two species groups, well-illustrated by Hill [1960], is that the tufted capuchins are more compact and robust in their tail, limbs, jaw, and skull, and the untufted capuchins are less robust, more slender, and longer-limbed (see Fig. 1). For this reason, they are now more generally categorized as either robust (tufted) or gracile (untufted) capuchin monkey groups.

The most recent appraisals of capuchin monkey systematics have been carried out by Torres de Assumpção [1983], who studied the tufted capuchin group for a doctoral thesis published in part posthumously [see Rylands et al., 2005; Torres, 1988], by Silva [2001], who studied both tufted and untufted capuchin monkeys, also for a doctoral thesis, and by Groves [2001] for his book *Primate Taxonomy*. Torres de Assumpção [1983] and Groves [2001] examined mainly fur color and patterns; Silva [2001] in addition made a thorough analysis of cranial morphology. As a result of some genetic studies [Seuáñez et al., 1986, e.g.] and the revisions of Groves [2001, 2005] and Silva [2001], a number of the subspecies of Hill [1960] are now classified as species [Rylands et al., 2000]. A new gracile species *Cebus kaapori* was described by Queiroz [1992]. The number of tufted species was subsequently augmented with the rediscovery of the previously enigmatic blonde capuchin monkey, *Cebus flavius* (Schreber, 1774), by Oliveira and Langguth [2006].

Capuchins form a monophyletic clade, estimated to have diverged from squirrel monkeys (*Saimiri*) at 13.8 millions of years ago (Ma) (12.1–16.1 Ma) [Chiou et al., 2011] or 15.5 Ma (12.5–19.6 Ma) [Lynch Alfaro et al., 2011]. Clearly, robust and gracile capuchins share many synapomorphic changes in comparison to their sister taxon, the squirrel monkey; most notably a large increase in body size (ca. 3 kg vs. 800 g),

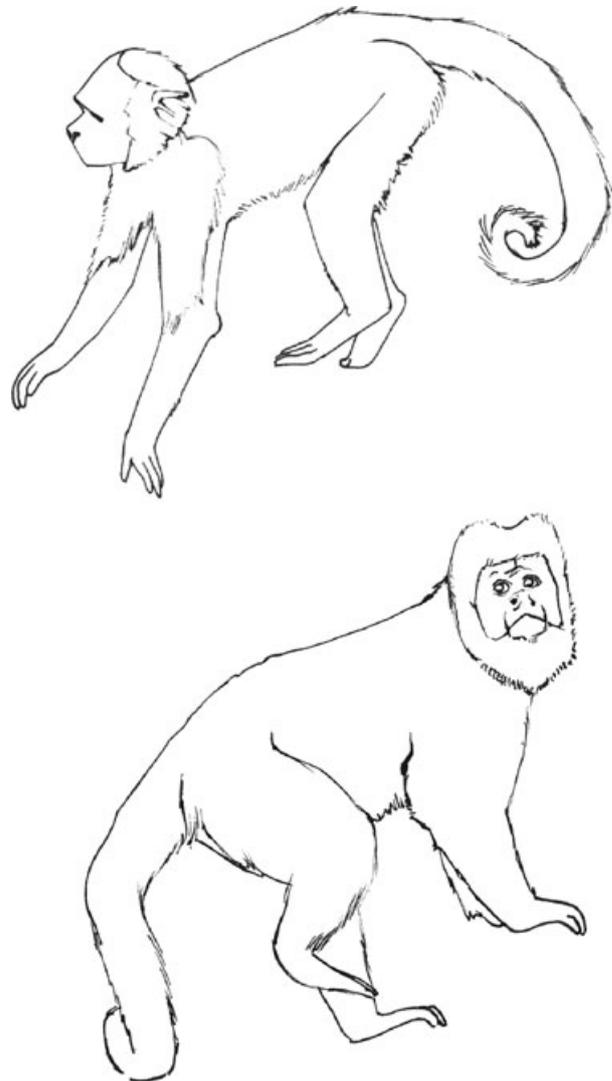


Fig. 1. Silhouettes of *Cebus* (top) and *Sapajus* (bottom). Drawings by Amisha Gadani.

a semi-prehensile tail, a higher encephalization quotient for at least *C. apella* (2.54 for *C. capucinus*, 3.49 for *C. apella*, and 2.63–2.80 for *Saimiri* [Jerison, 1973; Milligan, 2010]), increased manual dexterity and food processing skills, and a delayed life history with significantly increased longevity [Fragaszy et al., 2004a].

An examination of capuchin monkey diversity, however, reveals far more genetic and morphological difference *between* robust and gracile species than *within* either group [Lynch Alfaro et al., 2011; Silva, 2001]. Contra Hershkovitz [1949] and Hill [1960] who lumped all robust capuchins as *C. apella*, there may be more genetic and species diversity in the robust group compared to the gracile [Lynch Alfaro et al., 2011; Silva, 2001]. On the other hand, recent studies of diversity in gracile capuchins [Boubli et al., 2012; Ruiz-García et al., 2010, 2012] suggest that untufted species' diversity has been underestimated

in large part by lumping together the paraphyletic and discontinuously distributed capuchins from the Amazon, Andes, Trinidad, and western Ecuador under the taxon *C. albifrons*.

Our understanding of differences between the gracile and robust capuchin species is limited because the behavior of many capuchin species and subspecies has never been studied. Until now there have been relatively few systematic behavioral comparisons across multiple species, but these kinds of comparisons are included here, that is, *C. nigritus* versus *C. libidinosus* for socioecology [Izar et al., 2012]; gracile versus robust species for anointing behaviors [Lynch Alfaro et al., 2012]; *C. nigritus* and *C. capucinus* for tool use [Garber et al., 2012]; *C. flavius* and *C. libidinosus* for stone tool use [Emidio & Ferreira, 2012]; and gracile versus robust species for sexual behavior [Matthews, 2012]. Here we review morphological, biogeographic, ecological, and behavioral differences that distinguish the robust from the gracile capuchin monkeys.

MORPHOLOGICAL VARIATION

The tufted, or crested, capuchins stand out as being significantly more robust in terms of cranial and dental characteristics [Ford & Corruccini, 1985; Jungers & Fleagle, 1980], with both cranial and postcranial specializations for the exploitation of hard and tough foods [Wright et al., 2009]. Sexual dimorphism in cranial characters is more pronounced in robust than gracile capuchins [Master-son, 1997; Silva, 2001]. Robust capuchin males have a sagittal crest that is lacking in gracile capuchins [Silva, 2001]. The sagittal crest is an adaptation for durophagy, providing a greater area for attachment of the temporalis muscle for biting and chewing. Robust capuchins also have thickened corpora, larger ascending rami, and shorter mandibles compared to gracile capuchins [Bouvier, 1986; Daegling, 1992; Fragaszy et al., 2004a; Silva, 2001]. A larger zygomatic arch provides a greater area of attachment for the masseter and the ability to resist greater loading, and further reflects adaptations for crushing hard objects [Bouvier, 1986; G. Jones in Fragaszy et al., 2004a]. Byron [2009] compared *C. apella* to *C. olivaceus*, *C. albifrons*, and *C. capucinus* and found that *C. apella* had a significantly more robust mandibular and temporal fossa morphology as well as more complex sagittal sutures than other *Cebus* species; these differences were interpreted as adaptations to *C. apella*'s durophagous diet. Similarly, the larger muscle mass of the masseter and the temporalis muscles in *C. apella* compared to *C. capucinus* and *C. albifrons* are functionally attributed to a more resistant diet [Taylor & Vinyard, 2009]. In a study of cranial variation across three species of robust capuchins, Masterson [2001] reported that *C. nigritus* and *C. robustus* were both significantly larger

than, and had significantly larger dental arcades, increased prognathism, and larger absolute cranium size compared to *C. libidinosus*. This is probably also the case in comparison to *C. apella* (sensu Silva, 2001), and especially *C. cay*, with adult crania that are so small they look like the juvenile ones in other robust species [Silva, personal observation].

With regard to postcranial functional morphology, robust capuchins have shorter forelimbs and relatively shorter hands and feet compared to gracile capuchins. Body proportion differences are present early in development, and *C. albifrons* and *C. apella* show divergent growth trajectories of limb length as a function of body mass [Jungers & Fleagle, 1980]. *C. albifrons* is longer-limbed in proportion to body mass than *C. apella* throughout development, and this difference increases as growth progresses [Young, 2005]. Ford & Hobbs [1996] presented preliminary results that *C. olivaceus* (n = 2 specimens) is the gracile capuchin most similar to the robust capuchins in postcranial morphology.

Silva [2001] concluded from his analysis of capuchin external morphology (see below) that capuchins should be divided into two subgenera: *Sapajus* Kerr, 1792, corresponding to the robust forms [*Cebus (Sapajus) xanthosternos*, *Cebus (Sapajus) robustus*, *Cebus (Sapajus) macrocephalus*, *Cebus (Sapajus) apella*, *Cebus (Sapajus) libidinosus*, *Cebus (Sapajus) cay*, *Cebus (Sapajus) nigritus*], and *Cebus* for the gracile forms [*Cebus (Cebus) capucinus*, *Cebus (Cebus) albifrons*, *Cebus (Cebus) olivaceus*, and *Cebus (Cebus) kaapori*].

The name *Sapajus* was first used as a subgenus by Kerr [1792] for the form *Simia Sapajus capucinus albulus*, which Hershkovitz [1949] concluded was "if identifiable, a synonym of *Cebus apella*" (p.346). Von Pusch [1941] subsequently used the name for his systematic arrangement of the genus *Cebus*, which he defined as having three subgenera: *Saimiri* Voigt, 1831; *Cebus* Erxleben, 1777; and *Sapajus* Kerr, 1792 [Hill 1960]. According to Von Pusch [1941], *Sapajus* comprised *albifrons* (with one subspecies) and *apella* (with 17 subspecies). Here we follow Silva [2001] in distinguishing the robust capuchin species using the name *Sapajus*, but at the generic rather than the subgeneric level. The type species for *Sapajus* is *Simia apella* Linnaeus, 1758, and for *Cebus* is *Simia capucina* Linnaeus, 1758.

Through qualitative analyses of 2,369 museum specimens from 412 localities, supplemented with observations of over 1,000 living animals in the wild and in captivity, Silva [2001] found the following characteristics to demonstrate a clear division in morphology between all tufted, robust *Sapajus* and all untufted, gracile *Cebus* species (see Figs. 2 and 3 for cranial differences):

Shape of the frontal bone: Wide and flat in *Cebus*, but projecting forward and up in *Sapajus*.

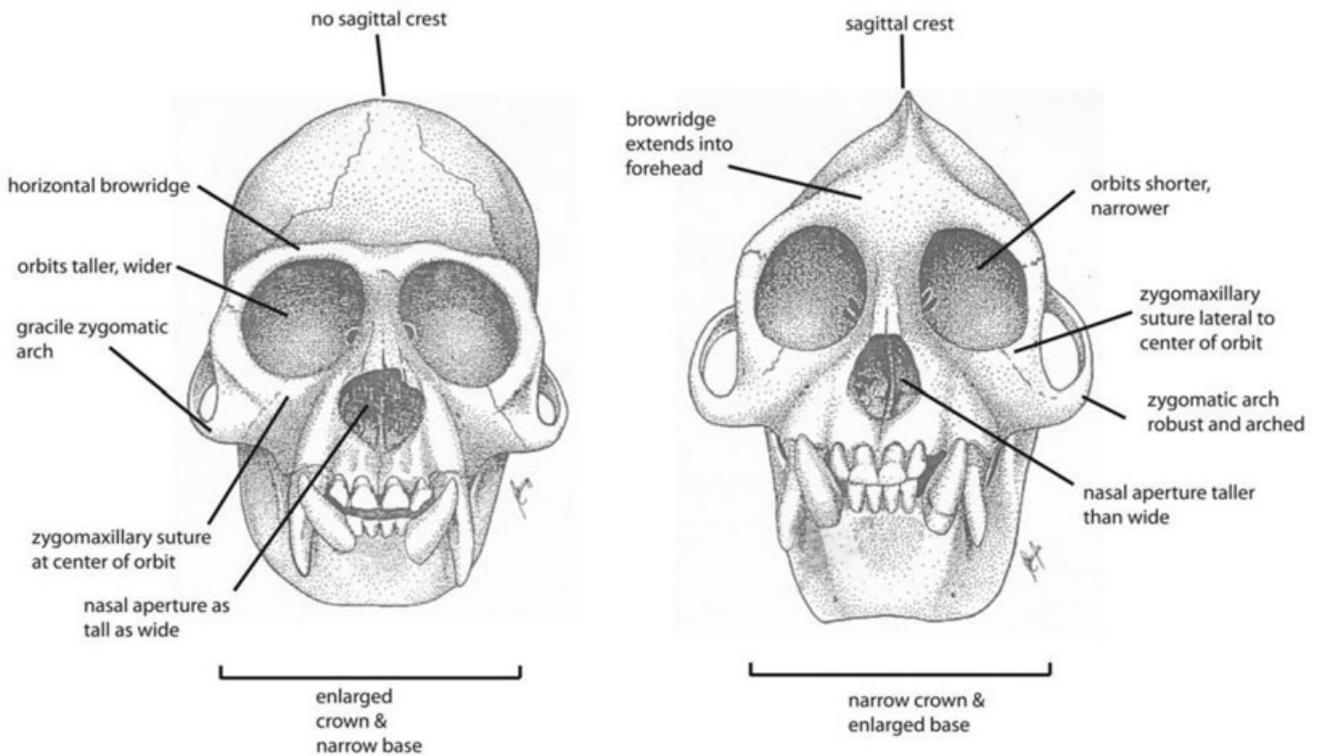


Fig. 2. Frontal view of crania of adult male *Cebus* (left) and *Sapajus* (right), annotated with key distinguishing differences. Modified from Silva [2001]. Drawings by Jair da Silva.

Zygomaxillary suture: In *Cebus*, the suture between the maxilla and zygomatic bone is found approximately in the center of the margin of the inferior orbit, and in *Sapajus* it is clearly lateral to the center of the margin of the inferior orbit. This is another invariable trait within each group that easily distinguishes *Sapajus* from *Cebus*.

Nasal aperture: The nasal aperture is approximately as tall as it is wide in *Cebus*, and taller than it is wide in *Sapajus*.

Shape of the wings of the vomer: Subdivided in *Cebus*, and fused in *Sapajus*.

Opening to the auditory meatus: The openings are relatively large and positioned lower in *Sapajus* species, and are small and laterally positioned in *Cebus*. This difference is consistent for all *Cebus* versus *Sapajus*, and is a good way to distinguish between the two quickly.

Canine shape: Regarding the canine length and the diameter of the base in relation to the thickness of the mandible, *Cebus* has long and slender canines, and *Sapajus* has relatively shorter, more robust canines.

Shape of the base of the mandible: There is little variation among *Cebus* species; all species have a straight mandible base. The base of the mandible is curved and irregular in all *Sapajus*, with more variation in shape across species.

Shape of the ascending ramus of the mandible: At a 90° angle in *Cebus*, but convex and projected back and down in *Sapajus*.

Silhouette: Looking at living capuchin monkeys from a side view, all *Sapajus* species have short limbs in proportion to body length, giving them a “compact” body shape, whereas all *Cebus* species have longer limbs in proportion to body length, giving them a more “lanky” silhouette (see Fig. 1).

Silva [2001] also found that the following qualitative characteristics were uniform across *Cebus* and different but variable in *Sapajus* (see Fig. 4 for species variation in face shape and pattern):

Crown in adult phase: Tuft absent in all *Cebus* (at least in adult males; some female *C. olivaceus* and *C. albifrons* have tufts); present in varying degrees and shapes in *Sapajus* (sometimes absent in *S. macrocephalus*).

Sideburns: None of the *Cebus* species has a dark preauricular stripe on the fur in the equivalent of “sideburns” [Groves, 2001], and all *Sapajus* species have either black or brown fur along the side of their faces in front of the ear (the only exception is *S. cay* that displays variation in having the darkened stripe—and this species is far from sympatry with any gracile species [Silva, 2001]).

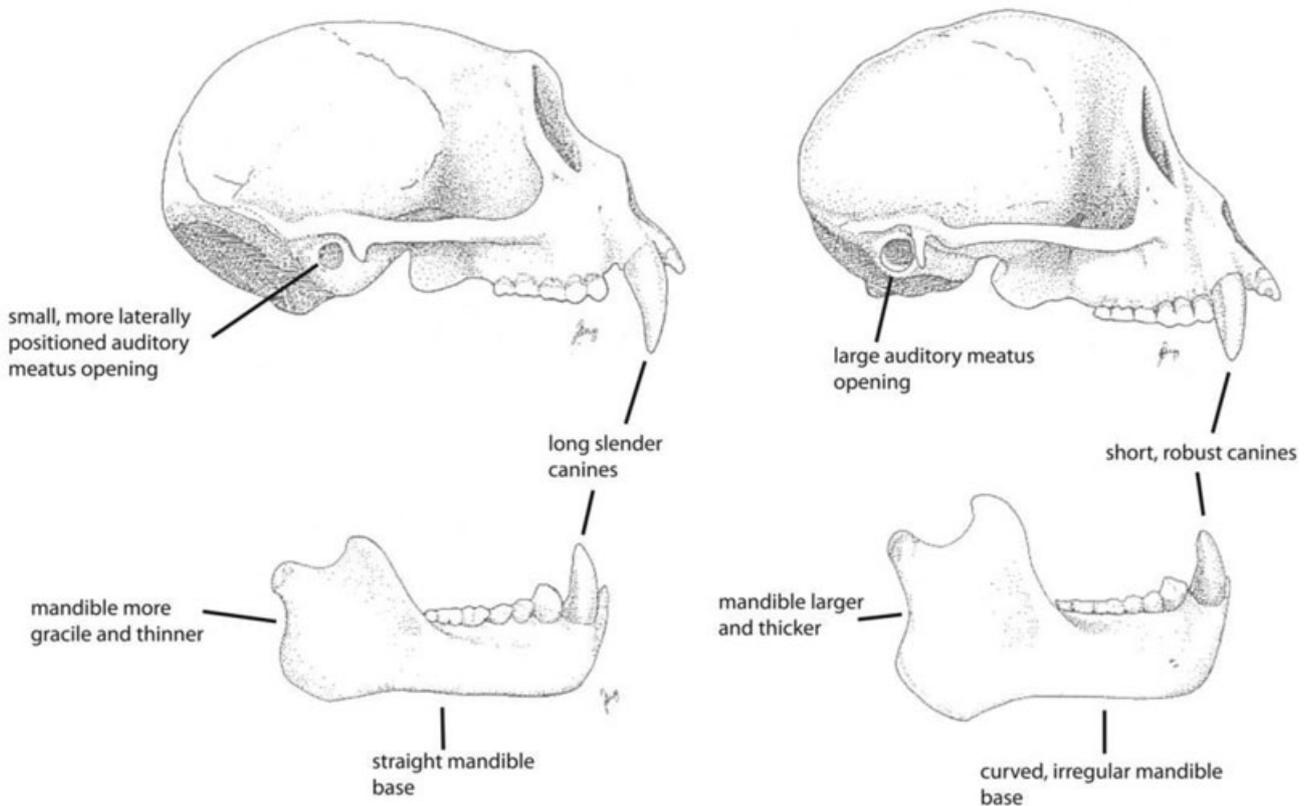


Fig. 3. Lateral view of crania of adult male *Cebus* (left) and *Sapajus* (right), annotated with key distinguishing differences. Modified from Silva [2001]. Drawings by Jair da Silva.

Outer eyebrows: *Cebus* lacks a dark brown stripe above and in front of the ear (a stripe from the lateral forehead in a curve around to the cheek exaggerating the eyebrows); all *Sapajus* have this trait, either continuous with the dark crown (in most species) or discontinuous with the crown in *S. xanthosternos*. This character also appears variable for the blonde capuchin, *Sapajus flavius*, not included in Silva's study.

Beard shape: None of the *Cebus* species has a beard, and *Sapajus* species do have beards, ranging from short to long.

There are also several characters that distinguish adult male *Cebus* and *Sapajus* from each other [Silva, 2001]:

Cranium shape: More rounded and bulging in *Cebus*, and larger compared to *Sapajus* in the medial and superior regions. The cranium in *Cebus* has a narrow base and a wide crown. In contrast, the base of the cranium is enlarged in *Sapajus*, and the crown of the head is narrower, with greater postorbital constriction.

Sagittal crest: Absent in *Cebus*, present in *Sapajus* but differing in prominence from small to large by species.

Skull height: Taller in *Sapajus*, in large part as a result of the sagittal crest that is present in *Sapajus* and absent in *Cebus*. However, the region around the vertebral column is more developed in *Cebus*, diminishing somewhat the overall difference in skull height.

Supraorbital ridges: Brow ridges (or supraorbital ridges) are more robust and expand up into the forehead in *Sapajus*; they are a well-developed nearly horizontal ridge in *Cebus* [see Groves, 2001].

Orbits: The orbits are both taller and wider in *Cebus* compared to *Sapajus*.

Zygomatic arch: *Sapajus* species have zygomatic arches that are much more robust and arched, making them wider than those in *Cebus*.

Mandible: Larger and thicker in adult male *Sapajus* compared to adult male *Cebus*.

Size of foramen magnum: The diameter of the foramen magnum is much larger in *Cebus* compared to *Sapajus*. The size of the occipital condyles is also larger and they project further in all directions in *Cebus*.

In a geographic analysis of morphological variation found in *Sapajus*, Silva [2001] found that tufted capuchins *sympatric* with *Cebus* showed the



Fig. 4. Adult male facial variation across different capuchin monkey species. Top row, left to right: *C. albifrons*, *C. olivaceus*, *C. kaapori*, *C. capucinus*; bottom row, left to right: *Sapajus nigritus*, *S. xanthosternos*, *S. flavius*, *S. apella*. Drawings by Amisha Gadani.

most difference in characters, that is, robustness in characters associated with increased durophagy. He suggested that this difference was a result of character displacement and niche partitioning between *Cebus* and *Sapajus*. Silva's [2001] morphometric analysis across *Sapajus* species suggested a hierarchy of *Sapajus* species relationships, and he subdivided them into three geographical groups:

- (1) Amazonian species (*S. macrocephalus* and *S. apella*)—At present, there is no genetic evidence that supports the distinction between these two species [Lynch Alfaro et al., 2011].
- (2) Species from the center of South America from the Cerrado (bush savanna of Central Brazil) and the Atlantic Forest north of the Rio Doce (*S. libidinosus*, *S. cay*, *S. robustus*, *S. xanthosternos*).
- (3) Species from the Atlantic Forest south of the Rio Doce (*S. nigritus*).

These divisions map well to the genetic variation found across *Sapajus* by Lynch Alfaro et al. [2011]; the phylogeographic data suggest that *S. nigritus* has been diversifying the longest as a species, and is sister to all other robust capuchins. *S. robustus* and *S. xanthosternos* form a clade, and within that clade, *S. cay*, *S. libidinosus*, *S. apella*, and *S. macrocephalus* form a less genetically diverse subclade.

PHYLOGENETICS AND EVOLUTIONARY HISTORY OF THE CAPUCHINS

Lynch Alfaro et al. [2011] sequenced the mitochondrial cytochrome *b* gene from 57 capuchin monkey specimens representing several species of both robust and gracile types of known provenance across their distribution: *C. olivaceus*, *C. capucinus*, *C. albifrons*, *S. apella*, *S. macrocephalus*, *S. xanthosternos*, *S. robustus*, *S. nigritus*, *S. cay*, and *S. libidinosus*. *C. kaapori*, and *S. flavius* were not included in this sample and require further investigation. Using a Bayesian discrete-states diffusion model, they reconstructed the most probable history of invasion across Central and South America. Their work showed that capuchin monkeys contained two well-supported monophyletic clades that corresponded exactly to Silva's [2001] morphologically distinct "gracile" *Cebus* and "robust" *Sapajus* groups [Lynch Alfaro et al., 2011]. The time-tree analysis estimated that *Cebus* and *Sapajus* diverged from one another during the Late Miocene (approximately 6.2 Ma) with a subsequent Plio-Pleistocene diversification in each of the two clades (starting at ca. 2.7 Ma for *Sapajus* and ca. 2.1 Ma for *Cebus*) [Lynch Alfaro et al., 2011]. Bayesian analysis of phylogeographic diffusion history indicated that *Sapajus* spent most of its evolutionary history confined to the Atlantic Forest, and that the current

wide-ranging sympatry of *Cebus* and *Sapajus* across much of the Amazon Basin resulted from a single rapid Late Pleistocene (ca. 400 thousands of years ago [ka]) invasion of *Sapajus* from the Atlantic Forest into the Cerrado and the Amazon.

These new data clarifying the biogeographical history of capuchins suggest a Late Miocene geographical isolation of the gracile and robust forms. Each form diversified independently, but during the Pleistocene, the robust *Sapajus* expanded its range from the Atlantic Forest into both the drier regions, such as the Cerrado and Caatinga (xerophytic forest and scrub of Northeast Brazil), and also to the Amazon, where it has now substantially encroached upon what was previously the exclusive range of the gracile *Cebus*. Lynch Alfaro et al. [2011] argued that, based on their findings, the genus *Cebus* as currently recognized should be split into two to reflect the Miocene divergence and two subsequent independent Pliocene radiations: *Cebus* from the Amazon and *Sapajus* from the Atlantic Forest.

ECOLOGICAL DIFFERENCES FOR *CEBUS* AND *SAPAJUS* IN SYMPATRY

The phylogeographic results shed light on longstanding questions about capuchin ecology, particularly in the Amazon where *Sapajus* and *Cebus* are found in sympatry (see Fig. 5). For *C. albifrons*, the relatively recent arrival by *Sapajus* may mean on-going competition for habitat and feeding resources, and a gradual reduction in range through competitive exclusion. Different outcomes seem to have occurred in different parts of the Amazon where both types of capuchins are found. It may be that the distribution of *C. albifrons* once extended throughout the Amazon and it has been extirpated gradually from the south and east (the direction *Sapajus* was predicted to have come from in Lynch Alfaro et al. [2011]). This might explain the absence of *Cebus* in eastern Amazonia; some other Amazonian primates such as *Saimiri*, *Saguinus*, and *Alouatta* range throughout the expanse of the tropical rainforest [Hershkovitz, 1977, 1984; Hill, 1962; Thorington, 1985]. However, there are other Amazon primate taxa that do not have representatives in eastern Amazonia, such as *Pithecia*, *Ateles*, *Callicebus*, and *Lagothrix*. What is unusual for *Cebus* is the disjunct distribution of *C. kaapori* in the far northeast Amazon, suggesting that there may have been a wider continuous distribution for *Cebus* in the past but that now many populations in the intermediate areas have been extirpated. However, other Guianan primates also have sister species that crossed the Rio Amazonas at its lowest reaches (*Saguinus midas/Saguinus niger* and *Chiropotes chiropotes/Chiropotes satanas*),



Fig. 5. Superimposed distributions of *Cebus* and *Sapajus* to show the wide area encompassed where the two genera are found in sympatry. Blue = *Cebus* only; Yellow = *Sapajus* only; Green = Sympatric or overlapping distribution of both *Cebus* and *Sapajus*. Note that there is local variation in the presence of either type of capuchin within the "green" distribution area.

so this question requires further paleogeographic exploration.

Habitat use and degree of overlap between *S. apella* and *C. albifrons* are variable across areas of sympatry. The gracile capuchins, with larger group sizes and larger home ranges, are generally found at lower densities than the robust species when the two types are found in sympatry [see, e.g., Bennett et al., 2001; Terborgh, 1983]. A study by Haugaasen and Peres [2005, 2009] of primate assemblages in flooded and unflooded forest found that, of 12 primate species, *S. macrocephalus* was the only true habitat generalist, with high population density in all kinds of forest; *C. albifrons* was found at a lower density than *S. macrocephalus* in terra firme forest, and rarely observed in the flooded forests, except at the height of the fruiting season. The difference in population density in the two species was considered a result of the heavy reliance of *C. albifrons* on widely dispersed fruits such as figs [Haugaasen & Peres, 2005; Terborgh, 1983]. In a survey of the Río Curaray in the Peruvian Amazon,

Heymann et al. [2002] found only *C. albifrons* on the north side of the river and *S. macrocephalus* on the south side, but suggested the difference was ecological (with *C. albifrons* restricted to the floodplain or riverine forest on the north of the river). In El Tuparro National Park, Colombia, Defler [1985] described only *C. albifrons* as using seasonally inundated forest, but *S. macrocephalus* and *C. albifrons* otherwise used similar forest, though their distributions were mutually exclusive. Defler [1985] considered historical precedence and competitive exclusion as explanations for the capuchins' contiguous and non-overlapping distributions in the region.

Phylogenetic analyses by Boubli et al. [2012] show that, like Amazonian *Sapajus*, *C. olivaceus* is a relatively recent radiation, with initial diversification around 700 ka in the northern Venezuelan Amazon. Outcomes regarding habitat sharing between *C. olivaceus* and *S. apella* are also variable. In Suriname, *S. apella* has a more generalized use of forest and edge habitats, and *C. olivaceus* prefers high terra firme rainforest, avoiding forest edge [Mittermeier and Van Roosmalen, 1981]. On Maracá Island in the northern Brazilian Amazon, Mendes Pontes [1997] found much overlap in habitat preferences between *C. olivaceus* and *S. apella* in terra firme forest, but *S. apella* was more of a habitat generalist, using the emergent canopy and the understory, while *C. olivaceus* was more restricted to intermediate levels of the forest. In Guyana, Sussman and Phillips-Conroy [1995] suggested that *C. olivaceus* had more limited habitat preferences and lower population density than *S. apella* where they occurred together. Lehman [2000] found in a survey of 16 sites in Guyana that the only negative association in primate species' occurrence was between *S. apella* and *C. olivaceus*. In particular, *C. olivaceus* sightings were greatly reduced in areas where they co-existed with *S. apella*; Lehman's explanation was scramble competition rather than intergroup competition between the two species. Oliveira et al.'s [2009] survey of Saracá-Taquëra National Forest, Pará, Brazil, found *S. apella* to be the most abundant primate, and they never directly observed *C. olivaceus*, despite reports of it living in the area and *C. olivaceus* museum specimens from there. Surveys in northern French Guiana showed that in 15 of 16 sites where both capuchin species were present, *S. apella* was more abundant than *C. olivaceus*. *S. apella* was recorded in all habitat types, but *C. olivaceus* only in upland forests [de Thoisy et al., 2005].

C. kaapori has been observed only in tall primary terra firme forest [Carvalho et al., 1999; Lopes & Ferrari, 1996; Silva & Cerqueira, 1998] and never in secondary forest, flooded forest, or open vegetation. In contrast, in areas of sympatry in the eastern Amazon, *S. apella* is common in most kinds of

habitats, including heavily degraded areas [Silva & Cerqueira, 1998]. *C. kaapori* tends to live in small groups at low population densities [Carvalho, 2003; Carvalho et al., 1999; Lopes & Ferrari, 1996; Silva & Cerqueira, 1998]; the low densities are attributed in part to interspecific competition with *S. apella* [see Carvalho et al., 1999].

What might be the advantage that allows *Sapajus* to consistently exhibit higher population densities than *Cebus* in areas of sympatry? The answer may well lie in the morphological and behavioral adaptations to durophagy shown by *Sapajus*. *Sapajus* species as a group are hard nut/palm fruit specialists [Haugaaen & Peres, 2009; Janson, 1986a,b; Spironello, 1991, 2001; Terborgh, 1983]. On Maracá Island, *S. apella* ate unripe fruit more than ripe fruit and exploited many more palm species than *C. olivaceus*, which fed on ripe fruits in almost 90% of the feeding records [Mendes Pontes, 1997]. At Manu, *S. macrocephalus* efficiently exploited palm nuts for food during the dry season—adult and juvenile *S. macrocephalus* could crush and open any palm nut with one bite; whereas *C. albifrons* adults would spend 5–10 min to open damaged nuts and were unable to open intact nuts at all [Terborgh, 1983].

Territoriality and ranging behavior also appear different between the two capuchin genera in areas of sympatry. In Manu, Peru, *S. macrocephalus* groups primarily used a core area, with a relatively small home range, large overlap between groups, and peaceful interactions across groups [Terborgh, 1983]. In contrast, *C. albifrons* groups aggressively defended a much larger, nearly exclusive territory and traveled longer distances, spending days in a particular part of the home range until the food sources were exhausted, and then moving on [Terborgh, 1983]. This difference in ranging was emphasized in the dry season when food was scarce: *S. macrocephalus* specialized on palm fruits and pith in a core area, while *C. albifrons* ranged more widely to find ripe fruit [Terborgh, 1983]. Defler (1979b) in Colombia found more tolerance between *S. macrocephalus* males than *C. albifrons* males within groups, and more tolerance across groups, as well as a lack of territoriality in *S. macrocephalus*. These differences are evidently fixed, at least for *C. albifrons*. In the Ecuadorian Amazon, Matthews [2009] found that where *S. macrocephalus* is absent, *C. albifrons* did not shift to occupy more of the *S. macrocephalus* niche, but instead showed similar ranging, feeding, and intergroup interaction patterns to those of *C. albifrons* studied elsewhere. *C. olivaceus* in Venezuela shows similar ranging and feeding behavior to *C. albifrons* [see Robinson, 1986]. In contrast, Izar et al. [2012] report that *Sapajus* species have a more flexible behavioral response to differences in resource availability and distribution.

BEHAVIORAL DIFFERENCES

Capuchin behavioral flexibility may mask the differences between *Sapajus* and *Cebus* because both are so adaptable to many habitat types and diets. There is wide variation in morphology and behavior across individuals, by age and sex class, and across populations within the same species. There is much more to be learned regarding behavioral diversity in capuchins; in fact, we are only beginning to scratch the surface for most species. For example, Jack et al. [2012] present a detailed analysis of natal dispersal data in *C. capucinus*: these authors found that group instability through group takeovers, short tenure length of a natal male's father, and small group size were all predictors of male natal dispersal, while males in stable groups were more likely to remain as residents in their natal group. Comparable data are lacking for all other capuchin species except perhaps for *S. nigritus* in Iguazú Falls [Janson et al., 2011].

We summarize here some areas where field studies indicate behavioral differences between *Cebus* and *Sapajus*, with the caveat that not all species of either of the two types have been well-studied for any of these behaviors:

Tool use: One striking, foraging-related difference between *Cebus* and *Sapajus* is in stone tool use in the wild. It would appear to be ubiquitous across robust capuchin populations in dry habitats (i.e., *S. flavius* [see Emidio & Ferreira, 2012]; *S. libidinosus* [see Emidio & Ferreira, 2012; Fragaszy et al., 2004b; Ottoni & Izar, 2008]; *S. xanthosternos* [see Canale et al., 2009]) and can occur even in forested areas (*Sapajus* spp. [see Ottoni & Mannu, 2001]), but it has not been recorded in other long-term studies of *Sapajus* in rainforest conditions (*S. nigritus* in southeast Brazil [Izar et al., 2012] and Argentina [Di Bitetti, 2001]; *S. apella* in Suriname [Gunst et al., 2010a,b], *S. macrocephalus* in Peru [Janson, 1986a,b] and Colombia [Izawa, 1979]). This can be explained in part because the alluvial floodplain of the central Amazon has no stones available for tool use [Spironello, 1991, 2001]. However, stone tool use has never been reported in the wild for any *Cebus* species, even, for example, in a savannah-like habitat where *C. albifrons* used the ground frequently and dedicated much effort trying to crack open palm fruits: nevertheless, it ignored the stones that were available [Defler, 1979a]. Garber and Brown [2004] and Garber et al. [2012] took an experimental approach to compare tool-use of monkeys using dowels as probes in the wild, and reported no significant differences between *C. capucinus* and *S. nigritus*.

Anointing: Both *Cebus* and *Sapajus* species perform anointing behaviors, in which they rub secretions of plant or animal matter, or mud, over them-

selves, sometimes in contact with up to several other individuals. *Cebus* anoints at a higher frequency than *Sapajus*, *Cebus* prefers plant matter for anointing and *Sapajus* prefers arthropods, and at least for *C. capucinus*, anointing has become a behavior independent of feeding, while *Sapajus* tends to eat the items with which it anoints [Lynch Alfaro et al., this issue].

Social conventions: Social conventions such as hand sniffing, sucking body parts, and inserting fingers into another individual's mouth have been described in *C. capucinus*; these behaviors usually occur in a reciprocal fashion in a relaxed atmosphere, and traditions may appear and be extinguished over a number of years [Perry et al. 2003a,b]. These social interactions are believed to test the strength of social bonds between individuals [Perry 2003a,b, 2008]. These kinds of behaviors have also been observed in *C. albifrons*, but not in *S. macrocephalus* at the same site; as Janson (personal communication) describes it: "*C. albifrons* is engaging in 'purely social' rituals that have been described for [*C.*] *capucinus* and seem totally alien to *Sapajus* as I know them (e.g., *Sapajus* don't stick their fingers up each other's noses . . .)." In fact, these kinds of behaviors have yet to be reported for *Sapajus* anywhere despite several long-term field studies [Perry, 2011].

Vocalizations: The description of vocalizations for *C. albifrons* by Defler [1979b] matches closely that for *C. capucinus* [Gros-Louis et al., 2008; Perry, 2008]. Robinson [1984] also described, albeit a limited number, calls for *C. olivaceus*, which seem to correspond to those for the other gracile species. In contrast, Di Bitetti [2002] described several quite different vocalizations for *S. nigritus*. For example, the "lost calls" or "arrawh" in *C. capucinus* are flat, atonal calls with lots of noise, uttered in 1–3 elements. "Arrh" calls are also found in *C. albifrons*, emitted when individuals are lost from the group, and are grouped in 2–4 calls per series [Defler, 1979b]. However, the call with the same function in *S. nigritus* in Iguazu, Argentina, is different; it is a musical long distance whistle series that can have 12–14 notes in quick succession [Di Bitetti, 2002]. The vocalizations accompanying the wheeze dance in *C. capucinus* include the wheeze, grunt, and squeak, and can occur during sexual displays or when two individuals reunite [Gros-Louis et al., 2008; Perry, 2008]. When *Sapajus* individuals reunite, however, they emit the sirena or reunion scream [Di Bitetti, 2001; Lynch Alfaro, 2008; Matheson et al., 1996]. *Sapajus* species may have additional calls that lack functional equivalents in *Cebus*; for example, the "wah wah wah" [Di Bitetti, 2001] or "rumble" [Resende et al., 2007] vocalization, which adult male *Sapajus* produces in response to explosive sounds such as thunder,

falling trees, or gunshots, has never been reported in *Cebus*.

Courtship, mating, and postcopulatory display: *Sapajus* displays the richest repertoire of sexual and courtship behaviors ever described for non-human primates [Fragaszy et al., 2004a]. This includes the alpha male's initial reluctance to mate, females' dogged persistence in soliciting male interest, mutual gaze between male and female and complex courtship signaling prior to mating, multiple mounts which can alternate between male-on-female and female-on-male mounts, and postcopulatory display—a continuation of courtship behaviors after copulation [Carosi et al., 2005; Fragaszy et al., 2004a; Janson, 1984; Lynch Alfaro, 2005]. In contrast, *C. capucinus* females in Santa Rosa, Costa Rica, exhibited little proceptive behavior, but instead tended to look and behave the same during fertile and nonfertile periods [Carnegie et al., 2005]. *C. albifrons* females at Tiputini Biological Station in Ecuador never showed the extended proceptivity displays commonly observed in *Sapajus* species [Matthews, 2012]. In courtship, *Sapajus* males and females raise their brows up and back and “grin,” pulling their lips back to expose their teeth in a grimace [Lynch Alfaro, 2005], but *C. capucinus* and *C. albifrons* instead protrude their lips in a “duck face,” which continues throughout copulation as well [Manson et al., 1997; Matthews, 2012; Perry, 2008]. This extreme difference in reproductive signaling suggests reproductive isolation. Janson [1984, 1986a,b] reported the difference in sympatric *S. macrocephalus* and *C. albifrons* in their courtship behaviors; *Sapajus* courtship lasted longer and was performed with greater vigor, and *Cebus* females lacked proceptive behaviors. Izar et al. [2012] noted that despite other significant differences in behavior and ecology, *S. nigritus* in the Atlantic Forest and *S. libidinosus* of the semi-arid Cerrado had very similar mating systems, suggesting that this is a conservative behavioral feature in *Sapajus*.

Group cohesion or fluidity: Capuchins tend to form stable groups across much of their range, but more fluid subgrouping or fission–fusion dynamics in response to resource availability can occur in *S. nigritus* (Minas Gerais, Brazil [Lynch Alfaro, 2007]; São Paulo, Brazil [Izar & Nakai, 2006]). Subgrouping or shifting group membership tends to occur in gracile *Cebus* only when there is an aggressive male take-over of a group [Perry, 2008] or when the group is in the process of permanent division into two groups [Robinson, 1988].

DISCUSSION

Morphological and taxonomic studies of *Sapajus* have increased the number of recognized species to

between five and eight. Silva [2001] recognized *S. apella*, *S. macrocephalus*, *S. libidinosus*, *S. cay*, *S. xanthosternos*, *S. robustus*, and *S. nigritus*. Groves [2001] decided on a rather different taxonomy: *S. apella* (with six subspecies), *S. libidinosus* (with four subspecies), *S. nigritus* (with three subspecies), and *S. xanthosternos*. *S. flavius*, also a valid taxon, was re-discovered only in 2006.

A literature review of the use of species/subspecies terms for *Cebus* in 1-year increments in Web of Science revealed that on average about 27% of articles in the last 4 years (2008–2011) for robust capuchins with *Cebus* in the title use a subspecies name or a species name other than *C. apella*—the 73% that use *Cebus apella* include almost all captive studies as well as the field studies in the range of *C. apella* sensu stricto. The use of *Cebus apella* has declined over time (it was used in 92% of article titles in 2000–2003, and 88% in 2004–2007), but is still ubiquitous for captive studies. The long-standing use of “*Cebus apella*” for all robust capuchins in captivity has obfuscated any understanding of tufted capuchin behavioral variation.

The umbrella usage of *C. apella* means that it is impossible to use most of the published karyological data on robust capuchins in a taxonomic framework. Almost all of the animals used in these studies were from zoos, from unknown provenance, and were never deposited in museums to allow for subsequent determination of taxonomic identity. The karyotypes of *Cebus* and *Sapajus* differ in fundamental number and diploid number, but the data at present do not allow for a coherent evolutionary analysis because of the blanket use of “*C. apella*” to describe the samples from the robust group.

Here we advocate the importance of a standardized use of *Sapajus* as a genus, and the careful discrimination of the identities of *S. apella*, *S. macrocephalus*, *S. libidinosus*, *S. cay*, *S. xanthosternos*, *S. robustus*, *S. nigritus*, and *S. flavius* as valid species (or the use of subspecies according to nomenclatural preferences) to place field observations and experimental results in context, allowing us to identify the within- and across-genus variation which is becoming so evident for capuchin monkeys. Captive researchers working with capuchin monkeys of unknown origin could now have cytochrome *b* and D-loop sequenced for their study animals and compare the sequences to published data to fit their group on the capuchin tree. Preliminary data from Lynch Alfaro (pers. obs.) suggests that the robust capuchins from many U.S. laboratories and zoos may be *S. apella* sensu stricto from the Guianas, and may be genetically homogeneous, coming to the U.S. from relatively few founder populations. This suggests that captive studies may be capturing only a small fraction of the genetic or geographic variation found in wild robust capuchins. The gracile capuchins are in a similar situation, being

composed of more species than was previously believed. *C. capucinus* evidently comprises two distinct species [Ruiz-García et al., 2012] and *C. albifrons* as currently defined has now been found to be paraphyletic [Boubli et al., 2012; Lynch Alfaro et al., 2011; Ruiz-García et al., 2010]. To understand the phylogeography of variation in the species (and subspecies) of capuchins it would be of great value if the taxonomic identity of subjects in captive research were carefully established.

Silva's [2001] assessment of morphological diversity across *Sapajus* species alone is that it is equivalent in magnitude to differences across the tamarin (*Saguinus*) species *S. mystax*, *S. midas*, *S. inustus*, *S. bicolor*, and *S. oedipus*; among owl monkeys, across both the "gray-neck" and "red-neck" species [as characterized by Hershkovitz, 1983]; across all *Saimiri* species, including both "gothic" and "roman" types; within the marmosets, both *Mico* and *Callithrix*; and within the saki monkeys *Pithecia*, the variation between *P. pithecia* and *P. monachus* species groups. No genus in the pitheciines or the atelines can be distinguished so easily by cranial architecture as can the robust and gracile capuchins [Silva, 2001].

Silva [2001] argues that except in *Callicebus* [see Hershkovitz 1988, 1990] and *Saguinus* [the mustached and saddle-back tamarins, see Hershkovitz 1977], there are no records of extensive sympatry within Neotropical primate genera other than for capuchin monkeys (see Fig. 5). Neotropical primates species within genera are generally parapatric or allopatric, and are morphologically different only in the structure and coloration of the fur [see Hershkovitz 1977, 1983, 1984, 1987; de Vivo 1991]. For example, in terms of cranial morphology, there are no characters that could assign species differences with confidence among specimens of *Pithecia*, *Chiropotes*, or *Cacajao* without known geographic origin and preserved skins [Silva, 2001]. In contrast, several cranial characteristics lead to the easy differentiation between the gracile and robust capuchins even for a skull of unknown provenance that lacks any associated pelage data (see Figs. 2 and 3).

With capuchin monkeys, primatologists have a perhaps unparalleled example of two distinct, successful radiations of monkeys that share many characters of interest with apes and humans: intelligence, delayed maturation, complex social relationships, local traditions, manual dexterity, extractive foraging, and tool use. Yet, these two groups have been evolving independently from one another in the Neotropics for ca. 6 Ma, the same time that humans and chimpanzees have been evolving independently from one another [Carroll, 2003]. It is of enormous interest to understand the behavioral diversity within these two radiations of capuchins, and to understand differences and convergences between the two types, in our effort to understand capuchins as a model for hominid evolution.

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