

RESEARCH ARTICLE

***Cebus* Phylogenetic Relationships: A Preliminary Reassessment of the Diversity of the Untufted Capuchin Monkeys**JEAN P. BOUBLI^{1*}, ANTHONY B. RYLANDS², IZENI P. FARIAS³, MICHAEL E. ALFARO⁴, AND JESSICA LYNCH ALFARO⁵¹Wildlife Conservation Society, Rio de Janeiro, Brazil²Conservation International, Arlington, Virginia³Laboratório de Evolução e Genética Animal, Universidade Federal do Amazonas, Manaus, AM Brazil⁴Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California⁵Center for Society and Genetics, University of California, Los Angeles, California

The untufted, or gracile, capuchin monkeys are currently classified in four species, *Cebus albifrons*, *C. capucinus*, *C. olivaceus*, and *C. kaapori*, with all but *C. kaapori* having numerous described subspecies. The taxonomy is controversial and their geographic distributions are poorly known. *Cebus albifrons* is unusual in its disjunct distribution, with a western and central Amazonian range, a separate range in the northern Andes in Colombia, and isolated populations in Trinidad and west of the Andes in Ecuador and northern Peru. Here we examine previous morphological and molecular hypotheses of the taxonomy and phylogeny of *Cebus*. We construct a time-calibrated phylogeny based upon mitochondrial DNA sequences from 50 *Cebus* samples from across their range. Our data indicate that untufted capuchins underwent a radiation at about 2 Ma, and quickly diversified in both the Andes and the Amazon. We provide a provisional reassessment for the taxonomy of untufted capuchins in the Amazon, the Llanos, the Andes, Trinidad, and Central America, splitting currently paraphyletic taxa into several species, including: at least two Amazonian species (*C. yuracus* and *C. unicolor*); a species from the Guiana Shield (most likely the same as Humboldt's *C. albifrons*); two northern Andean species, *C. versicolor*, *C. cesarae*; *C. brunneus* (with *trinitatis* a junior synonym) on the Venezuelan coast, and *C. adustus* in the region of Lake Maracaibo; *C. capucinus* in northwestern Ecuador and Colombia, and Panama; *C. imitator* in Central America; *C. olivaceus* and *C. castaneus* occupying a large part of the Guiana Shield; and *C. kaapori* in the eastern Amazon, south of the Rio Amazonas. More intensive and extensive geographic sampling is needed, including that for some subspecies not represented here. Taxa from the southwestern Amazon (*yuracus*, *cuscinus*, and *unicolor*) and the phylogenetic position of Humboldt's *Simia albifrons* from the Orinoco remain particularly poorly defined. Am. J. Primatol. 00:1–13, 2012. © 2012 Wiley Periodicals, Inc.

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INTRODUCTION

Untufted capuchins are medium-sized (2–4 kg) monkeys of Central and northern South America, occurring in lowland, premontane, and montane forests, from sea level to over 2000 m [Aquino & Encarnación, 1994; Fragaszy et al., 2004; Hernández-Camacho & Cooper, 1976; Tirira, 2007]. Hershkovitz [1949, 1955] and Hill [1960] provided excellent accounts of the extremely confused taxonomic history of the capuchin monkeys. Hershkovitz [1949; see also Cruz Lima, 1945] recognized three species of the so-called untufted group—the white-fronted capuchin *Cebus albifrons* (Humboldt, 1811), the white-faced capuchin *C. capucinus* (Linnaeus, 1758), and the wedge-capped or weeper capuchin *C. olivaceus* (Schomburgk, 1848; formerly *nigrivittatus* Wagner, 1848, see Rylands [1999]; Groves [2001, p.151]). A

fourth species, *C. kaapori*, was described by Queiroz in 1992. Hershkovitz [1949] accommodated the diversity of this wide-ranging group at the subspecies

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level. In all, he recognized 13 subspecies of *C. albifrons*, five of *C. olivaceus* and five of *C. capucinus*.

Subsequent authors have simplified Hershkovitz's [1949, 1955] scheme [e.g., Defler, 2004; Groves, 2001, 2005; Hernández-Camacho & Cooper, 1976; see below]. However, untufted capuchins occur over a large part of northern South America and Central America, and remain undersampled; there are large areas where the occurrence and identity of capuchin monkeys are presumed rather than known. The lack of available material across much of their range requires that any taxonomic simplification should be taken with caution, as it is likely that more taxa will be revealed as more samples emerge from new regions, especially remote Amazonian interfluvia. Hershkovitz [1949] himself concluded that it was desirable "to retain these named subdivisions of the species pending a thorough study of ample material" (p. 347).

Lynch Alfaro et al. [2011] analyzed the evolutionary radiations of *Cebus* (untufted capuchins) and *Sapajus* (the tufted capuchins). Their molecular analysis placed the initial diversification of *Cebus* at 2.1 Ma and identified two main clades: one included Amazonian *C. albifrons* and *C. olivaceus*, and the other Andean *C. albifrons* and *C. capucinus*. This suggested that *C. albifrons* as currently recognized was paraphyletic, and needed taxonomic revision.

Here we perform a BEAST [Drummond & Rambaut, 2007] analysis of a concatenated data set of cytochrome *b* and D-loop for 50 samples of untufted capuchins. The samples include representatives of the three untufted capuchin species recognized by Hershkovitz [1949]: *C. capucinus*, *C. albifrons*, and *C. olivaceus*. Our objective is to further consider the molecular diversification across untufted *Cebus* species and subspecies, and to understand their phylogenetic relationships based on molecular data. We assess the genetic data in relation to *Cebus* geographic distributions and previously published morphological and molecular hypotheses concerning *Cebus* taxonomy. Below we provide details about the historical basis for the current taxonomy for the untufted capuchins.

The White-Fronted Capuchin, *C. albifrons*

Hershkovitz's [1949] treatment of *C. albifrons* was as follows: (1) *C. albifrons albifrons* [Humboldt, 1811], from the banks of the Orinoco, near the mouth of the Río Ventuari; (2) *C. a. hypoleucus* [Humboldt, 1811], from near Zapote, Río Sinu (mouth of), Bolívar, Colombia; (3) *C. a. malitiosus* Elliot, 1909, from the Sierra Nevada de Santa Marta, Colombia; (4) *C. a. cesarae* Hershkovitz, 1949, from the Río Cesar, Magdalena Valley, Colombia; (5) *C. a. pleei* Hershkovitz, 1949, from Mompós, west bank of the Río Magdalena, at the base of the northern extremity of the Cordillera Central, Colombia; (6) *C. a. versicolor*

Pucheran, 1845, from the middle Río Magdalena, Colombia; (7) *C. a. leucocephalus* Gray, 1866, from the Río Lebrija, Santander, Colombia; (8) *C. a. adustus* Hershkovitz, 1949, from the eastern base of the Sierra de Perijá in Venezuela and Colombia; (9) *C. a. unicolor* Spix, 1823, from the Rio Tefé, Amazonas, Brazil; (10) *C. a. yuracus* Hershkovitz, 1949, from the ríos Marañón and Napo, eastern Ecuador and northern Peru; (11) *C. a. cuscinus* Thomas, 1901, from the upper Río Madre de Dios, Peru; (12) *C. a. aequatorialis* Allen, 1921, from the Pacific coast in western Ecuador (and probably also the Tumbes region in northern Peru [Encarnación & Cook 1998]); and (13) *C. a. trinitatis* Von Pusch, 1941, from Trinidad.

Hershkovitz [1955] subsequently found that no representative of *C. albifrons* occurs west of the Río Magdalena-Cauca, and that no white-fronted capuchins occur at the type locality of the captive specimen that Humboldt named *Simia hypoleuca*. As a result, he considered the name *hypoleuca* to be an unavailable synonym of *albifrons*. Cabrera [1957] argued that the type specimen was taken from the east of the Río Magdalena, and that *hypoleuca* is a senior synonym of *malitiosus* described by Elliot [1909]. Although acknowledging Hershkovitz [1955], Hill [1960] continued to recognize *hypoleucus*, explicitly following Cabrera [1957], but ignoring Cabrera's argument that it is the same animal as Elliot's *malitiosus*. Hill [1960] also recognized *malitiosus*. Groves (2001) ascribed authorship of *C. hypoleucus* to É. Geoffroy (1812) and considered it a junior synonym of *C. capucinus*. Cabrera [1957] made no mention of the form *trinitatis*.

Hernández-Camacho & Cooper [1976; see Fragaszy et al., 2004] reinterpreted the arrangement of the Colombian forms proposed by Hershkovitz [1949]: (1) *C. a. malitiosus* from the northern slopes of the Santa Marta Mountains; (2) *C. a. cesarae*, from the Río Cesar, Department of Magdalena, southward from Ciénaga Grande, and the lowlands of the Department of Cesar, north to the deciduous and gallery forests of the Río Ranchería, Department of Guajira; (3) *C. a. versicolor*, a complex from the Cauca-Magdalena interfluvium with the forms *leucocephalus* and *pleei* as regional variants; (4) *C. a. adustus* possibly from the piedmont forests of western Arauca, the northern tip of Boyacá and north Santander, the Lake Maracaibo region and upper Apure basin of Venezuela; (5) *C. a. albifrons* Humboldt type specimen, not preserved, from the Orinoco region of Venezuela and Colombia; (6) *C. a. unicolor*, from Tefé, widespread in the upper Amazon; and (7) *C. a. yuracus* from south of the Río Putumayo. Defler and Hernández-Camacho [2002; Defler, 2004] made a particular study of the type locality of *C. a. albifrons* and, because the *C. a. albifrons* type specimen has been lost, they established a neotype. They argued that *C. a. unicolor* from the central Amazon was a junior synonym of *C. a. albifrons*.

Groves [2001, 2005] further reduced the number of subspecies of *C. albifrons* to six, recognizing just one northern Colombian form, *C. a. versicolor* (*leucocephalus*, *malitiosus*, *adustus*, *cesarae*, and *pleei* as synonyms), and three Amazonian forms, *C. a. albifrons*, *C. a. cuscinus* (*yuracus* as a junior synonym), and *C. a. unicolor*, along with *C. a. trinitatis* from Trinidad, and *C. a. aequatorialis* from the Pacific coast in Ecuador and Peru.

The Wedge-Capped or Weeper Capuchin, *C. olivaceus*

Hershkovitz [1949] listed five subspecies of *C. nigrivittatus*: *C. n. nigrivittatus* Wagner, 1848, from the upper Rio Branco, Brazil; *olivaceus* Schomburgk, 1848, from the southern foot of Monte Roraima, Brazil; *castaneus* I. Geoffroy, 1851 described from Cayenne, French Guiana; *apiculatus* Elliot, 1907, from La Unión, Río Cuara, Venezuela; and *brunneus* Allen, 1914, from north-western coastal Venezuela. Neither Silva Jr. [2001, 2002] nor Groves [2001, 2005] considered any of the subspecies to be valid. Bodini & Pérez-Hernández [1987] recognized *C. olivaceus brunneus*, *C. o. nigrivittatus*, *C. o. apiculatus*, *C. o. olivaceus*, and an undescribed subspecies (llanos north of the Río Orinoco) as occurring in Venezuela. In his review of Venezuelan primates, Linares [1998] indicated just two subspecies: *C. o. brunneus* and *C. o. olivaceus*.

The Ka'apor Capuchin, *C. kaapori*

Occurring to the south of the lower Río Amazonas, the Ka'apor capuchin was first described as a distinct species by Queiroz in 1992, although its existence had been registered previously, as *C. capucinus*, by Goeldi & Hagmann [1906], who recorded six specimens (five from the Río Acará, and one from the Río Capim in southern Pará) in the collection of the Museu Paraense Emílio Goeldi, Belém. Harada & Ferrari [1996] argued that *C. kaapori* should be considered a subspecies of *C. olivaceus*, and Rylands et al. [2000] listed it as such, although later authors continue to consider it a full species [e.g., Fragaszy et al., 2004; Groves, 2001; Rylands & Mittermeier, 2008].

The White-Faced Capuchin, *C. capucinus*

Hershkovitz [1949] listed five subspecies of the Central American *C. capucinus*, although he himself did not consider any of them valid: (1) *C. c. capucinus* (Linnaeus, 1758), from "northern Colombia", (2) *C. c. curtus* Bangs, 1905, from the Colombian island of Gorgona in the Pacific, (3) *C. c. nigripictus* Elliot, 1909, from the Cauca Valley, Colombia, (4) *C. c. imitator* Thomas, 1903, from Boquete, Chiriqui, Panama, and (5) *C. c. limitaneus* Hollister, 1914, restricted to

Cabo Gracias a Dios at the mouth of the Río Segovia, eastern border between Honduras and Nicaragua. Hernández-Camacho & Cooper [1976], and Groves [2001, 2005] agreed with Hershkovitz [1949] that the above subspecies are not valid taxa. However, all are still in current use. Defler [2004] recognized and illustrated three of them for Colombia: *C. c. capucinus*, *C. c. nigripictus*, and *C. c. curtus*. In contrast, Hall [1981; see also Rylands et al., 2006] recognized *C. c. capucinus* in Panama and northern Colombia, *C. c. imitator* for Panama (including the islands of Coiba and Jicarón), Costa Rica, and Nicaragua, and *C. c. limitaneus* in Nicaragua and Honduras.

METHODS

Field and Museum Collection

This study made use of tissues collected in the field and tissues sampled from museum collections. New specimens of untufted capuchins were obtained in different parts of the Rio Negro–Rio Branco interfluvium by J.P.B. during a series of expeditions to the region between 2001 and 2008. Field samples were also collected in Costa Rica by J.L.A. and students, in collaboration with the University of Costa Rica. Samples from museum specimens of known provenance from Brazil, Venezuela, Colombia, Peru, Honduras, Ecuador, Guyana, Panama, and Costa Rica were obtained by J.L.A. Sequences were also downloaded from GenBank. Our samples of *C. albifrons* were from locations in the ranges of the following subspecies as identified by Hershkovitz [1949] and Aquino and Encarnación [1994]: *C. a. pleei*, *C. a. cesarae*, *C. a. leucocephalus*, *C. a. yuracus*, *C. a. unicolor*, *C. a. albifrons*, and *C. a. trinitatis* (see Table I). According to Hernández-Camacho & Cooper [1975, p.58], the sample from Apure, Venezuela (no. 35 in Table I) would be a (possible) light phase population of *C. a. adustus*, otherwise indicated as occurring to the north, west of Lake Maracaibo, and not *C. a. leucocephalus* as indicated by Hershkovitz [1949]. No samples were obtained from the putative ranges of *C. a. versicolor* from northern Colombia, *C. a. albifrons* from eastern Colombia and Orinoco (but collected in the Rio Branco–Rio Negro interfluvium), and *C. a. cuscinus* (southern Peru and northern Bolivia). Although we obtained a sample said to be from within the range of *C. a. aequatorialis* and labeled as such (sample 12), this was a specimen that came from a zoo and we believe it is actually *C. capucinus*, which is known to occur in northern Ecuador [Tirira, 2007]. Thus, we had no samples of *C. a. aequatorialis* in this study. For *C. olivaceus*, we sampled specimens of capuchins from the ranges of *C. o. brunneus*, *C. o. apiculatus*, *C. o. castaneus*, *C. o. nigrivittatus*, and *C. o. olivaceus*, as indicated by Hershkovitz [1949], and two from the north of the Río Orinoco, which Bodini & Pérez-Hernández [1987] indicated may be an

TABLE I. Specimens Used in cytB Plus D-Loop Analysis, With Latitude and Longitude Indicating Provenance of Specimens; Locality Number According to Map on Fig. 2.

Code	Taxon	Latitude	Longitude	GenBank Cyt b	GenBank D-loop	Location	Sample ID
1	<i>Cebus c. limitaneus</i>	15.26	-83.78	n/a	JQ317620	Connor	65-105
2	<i>Cebus c. imitator</i>	10.35	-85.35	JN400552	JQ317621	UCR	CC56
3	<i>Cebus c. imitator</i>	10.08	-84.47	JN409287	JQ317622	UCR	CC02
4	<i>Cebus c. imitator</i>	9.95	-84.55	JN409288	JQ317650	UCR	CC51
5	<i>Cebus c. imitator</i>	9.78	-84.93	JN409306	JQ317651	UCLA	CU005
6	<i>Cebus c. imitator</i>	9.45	-84.15	JN409307	JQ317652	UCR	CC19
7	<i>Cebus c. imitator</i>	9.73	-82.85	JN409308	n/a	UCLA	J048
8	<i>Cebus c. imitator</i>	8.38	-83.28	JQ317658	JQ317623	UCLA	M004
9	<i>Cebus c. capucinus</i>	9.48	-79.56	JN409309	JQ317653	USNM	171487
10	<i>Cebus c. capucinus</i>			AY065907	JQ317654	GenBank	AY065907
11	<i>Cebus c. capucinus</i>	8.1	-77.24	pending	n/a	USNM	338120
12	<i>Cebus c. capucinus</i>			pending	n/a	USNM	114648
13	<i>Cebus o. brunneus</i>	10.62	-68.41	JN409289	JQ317624	USNM	372765
14	<i>Cebus o. brunneus</i>	10.9	-68.77	JN409310	JQ317655	USNM	443218
15	<i>Cebus olivaceus ssp.</i>	10.66	-62.5	JN409311	n/a	USNM	261319
16	<i>Cebus olivaceus ssp.</i>	9.74	-61.42	JN409290	JQ317625	LACM	14378
17	<i>Cebus o. apiculatus</i>	7.65	-66.17	JN409312	JQ317626	USNM	296608
18	<i>Cebus o. apiculatus</i>	3.62	-65.68	JN409313	JQ317627	USNM	388187
19	<i>Cebus o. apiculatus</i>	3.62	-65.68	JQ317659	JQ317628	USNM	388188
20	<i>Cebus o. apiculatus</i>	7.5	-65.78	JQ317666	JQ317656	USNM	406451
21	<i>Cebus o. olivaceus</i>	6.29	-61.32	JQ317660	JQ317629	USNM	374805
22	<i>Cebus o. olivaceus</i>	6.29	-61.32	JN409291	JQ317630	USNM	374796
23	<i>Cebus o. olivaceus</i>	5.03	-60.95	JN409314	JQ317631	USNM	449466
24	<i>Cebus o. olivaceus</i>	6.29	-61.32	JQ317661	JQ317632	USNM	374810
25	<i>Cebus o. olivaceus</i>	4.42	-61.58	JN409315	JQ317633	USNM	443211
26	<i>Cebus o. castaneus</i>	3.3	-58.88	JN409316	JQ317634	USNM	339662
27	<i>Cebus o. nigrivittatus</i>	-0.96	-62.92	FJ529106	n/a	GenBank	FJ529106
28	<i>Cebus o. nigrivittatus</i>	0.5	-64	JN409335	JQ317635	INPA	JPB OLIO
29	<i>Cebus o. nigrivittatus</i>	0.85	-63.48	JQ317667	JQ317636	INPA	JPB 130
30	<i>Cebus o. nigrivittatus</i>	0.5	-64	JQ317664	JQ317637	INPA	JPB OLIA
31	<i>Cebus a. cesarae</i>	9.14	-73.57	JN409292	JQ317638	LACM	27327
32	<i>Cebus a. cesarae</i>	9.14	-73.57	n/a	JQ317639	LACM	27333
33	<i>Cebus a. adustus</i>	9.2	-72.64	JQ317668	JQ317640	USNM	443501
34	<i>Cebus a. adustus</i>	9.2	-72.64	JN409319	JQ317641	USNM	443503
35	<i>Cebus a. leucocephalus</i>	7.32	-71.96	JN409293	JQ317642	USNM	443629
36	<i>Cebus a. adustus</i>	9.18	-72.7	JQ317662	n/a	USNM	443642
37	<i>Cebus a. pleei</i>	9.23	-74.42	JQ317669	n/a	USNM	281628
38	<i>Cebus albifrons ssp.</i>			JN409318	JQ317643	USNM	398449
39	<i>Cebus a. trinitatis</i>	10.39	-61.3	JN409317	JQ317644	AMNH	24201
40	<i>Cebus a. unicolor</i>	-10	-71.02	JN409295	JQ317645	LSUMZ	9922
41	<i>Cebus a. yuracus</i>	-0.7	-76.35	JQ317670	JQ317646	NYU	F198
42	<i>Cebus a. yuracus</i>	-0.7	-76.35	JN409322	JQ317657	NYU	217
43	<i>Cebus a. yuracus</i>	-4.45	-78.27	JN409294	JQ317647	MVZ	153479
44	<i>Cebus a. unicolor</i>	-8.67	-72.78	n/a	JQ317648	MVZ	193675
45	<i>Cebus a. unicolor</i>	-8.67	-72.78	JN409323	JQ317649	MVZ	193676
46	<i>Cebus a. unicolor</i>	2.25	-65.28	JN409321	n/a	USNM	406439
47	<i>Cebus a. unicolor</i>	-0.96	-62.92	FJ529109	n/a	GenBank	FJ529109
48	<i>Cebus a. albifrons</i>	0.62	-65.92	JQ317671	JQ317615	INPA	JPB 73
49	<i>Cebus a. albifrons</i>	0.49	-65.27	JQ317663	JQ317616	INPA	JPB 107
50	<i>Cebus a. albifrons</i>	0.49	-65.27	JN409336	n/a	INPA	JPB 100
51	<i>Sapajus nigrinus</i>	-23	-44.3	JN409333	JQ317617	USNM	518478
52	<i>Sapajus robustus</i>	-17.85	-41.5	JQ317672	JQ317618	USNM	518434
53	<i>Sapajus macrocephalus</i>	-0.478	-64.41	JQ317665	JQ317619	INPA	JPB 80

The identity of each taxon follows Hershkovitz [1949] and Bodini and Pérez-Hernández [1987].

Connor=Connor Museum, Washington State University; UCR=University of Costa Rica; UCLA=University of California, Los Angeles; USNM=Smithsonian (National Museum of Natural History), Washington D.C.; LACM=Natural History Museum of Los Angeles County; INPA=National Institute for Amazonian Research, Manaus, Brazil; AMNH=American Museum of Natural History, New York; LSUMZ=Louisiana State University Museum of Zoology; NYU=New York University; MVZ=Museum of Vertebrate Zoology, California.

^aA specimen from the Honduras Zoo.

^bA specimen from the Guayaquil Zoo, Ecuador. Evidently from northern Ecuador.

^cBelieved to be an undescribed subspecies by Bodini & Pérez-Hernández [1987, p. 240].

^dFollowing Hershkovitz [1949] and Bodini and Pérez-Hernández [1987], but possibly a light phase of *C. a. adustus* according to Hernández-Camacho and Cooper [1976, p. 58].

^eFrom Barranquilla, outside the range of *C. albifrons* but a port of monkey export.

TABLE II. Primers for D-loop (Mitochondrial Control Region)

CR.HowRai F	5'- CTR CCR TCA ACA CCC AAA G -3' [Cortes-Ortiz et al., 2003]
CR.A Daniela F	5'- TAA TAC AWA GTA CTA CAM ATG C -3'
CR.B Daniela F	5'- TAA TGT ACA GTA CTG AGA ATG C -3'
CR.A Rasheed R	5'- CAT CCA GTG ACG CGG TTA AGA -3'
CR.B Rasheed R	5'- GTT CCT GTG ACG CGG TTA AGA -3'

undescribed subspecies. For *C. capucinus* sampled specimens were of *C. c. limitaneus* from Honduras, *C. c. imitator* from Costa Rica, and *C. c. capucinus* from Panama (See Table I).

DNA Extraction, Amplification and Sequencing

We sequenced portions of two mitochondrial genes for our analysis of *Cebus* divergence times: 404 bp of D-loop and 952 bp of cytochrome b (cytB). For degraded museum samples, this sometimes required the use of multiple overlapping internal sets of primers (Table II for D-loop, [see Lynch Alfaro et al., 2011 for cytB primers]). For some samples, we were not able to recover the entire length of each fragment, and the missing bases were treated as missing data. Blood samples were extracted using a DNeasy Blood & Tissue Kit (QIAgen, <http://www.qiagen.com>) and fecal samples were collected in RNAlater (QIAgen) and extracted using a modified QIAgen QIAamp DNA Stool Kit [see Di Fiore et al., 2009]. Museum samples were extracted in Chelex following Barber [2004]. Preventative laboratory techniques to control for the possibility of numts and contamination are described in Lynch Alfaro et al. [2011].

Polymerase chain reaction (PCR) amplifications for D-loop consisted of 10 min activation at 94°C, followed by 60 cycles of 30 sec at 94°C, 30 sec at 55°C, 1 min at 72°C, with a final annealing of 10 min at 72°C. The thermal cycling program for cytB included 10 min activation at 84°C, followed by 60 cycles of 30 sec at 84°C, 30 sec at 55°C, 1 min and 20 sec at 72°C, with a final annealing of 10 min at 72°C. PCR amplification specifications for cytB follow Lynch Alfaro et al. [2011].

Template volume, number of cycles, annealing temperature, and MgCl₂ concentration varied by primer pair, tissue type, and template concentration. All PCR products were further purified for sequencing by EXO/SAP (Exonuclease I—Shrimp Alkaline Phosphatase). The 10 µl Master Mix (MM) included 6 µl was DNA template, 2 µl ddH₂O, 1 µl SAP, 0.5 µl Buffer, and 0.5 µl EXO. The thermocycler program included one cycle of 30 min at 37°C, 15 min at 80°C, and a final temperature of 4°C.

All sequencing was conducted using an Applied Biosystems Prism (Life Technologies) 373 capillary sequencer housed in the Bioinformatics User Laboratory at Washington State University, or an Ap-

plied Biosystems 3730xL DNA Analyzer at the Yale Sequencing Laboratory at Yale University. Samples deposited at INPA were sequenced on Applied Biosystems 3130xl DNA Analyzer at Universidade Federal do Amazonas. We deposited all sequences to GenBank (see Table I for accession numbers).

Time Tree Analysis

To construct a time tree for a concatenated data set of cytochrome *b* plus D-loop for *C. albifrons*, *C. olivaceus*, and *C. capucinus*, we inferred divergence times under a relaxed clock model of uncorrelated, lognormally distributed rates using BEAST 1.61. We assigned each gene (D-loop and cytochrome *b*) separate (unlinked) HKY + G models. We used a coalescent expansion growth tree prior and default priors on other model parameters. There are no fossils that can be reliably assigned to the *Cebus-Sapajus* crown group. However, a previous divergence time analysis of platyrrhines [Lynch Alfaro et al., 2011] that incorporated five fossil calibrations yielded a mean age of the split between *Cebus* and *Sapajus* of 6.9 millions of years ago (MYA) (95% Highest Posterior Density: 4.3–9.9 MYA). We incorporated this estimate in our divergence time analysis by assigning a truncated normal prior to the root of the tree with mean of 6.9 MYA, SD 2, and min-max of 4.3 and 9.9 MYA.

We ran the Markov chain for 100,000,000 generations, sampling every 5,000 steps. We visually assessed convergence using Tracer 1.5 [Rambaut & Drummond, 2007] and AWTY to check effective sample size for parameters, stationarity of parameter samples, and estimates of clade posterior probabilities.

This research adhered to the Brazilian laws that govern primate research and the American Society of Primatologists' principles for the ethical treatment of primates. Research permits were granted through FUNAI and IBAMA, and institutional IACUC committees.

RESULTS

Our molecular time tree (Fig. 1) indicates that the untufted capuchins experienced a rapid diversification early in their evolutionary history, with major splits occurring at 2.5–2.1 Ma, during the Middle to Late Pliocene. The first untufted clade diverged at approximately 2.5 Ma, forming a Western

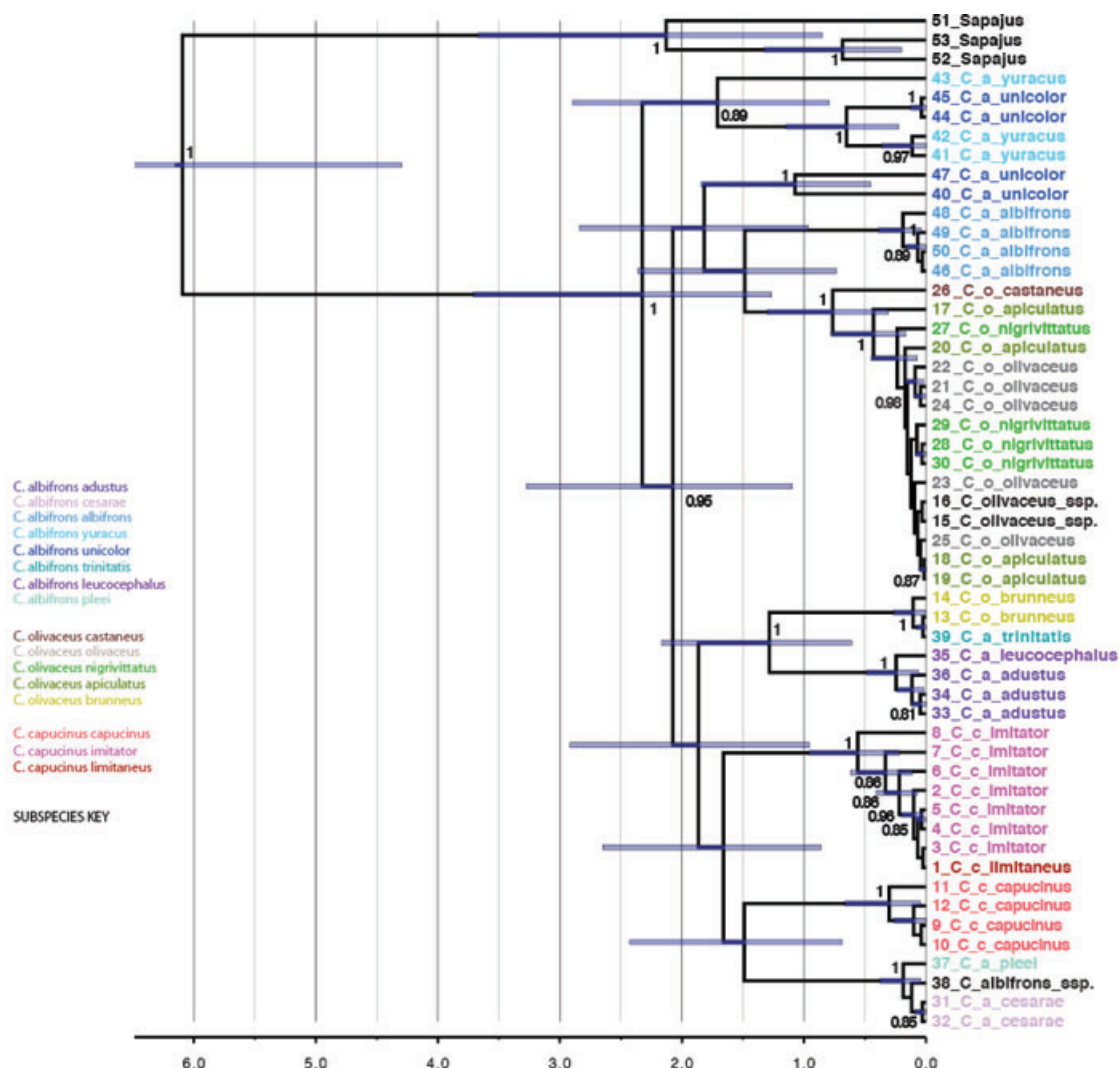


Fig. 1. Time tree for untufted *Cebus* diversification, using cytochrome *b* and D-loop markers. Numbers correspond to samples in Table I.

Amazonian clade (Group A in Fig. 2). This group encompasses our samples from Peru (43) and Amazonian Ecuador (41 and 42), as well as samples 44 and 45 from the upper Rio Juruá, Acre in Brazil (Fig. 2). According to Hershkovitz [1949; also Aquino and Encarnación, 1994] these samples are within the ranges of *yuracus* (nos. 41, 42 and 43, north of the Río Marañón) and *unicolor* (nos. 44 and 45, south of the Río Marañón). In our results they form a distinct clade, with the Peruvian specimen 43 in the west being a sister taxon to the samples to the north and south.

In addition to this Western Amazonian clade (Group A), two distinct untufted radiations originated at about 2 Ma: Group B an Amazonian plus Guiana Shield radiation that includes what are currently considered *C. a. unicolor*, *C. a. albifrons*, and subspecies of *C. olivaceus*; and Group C, a Western and Northern Andes plus Central American radia-

tion including what are currently considered *C. olivaceus brunneus*, *C. a. trinitatus*, *C. a. leucocephalus*, *C. a. adustus*, *C. c. imitator*, *C. c. limitaneus*, *C. c. capucinus*, *C. a. cesarae*, and *C. a. pleei*.

The Amazonian plus Guiana Shield radiation (B) contains two distinct groups or subclades separated by the Rio Negro:

(B.1) Amazonian—This area is insufficiently represented in our study, with only two samples (both in the range of *C. a. unicolor* as indicated by Hershkovitz [1949]), one from Barcelos on the right bank of the Rio Negro (no. 47) and the other from the Río Curanja, upper Río Purus (no. 40) in the Department of Loreto in Peru near the Brazilian border. These two samples, from localities more than 1,000 km apart, have been separated by more than 1 million years. The type locality of *C. a. unicolor* is Tefé, south of the Rio Amazonas, between the localities of the two samples (Fig. 2).

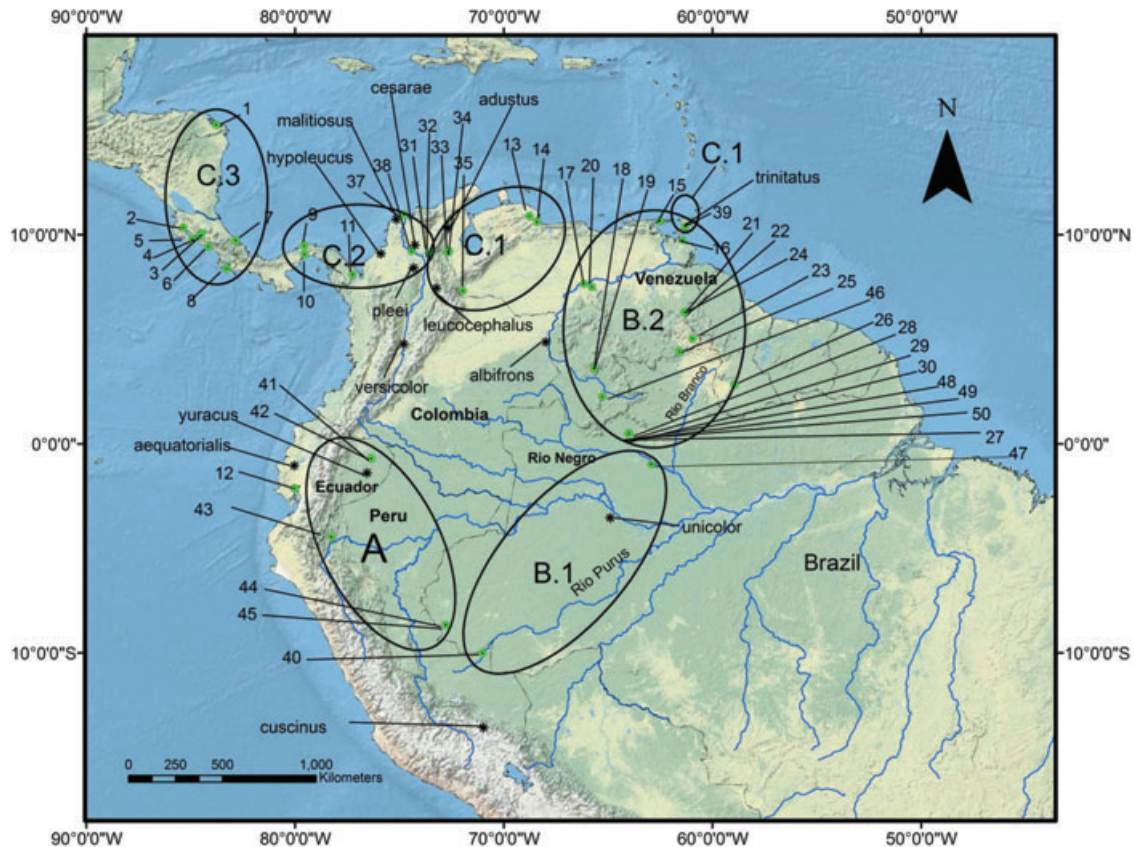


Fig. 2. Map of provenance of capuchin monkey specimens used in the time tree analysis. See Table I for more information on samples by number. Map includes major rivers and six phylogeographic regions that correspond to one or more distinct capuchin groups, as determined by the divergence time analysis: Group A—West Amazon, *Cebus yuracus*, Group B.1—Central Amazon, *C. unicolor*, Group B.2—Guyana Shield, *C. albifrons*, and *C. olivaceus*, Group C.1—Northern Andes, *C. brunneus* and *C. adustus/leucocephalus*, Group C.3—Central America, *C. imitator* and Group C.2—Northwestern Andes, *C. pleei*, *C. cesarae*, and *C. capucinus*. *Type localities for Hershkovitz's *albifrons* subspecies are indicated by an asterisk.

(B.2) Guiana Shield—At about 1.5 Ma, a branch of the untufted capuchins from the B.1 subclade evidently crossed the Rio Negro and rapidly spread further north and east through the Guiana Shield. This group diversified into two major clades: (1) Rio Negro and Orinoco white-fronted capuchins that were also considered by Hershkovitz [1949] to be *C. a. unicolor* (while just plotting the type locality of *C. a. albifrons* on the Rio Orinoco, just to the north, see below); and (2) the forms that have been variously described as subspecies of weeper or wedge-capped capuchins *C. olivaceus* (the *C. nigrivittatus* group of Hershkovitz [1949]) except for *brunneus* of the Venezuela coast that originated from Group C (see below).

Based on the samples included in this study, the crown age for living *C. olivaceus* is about 0.7 Ma. Excluding *C. o. brunneus*, there is no evidence for subspecies distinctions among *C. o. olivaceus*, *C. o. nigrivittatus*, and *C. o. apiculatus* (see Fig. 2). The sample from Guyana (*C. o. castaneus*, Fig. 2, no. 26) is the most geographically distant from the other *C. olivaceus* samples and the most genetically divergent (estimated divergence time from other *C. olivaceus*

at 0.7 Ma). There is a small area of overlap between these *albifrons* and *olivaceus* forms (see Fig. 3) in the Branco–Negro interfluvium, between the rios Demini and Padauri, both left bank tributaries of the Negro (J.P.B., personal observation). In this study, we are assuming that the *albifrons* samples from the Branco–Negro interfluvium are aligned with the neotype for Humboldt's *C. albifrons* established by DeFler and Hernández-Camacho [2002] (and thus, not *unicolor* as assumed by Hershkovitz 1949) on the left bank of the Río Orinoco: about 10 km north of Maypures, 200 km north of the Cerro Rocosó, El Tuparro National Park, Department of Vichada, Colombia. Samples from that locality in Colombia, however, are required to confirm this. If future studies prove our Negro–Branco samples to be different from Colombian *C. a. albifrons*, then a new name will be needed for these white-fronted capuchins.

Group C comprises the Northern Andean plus Western Andes and Central American radiation of the untufted capuchins. Group C capuchins split off about 1.9 Ma into a northeastern branch (C.1), east of the Eastern Cordillera today, east of the Serra de



Fig. 3. (A) Skull and live specimen of *Cebus olivaceus* from Río Aracá (photo courtesy of Francisco Pontual) and, (B) *C. albifrons* from Pico da Neblina with a baby howler monkey on his back in the Maturacá Yanomami village, AM. Both from Brazil Negro-Branco rivers interfluvium (Group B.2).

Perijá and extending to the Venezuelan Coast (*brunneus*) and around Lake Maracaibo (*adustus*), a western branch (C.2) up the Pacific Coast of northwestern Ecuador, into western Colombia and Central America (*C. capucinus*) with a part isolated (branching off about 1.5 Ma) in the Magdalena-Cauca-Cesar valleys and extending to the extreme north of Colombia, Sierra Nevada de Santa Marta (*versicolor*, *pleei*, *cesarae*, *malitiosus*) between the central and eastern cordilleras, and the Central American *C. capucinus imitator* branch (C.3). Note that the branching pattern in Fig. 2 indicates that an ancestral white-faced capuchin was first isolated in Central America in Costa Rica, Nicaragua, and Honduras about 1.7 Ma (Group C.3—*C. c. imitator* and *C. c. limitaneus*).

The white-faced capuchin of northern Colombia (*C. c. capucinus*), west of the Río Magdalena, subsequently occupied Panama and the Pacific coasts of Colombia and northwestern Ecuador.

There is no indication here that *C. capucinus imitator* and *C. capucinus limitaneus* are distinct. The single specimen from Trinidad (*trinitatis*) formed a clade with *C. brunneus* (Group C.1).

DISCUSSION

Our results indicate that the current morphology-based untufted capuchin monkey taxonomy—that separates the untufted capuchins, *Cebus*, into three groups, that is, white-fronted



Fig. 4. A sample of the coat-pattern variation in *Cebus*. From left to right, specimens from: Bolívar, Venezuela; Kartabo, Guyana; Rio de Oro, Ecuador; Rio Tapajos, Brazil; Solano, Venezuela; Solano, Venezuela; Catacomas, Honduras. Samples photographed from the American Museum of Natural History Collection in New York.

capuchins (*C. albifrons* ssp.), wedge-capped capuchins (*C. olivaceus* ssp.), and white-faced capuchins (*C. capucinus* ssp.)—is untenable. Our analysis has indicated paraphyly in the current taxonomic arrangements of *C. o. brunneus* in coastal northwest Venezuela with the remaining subspecies of weeper capuchins (*C. olivaceus*), and, more extensively, among three groups of capuchins currently considered subspecies of the white-fronted capuchin (*C. albifrons*) as well as white-faced capuchins (*C. capucinus*). The relative age when most of the present diversity arose, Late Pliocene to Early Pleistocene, implies that for notably divergent clades of *C. albifrons*, species status is more justifiable than their classification as subspecies. More samples are necessary, however, to assess the relationships of these groups. We expect to find greater diversity in the enormous geographic range of untufted capuchins (see Fig. 4).

Another recently published study of the phylogenetic relationships of untufted capuchins is that of Ruiz-García et al. [2010]. In their study of the molecular phylogenetics of *C. albifrons*, they also found a distinct division of Amazonian forms from the Río Vaupés, Colombia, and forms south of the Amazon. In that analysis, the Colombian Río Vaupés specimens were a sister group to the northern Colombian Andes forms, which they listed as *versicolor*, *pleei*,

and *cesarae* (in our Group C.3). However, the Ruiz-García et al. [2010] tree did not include any representatives of *Sapajus* (tufted capuchins, the sister taxon to untufted capuchins [Lynch Alfaro et al., 2011]), leaving the rooting of their tree uncertain. Our findings and those of Ruiz-García et al. [2010] question the proposition of Defler and Hernández-Camacho [2002] that *unicolor*, with its type locality in Tefé, south of the Río Solimões, is a junior synonym of Humboldt's *albifrons*. We argue instead that these authors were probably right concerning the affiliation of white-fronted capuchins from the north of the Rio Negro named *C. a. unicolor* by Hershkovitz [1949] with *C. a. albifrons*, but to the south (right bank) of the Rio Negro (Barcelos), the white-fronted capuchin is more closely related to the capuchin we sampled from the upper Rio Purus (which may or may not be Hershkovitz's *C. a. unicolor*). Further sampling is required, especially at or near Tefé, the type locality of *unicolor*. It is possible that the Barcelos specimen is a distinct taxon.

Our data suggest that *C. olivaceus* is a successful recent radiation in this region. Our findings confirm the conclusions of morphological assessments by Groves [2001] and Silva Jr. [2001, 2002] that *C. olivaceus* should not be divided into subspecies. They are also concordant with Valderrama-Aramayo's [2002] molecular study in Venezuela that

described *C. olivaceus* mitochondrial D-loop haplotypes as depauperate in variability within and among populations. There is no convincing molecular or morphological evidence for population isolation among the putative subspecies in the weeper capuchins of our Group B.2 and they should be considered a single species *C. olivaceus*, with the exception perhaps of the Guyana specimen (no. 26), which is the most genetically divergent. The analysis of further specimens from Guyana, Suriname, French Guiana, and far north-eastern Brazil is needed, including especially *C. o. castaneus* [I. Geoffroy, 1851], from its type locality.

The present success of *C. olivaceus* in the Llanos may stem from the fact that it is not sympatric with *Sapajus apella* there. *Sapajus* is also absent from the east of the Rio Branco and northeast of the Negro (J.P.B., personal observation). *Cebus olivaceus* has the most robust morphology of the untufted group (but *C. a. aequatorialis* is likely as robust, J.P.B. personal observation), and appears to have filled the niche presently occupied elsewhere by *Sapajus*. The overall rarity of untufted capuchins throughout the Brazilian Amazon (excluding the Negro–Branco interfluvium, J.P.B., personal observation) might be a result of the relatively recent arrival of *Sapajus* to the Amazon Basin (ca. 0.4 Ma [Lynch Alfaro et al., 2011]). In some areas east of the Essequibo, *C. olivaceus* is relatively rare and seems to occupy habitats not preferred by *Sapajus* (for example in Brownsberg, Suriname, J.P.B., personal observation). We speculate that this is due to competitive exclusion with sympatric *S. apella* [see Lynch Alfaro et al., 2011]. Thus, the Negro–Branco interfluvium may be a stronghold for untufted capuchins against the gradual invasion of their original range by *Sapajus*.

Although not sampled here, *C. kaapori* is going through a similar process in which both forest destruction and long-term competitive replacement by *S. apella* may be contributing to its endangered status [Lynch Alfaro et al., 2011]. Although *C. kaapori* was not included in our analysis, we predict that this species is sister to, or nested in, the clade of Group B.2.

The affinities of *C. a. aequatorialis* have yet to be determined. Geographically, west of the Andes in Ecuador and northernmost Peru, it may form part of Group C.2, or it may be an entirely separate offshoot of Group A. Unfortunately, we were unable to obtain samples from this taxon. Ruiz-García et al. [2010] studying the COII gene sequences of a broad sample of white-fronted capuchins, analyzed one specimen from Cantón Jama, Manabí, Ecuador, and found it to be aligned with a clade including central Amazonian capuchins from Tefé, Brazil (type locality of *unicolor*), Leticia, Colombia, and the ríos Ucayali, Napo, and Pachitea, and Sierra Escalera, San Martín (in the region identified by Aquino and Encarnación

[1994] as an undescribed subspecies), in Peru. Geographically, this is difficult to interpret.

Group C.1 includes samples of *C. o. brunneus* and *C. a. adustus* (number 35 from Apure, Venezuela, is possibly *leucocephalus*) from the northernmost extremity of the Andes, and *C. a. trinitatis* from the island of Trinidad. As noted above, *C. olivaceus* is paraphyletic; *C. o. brunneus* is part of a clade entirely separate from that of Group B.2 weeper capuchins—its sister species is evidently the capuchin from the region of Lake Maracaibo from which it diverged about 1.2 Ma—and it should be considered a separate species: *C. brunneus* [Allen, 1914]. An unexpected result was that the specimen from Trinidad, *C. a. trinitatis*, is genetically similar to *brunneus* and may be from a population introduced to the island, or a relict population from an earlier radiation of Andean *C. albifrons* in Venezuela that has been replaced by the Amazonian/Llanos *C. olivaceus* radiation. More samples are needed from Trinidad to see if there is a mix of *Cebus* haplotypes represented on the island.

The capuchins from Lake Maracaibo, extending across the northern half of the Sierra de Perijá, distinct from the capuchins in the northern Andes to the west were named *adustus* by Hershkovitz [1949]. The type, apparently paler than *leucocephalus* to the west, came from near the headwaters of the Río Cogollo (Apón), 5 km northwest of Machiques, Zulia, Venezuela. These samples (nos. 33, 34 and 36) came from the area delimited by Hershkovitz [1949] as belonging to *adustus*. Sample no. 35 from Nulita in the Selvas de San Camilo, Apure, Venezuela, came from within the range that Hershkovitz indicated for *leucocephalus* Gray, 1866 (1865). Gray's type locality for this species was Colombia, but Hershkovitz [1949] restricted it to El Tambor, Río Lebrija, 25 km northwest of Bucaramanga, Santander. Gray (1865) believed that *leucocephalus* might be a variety of *C. versicolor*, and Hernández-Camacho and Cooper (1976) and Defler (2004) believed so too, except with regard to a population they identified in the west of the Department of Arauca in Colombia on the Venezuelan border, immediately south of the Selvas de San Camilo, Apure, which they believed might be *adustus*. Our study certainly showed that the Apure population is aligned with *adustus* to the north. Provisionally it would seem that *C. adustus* Hershkovitz, 1949, would be the correct name for these specimens but the question remains open. The molecular genetic study of Ruiz-García et al. [2010] included specimens which they recorded as *leucocephalus* from Norte de Santander (Cúcuta) and Santander (Puerto Villamizar, Rubio, Catatumbo, and the type locality Bucaramanga). They fell into a distinct clade which was a sister group to the large majority of the white-fronted capuchins they analyzed, including clades they identified as *unicolor*, *albifrons*, *versicolor*, and *cesarae*, and they concluded

that *leucocephalus* is more related to the Amazonian *C. albifrons* lineages than to the other northern Andean forms. From their findings, *leucocephalus* is distinct from *versicolor*, *pleei*, and *cesarae* which form the Northern Andean Group C.2. The forms *adustus* and *leucocephalus* may be distinct taxa, but if *adustus* is found to be the same as *leucocephalus*, *leucocephalus* would be the senior synonym for the sister species of *C. brunneus*.

Our study and that of Ruiz-García et al. [2010] revealed a single distinct haplogroup of *C. capucinus* occurring in Costa Rica, Nicaragua, and Honduras, splitting from Colombian and Panamanian capuchins about 1.7 Ma. In concordance with Ruiz-García et al. [2012] we found no evidence for a subspecific distinction of *limitaneus* in Honduras and *imitator* in Costa Rica. *Cebus limitaneus* is the junior synonym of this group of white-faced capuchins that should be considered a distinct species: *Cebus imitator* [Thomas, 1903].

The diversification of Group C.2 was without doubt influenced by the ongoing and, in geological time, rapid uplifting of the Northern Andes, notably the Eastern Cordillera, 5–2 Ma [see, e.g., Gregory-Wodzicki, 2000]. The rather complex grouping of northern Colombian capuchins is divided by the ríos Magdalena and Cauca. The diversity in morphology in this area resulted in Hershkovitz [1949] indicating four subspecies of *C. albifrons* east of the Magdalena and two of *C. capucinus* (*capucinus* and *nigripectus*) to the west.

East of the Río Magdalena, Ruiz-García et al. [2010] identified two distinct sister taxa, a northern form combining *pleei* and *cesarae* (both described by Hershkovitz [1949]) and a southern form in the Magdalena and Cauca river valleys; *versicolor* [Pucheran, 1845]. Our samples (nos. 31, 32, and 37) were from specimens in the putative ranges of *pleei* and *cesarae*, which formed a single clade and corresponded to Ruiz-García et al.'s *cesarae/pleei* cluster. If a single taxonomic unit, the appropriate name could be *C. cesarae* (if only because its description by Hershkovitz [1949] is on page 356, whereas that of *pleei* is on page 360). Further studies are needed to delineate the border between *versicolor* and *cesarae*.

The validity of *malitiosus* on the Colombian coast from the northwestern base and foothills of the Sierra Nevada de Santa Martha is yet to be ascertained. Our study did not include any samples from its supposed range, and the one sample believed to be *malitiosus* (from Pueblito, Tayrona National Park) in the analysis of Ruiz-García et al. [2010] was nested in an early branch which included two capuchins from the Colombian Amazon (Puerto Rastrojo and Villaflor) and one from the Río Napo in Peru.

The capuchins west of the Río Magdalena extending into Panama formed a distinct clade, which was also identified by Ruiz-García et al. [2010, 2012].

Ruiz-García et al. [2012] identified three mitochondrial haplogroups for Colombian/east Panamanian *C. capucinus* and for each the diversity was high, but the three haplogroups were intermixed geographically. Ruiz-García et al. [2012] suggested that this geographic and genetic signature was generated from small and initially isolated populations subject to intense gene drift during the completion of the Panama land bridge and climatic changes in the Quaternary; parapatric prespeciation processes of populations that subsequently expanded and intermixed (see also Ford [2006], for a historical biogeographic review of the Central American capuchins).

CONCLUSIONS

Our molecular genetic analysis indicates that untufted capuchins are rather more diverse than has been indicated by Groves [2001; 2005; also Silva Jr., 2001] and approximates more closely the assessment of Hershkovitz [1949, 1955]. Hershkovitz's [1949] most helpful appraisal maintained the names of the numerous forms, even though he himself was doubtful of the validity of a number of them, and with *C. albifrons* he contributed descriptions of four previously undescribed subspecies (*cesarae*, *pleei*, *adustus*, and *yuracus*). One of our key findings is that both *C. olivaceus* and *C. albifrons* as defined by Hershkovitz are paraphyletic. The form *brunneus* has an origin distinct from the other weeper capuchins of Hershkovitz and is aligned with the white-fronted capuchins of the region of Lake Maracaibo. The capuchins of the Magdalena–Cauca valleys form a distinct clade, with white-faced capuchins as the sister group, and white-fronted capuchins of the Rio Negro–Branco interfluvium have the entire Guiana shield radiation of weeper capuchins as their sister group. Avoiding an elaborate—contrived even—arrangement of species and subspecies, and using the Phylogenetic Species Concept as recommended by Groves [2001, 2004], we point to a provisional taxonomy of species.

Our molecular analysis suggests the division of sampled individuals into six phylogeographic groups and nine full species: Group A—*C. yuracus*; potentially *C. cuscinus* and an yet unknown taxon; Group B.1—*C. unicolor*, and probably one or more species as yet undescribed; Group B.2—*C. albifrons*, *C. olivaceus*, and *C. castaneus*; Group C.1—*C. brunneus* and *C. leucocephalus/adustus*; Group C.2—*C. capucinus*, *C. cesarae*, and *C. versicolor*; and Group C.3—*C. imitator*.

This is of course provisional, pending most especially the analysis of a considerably expanded sample from the southern and western Amazon (*cuscinus* and *unicolor*, and probably as yet unnamed taxa), and of further specimens in the regions of the Sierra Nevada de Santa Marta (*malitiosus*) and Lake Maracaibo (*adustus/leucocephalus*). Further study

of the untufted capuchins of the Guianas is needed to establish the validity of *castaneus* as distinct from *olivaceus*. *Cebus kaapori* we maintain as a distinct species but it would be of interest to see how, for example, it may relate to *castaneus*. We are still ignorant of the exact distributional limits for the large majority of these untufted capuchins.

Although we have so few samples from the southern Amazon, the results are intriguing in that they indicate that the origin of this radiation was in the western Amazon. About 2 Ma, the ancestral *Cebus* in the southwestern Amazon evidently divided along a north–south axis to form a south central clade which in turn suffered a divide along an east–west axis. The northern group gave rise to the two radiations occupying northern South America and Central America. Not sampled here was *C. kaapori* from southern Pará, Brazil, which we predict future analyses will confirm as a sister group to the Guiana Shield weeper capuchins.

Our findings point to the importance of revising the taxonomy of New World Primates for conservation purposes. We show here that the apparently wide-ranging and non-threatened white-fronted capuchin is actually a diverse and old radiation of primates. Some of them appear to have very restricted ranges and their conservation status should be urgently assessed as is the case of the northern Andean taxa. With an increase in habitat fragmentation in this Andean region, knowing the population status of these different species is fundamental for conservation planning.

Finally, we would like to comment on the potential role that interspecific competition may have played in Amazonian history to determine the diversity and distribution of species. Although this role has been largely overlooked by scientists interested in the origins of species diversity in Amazonia [e.g., Haffer, 1997], Boubli et al. [29] suggest that interspecific competition is an important factor shaping the phylogenetic and geographic distributional patterns of primates, as in the case of the pitheciines they studied north of the Rio Negro. In the present study, we mention the potentially negative effect that the relatively recent invasion of *Sapajus* in Amazonia might have had on the abundance and distribution of untufted capuchins, a natural process and an example of evolution in action [see also Lynch et al., 2011]. We believe that this process may also be occurring in other places in Amazonia; for example, *Saguinus midas* and bare-faced tamarins [see Rohe 2006].

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