



A Taxonomic Reassessment of *Cacajao melanocephalus* Humboldt (1811), with the Description of Two New Species

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Abstract The author of the last published systematic review of *Cacajao* recognized 2 subspecies of black-headed uakaris (black uakaris): *Cacajao melanocephalus melanocephalus* and *C. m. ouakary*. As a result of a series of black uakari surveys and collecting expeditions to several tributaries of the Rio Negro and of morphological and molecular analyses of museum specimens and specimens we collected during field expeditions, we reassess their taxonomy. We describe a newly discovered species of black uakari from the Rio Aracá, a left bank tributary of the Rio Negro, Amazonas, Brazil. We also show that *ouakary* is a junior synonym of *melanocephalus* and provide a new name and a new description for *Cacajao melanocephalus melanocephalus* in the Pico da Neblina region of Brazil and Venezuela. Based on genetic, morphological, and ecological evidence, we propose that there are 3 species of black uakaris. We named the Rio Aracá species *Cacajao*

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ayresi sp. nov. (Ayres uakari) in honor of the late José Márcio Ayres, a pioneer in uakari research and conservation. We named the Neblina black uakari *Cacajao hosomi*, after the Yanomami word for uakaris. The new taxonomic arrangement provided here implies that the conservation status of black uakaris needs to be reassessed.

Keywords Amazonia · black-headed uakari · Brazil · *Cacajao melanocephalus* · cytochrome *b* · geographic distribution · New World primates · Pitheciines · Pleistocene · rain forest · speciation · phylogeny

Introduction

Black-headed uakaris, *Cacajao melanocephalus* ssp. (black uakaris) are specialized seed-eating Pitheciinae that inhabit remote areas of the Rio Negro and Rio Orinoco Basins and parts of the Pantepui biogeographic region of Brazil, Colombia, and Venezuela (Boubli 1993; Hershkovitz 1987). They are diurnal medium-sized monkeys, with males slightly larger and more robust than females (this study; Hershkovitz 1987). Uakaris have very short tails, distinguishing them from all other New World primates. The tail length of black uakaris is less than half that of the head and body combined (this study; Hershkovitz 1987). Primatologists currently recognize 2 taxa: *Cacajao melanocephalus melanocephalus* and *C. m. ouakary* (Groves 2001; Hershkovitz 1987). According to Boubli (1993), *Cacajao melanocephalus melanocephalus* inhabits the area delimited by the Rio Negro to the south and west and the Rio Aracá to the east, with no specified limit to the north and *C. m. ouakary* ranges south and west of Rio Negro, north of the Rio Japurá and south of the Rio Guaviari in Colombia; the Rio Negro marks the boundary between the 2 taxa (Boubli 1993).

Since 1991, Boubli has conducted primate surveys and collecting expeditions to several tributaries of the Rio Negro and mountains of the Pantepui region as part of a systematic study of the ecology and biogeography of black uakaris (Boubli 1997, 1999). In light of new evidence gathered in these field trips and as a result of morphological and molecular analyses of field-collected and museum specimens, we reassess the taxonomic status of black uakaris. We include a description of a newly discovered black uakari from the Rio Aracá region, a left bank tributary of the Rio Negro, Amazonas, Brazil. We also show that *ouakary* is a junior synonym of *melanocephalus* and provide a new nomen and description for *Cacajao melanocephalus melanocephalus*. Based on genetic, morphological, and ecological evidence, we consider the 3 black uakaris described here as full species. To avoid inevitable confusion with the different names discussed here, we henceforth refer to the subspecies *Cacajao melanocephalus melanocephalus* as Neblina uakaris because most of our specimens are from Pico da Neblina National Park in Brazil. We refer to the subspecies *Cacajao melanocephalus ouakary* as golden-backed uakaris as proposed by Barnett and Cunha (1991), and finally, we refer to the newly discovered black uakaris as Aracá uakaris, alluding to their type locality.

Methods

Field Surveys

We carried out surveys of black uakaris along first- and second-order tributaries of the upper Rio Negro (Uaupés, Uneiuxi, Iá, Iá-Mirim, Cauaburi, Marauíá, Preto, Padauri, Erere, Aracá, Madixi, Jauari, Cuieiras, and Demeni) and several mountains of the Pantepui (Pico da Neblina, Baruri, Padre, Imeri, Tapirapecó, and Aracá) from 1991 to 2007. We conducted surveys around transient camp sites for 2–3 days by foot (mountains) and canoes (tributaries). When we found a group of uakaris, we determined their geographical location via a global positioning system (GPS) and collected a specimen when possible. We preserved specimens initially in ethanol and later prepared their skins and skulls either at the Museu Nacional (MN)/UFRJ, Rio de Janeiro or at INPA, Manaus, Brazil.

We spoke with Indians and settlers along the way, asking them about the composition of the local primate communities. We also collected discarded monkey bones around Yanomami hearths and traded for decorative artifacts containing monkey skins in the villages of Maturacá, Nazareth, and Xamatá and at a Baniwa village in the Rio Içana.

Molecular Analysis

We extracted total genomic DNA from muscle tissues preserved in alcohol per the standard protocol of Sambrook *et al.* (1989) and from uakari bones and skins obtained at the Yanomami villages. We amplified the mitochondrial cytochrome *b* gene (*cyt b*) via the polymerase chain reaction (PCR) with the primers L14725 (Kocher *et al.* 1989) and H15915 (Irwin *et al.* 1991). We carried out PCR reactions in a total volume of 25 μ l, containing 2.5 μ l of dNTPs (2.5 mM); 2.5 μ l of 10 \times buffer (100 mM Tris-HCl, 500 mM KCl); 2 μ l from each primer (0.2 μ M), 3 μ l of MgCl₂ (25 mM); 1 μ l of DNA (*ca.* 10 ng), and 1 U of *Taq* DNA polymerase. We carried out the amplification cycles under the following conditions: denaturing at 92°C for 1 min; annealing at 52°C for 35 s; and extension at 72°C for 90 s. We carried out a final extension cycle at 72°C for 5 min. After purification, we sequenced PCR products via a ET Terminator Cycle Sequencing kit (Amersham Bioscience) and resolved on the MegaBACE 1000 (Amersham Pharmacia) automatic sequencer per the manufacturer's instructions. We edited and aligned sequences in Clustal W (Thompson *et al.* 1996) using the default setting and edited by eye. Clustal W is implemented in BioEdit (Hall 1999). We conducted phylogenetic analysis via PAUP* version 4.0b10 (Swofford 2002). We performed a heuristic search with a branch-swapping algorithm (tree bisection reconnection) under maximum parsimony (MP). Nonparametric bootstrapping was based on 1000 replicates. We used Modeltest 3.7 (Clement *et al.* 2000) to determine the best model of sequence evolution that fits the evolutionary parameter values for the data. We determined the Tamura Nei with the γ parameter (TrN+G) model of molecular evolution (Rodríguez *et al.* 1990) to be the most likely model of sequence evolution. We performed Bayesian inference analysis in MrBayes 3.01 (Ronquist and Huelsenbeck 2003) under the Tamura-Nei+G model. We generated pairwise distances under the Tamura-Nei+G model of molecular evolution in PAUP* 4.0b10 (Swofford 2002).

Table 1 Localities surveyed indicating where we observed/collected uakaris and the elevation; locality number according to Fig. 1.

Locality	Locality name	Elevation (m)	Species observed	Collected	Voucher specimen museum number (field number ^a)
1	Matapi island, Rio Uaupés	83	<i>Cacajao melanocephalus</i>	No	–
2	Rio Içana	–	<i>C. melanocephalus</i>	Yes	– (open skin 3 in Fig. 3)
3	Morro Seis Lagos	100	<i>C. hosomi</i>	No	–
4	Rio Iá	70	<i>C. hosomi</i>	Yes	–
5	Maturacá road	87	<i>C. hosomi</i>	No	–
6	Bebedor, mid- Rio Cauaburi	84	<i>C. hosomi</i>	No	–
7	Serra do Demiti., road side	120	<i>C. hosomi</i>	Yes	INPA 5252 (JPB 152)
8	Salto Huá, Canal Maturacá	105	<i>C. hosomi</i>	No	–
9	Igarapé Waputa	104	<i>C. hosomi</i>	Yes	INPA 5249; INPA 5251 (JPB 153); INPA 5250 (JPB 154)
10	Maturacá village	180	<i>C. hosomi</i>	No	–
11	Igarapé Tukano	150	<i>C. hosomi</i>	No	–
12	Upper Rio Cauaburi	144	–	–	–
13	Pico da Neblina	1500	<i>C. hosomi</i>	No	–
14	Serra do Imeri	808	<i>C. hosomi</i>	Yes	MN68611 (JPB102); MN68613 (JPB106)
15	Zê Maria, Marauíá River	–	–	–	–
16	Serraria, Rio Negro	35	<i>C. melanocephalus</i>	Yes	MN68616 (JPB 110)
17	Rio Aiuanã	35	<i>C. melanocephalus</i>	No	–
18	Ecunauí, Rio Negro	35	<i>C. melanocephalus</i>	No	–
19	Rio Mandiquié	–	–	–	–
20	Marari, village	–	–	–	–
21	Pico Tamacuari, Tapirapecó	–	–	–	–
22	Balawa-ú village	–	–	–	–
23	Novo Demeni village	–	–	–	–
24	Igarapé Anta	–	–	–	–
25	Serra do Aracá	–	–	–	–
26	Igarapé Cuieiras	–	–	–	–
27	Lago da Serrinha, Rio Aracá	–	–	–	–
28	Rio Demeni	–	–	–	–
29	Igarapé Madixi	–	<i>C. ayresi</i>	Yes	INPA 5246 (JPB 135)
30	Lower Rio Aracá	–	<i>C. ayresi</i>	Yes	INPA 5247 (JPB 138); INPA 5248 (JPB 139)
31	Rio Negro	–	–	–	–
32	Igarapé Preto	–	–	–	–
33	Malalaha village	–	–	–	–
34	Igarapé Peixe–boi	–	–	–	–
35	Cuacu village	–	–	–	–
36	Igarapé Erere	–	–	–	–
37	Roçado village	–	<i>C. melanocephalus</i>	No	–
–	Sao Gabriel da Cachoeira, township	–	<i>C. hosomi</i>	Yes	INPA 5242 (JPB 001)
–	Rio Solimões, Lago Amanã, ca. 100 km upstream from Manacapuru	–	<i>C. melanocephalus</i>	Yes	INPA5238 (MvR 021)

Table I (continued)

Locality	Locality name	Elevation (m)	Species observed	Collected	Voucher specimen museum number (field number ^a)
–	Rio Solimões, Lago Amanã, ca. 100 km upstream from Manacapuru	–	<i>C. melanocephalus</i>	Yes	INPA 5239 (MvR 022)
–	Lake on the left bank of the Rio Solimões, ca. 1 h upstream from Manacapuru	–	<i>C. melanocephalus</i>	Yes	INPA 5240
–	Sacado do Tarauacá	–	<i>C. calvus calvus</i>	Yes	INPA 5241

^a Collector initials: JPB = Jean Phillippe Boubli; MvR = Marc van Roosmalen.

Molecular and Morphological Analysis

We performed molecular analysis via cytochrome *b* gene sequences of newly collected and museum specimens of *Cacajao calvus* ($N=1$), Neblina uakaris ($N=7$), golden-backed black uakaris ($N=4$), and Aracá uakaris ($N=3$). The final alignment comprised ca. 1095 nucleotides of nearly complete cytochrome *b* gene and 10 nucleotides of tRNA threonine (GenBank accession nos. EU560408–EU560422). We included sequences of cytochrome *b* of Uta Hicki's bearded sakis *Chiropotes utahicki* (GenBank AY226185) and brown-backed bearded sakis *C. israelita* (GenBank AY226190) as outgroups. On average, genetic distance between black uakaris across the Rio Negro, i.e., between Neblina and Aracá uakaris versus golden-backed black uakaris, was 2.3%, which is greater than that between the 2 species from the left bank, viz., Neblina and Aracá uakaris (0.5%). Bayesian inference and strict consensus maximum parsimony trees provide support for distinctiveness of the 3 focal forms of black uakaris (Figs. 2 and 3). Neblina and golden-backed black uakaris are distributed allopatrically, with the Rio Negro forming a geographic barrier, are reciprocally monophyletic (Fig. 2), are supported by diagnostic characters (Table II), differ in color pattern of pelage, and occupy different habitats; therefore we consider them full species. Neblina and Aracá uakaris are separated by ≥ 3 mutations in the analyzed section of the cytochrome *b* gene; however, genetic divergence within each taxon is ≤ 4 mutations. The data suggest that the 2 reciprocally monophyletic species are the result of historical fragmentation followed by incipient differentiation. The 2 taxa also clearly differ in pelage color pattern, and have disjunctive distributions, which leads us to conclude that they are following unique evolutionary trajectories under the Evolutionary Species Concept (Moritz 2002).

Time of Divergence Among the 3 Taxa

Despite existing controversy with respect to rates of molecular evolution in primate mitochondrial amino-acid coding genes, the lower-bound (1% per million yr; Brown *et al.* 1979) and the upper-bound (1.5% per million yr; Ho *et al.* 2005) substitution rates result in an estimate of the last common ancestor of Neblina and Aracá uakaris at 0.5–0.3 Ma, respectively, corresponding to the mid-Pleistocene. The divergence

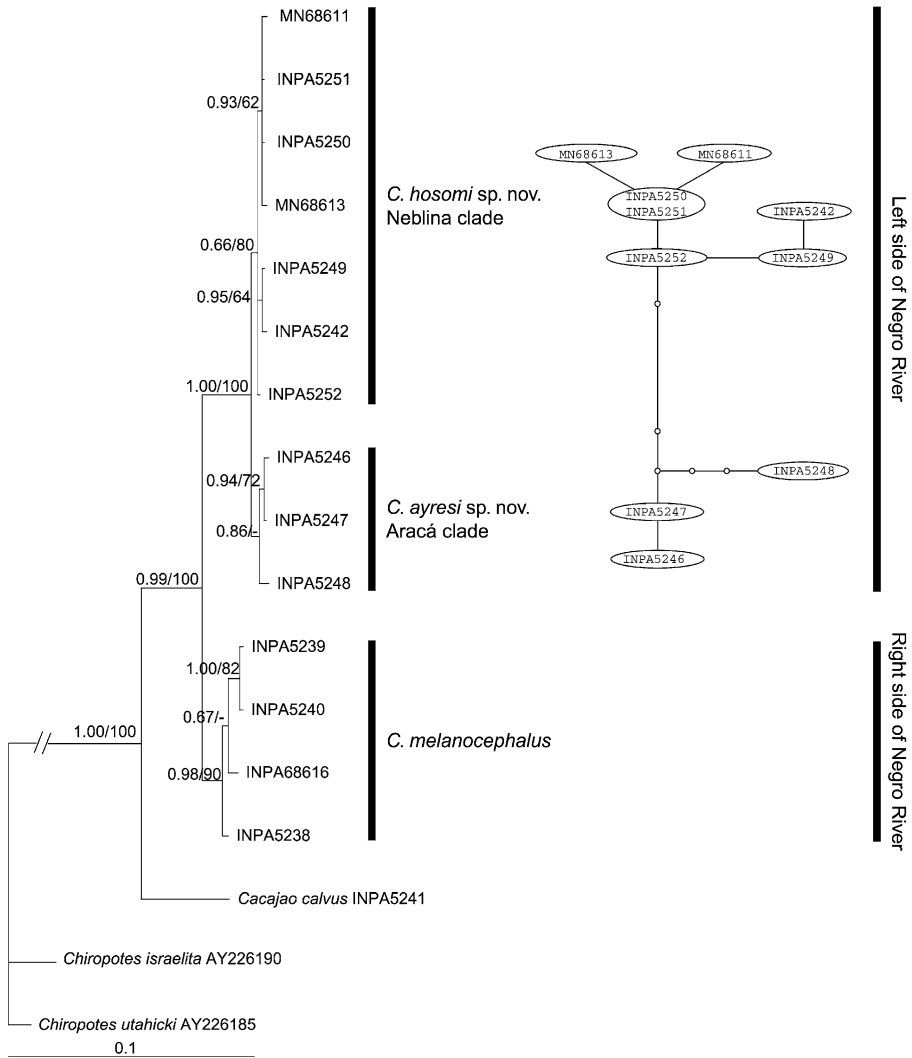


Fig. 2 Bayesian inference topology based on cytochrome *b* data obtained using TN+G distance. Numbers on left and right of the branches are posterior probabilities and bootstrap values (only values >50 are shown). Haplotype network represents haplotype relationship among subclades.

time estimated for the last common ancestor of left (Neblina and Aracá uakaris) and right (golden-backed black uakaris) bank Rio Negro clades are between 2.5 and 1.6 Ma corresponding to the late Pliocene. Pairwise divergence among all analyzed specimens is in Table III.

Taxonomic Accounts

Alexander von Humboldt (1811) first observed and described black uakaris during his expedition to the upper Orinoco and Cassiquiare regions of southern Venezuela (Humboldt and Bompland 1907). Humboldt never saw black uakaris in the wild and



Fig. 4 *Simia melanocephala* (Humboldt 1811) and *Brachyurus ouakary* (Spix 1823) (= *Cacajao melanocephalus*).

different in the markedly yellowish coloration of the sides and back without any obvious reddish tinge. (Hernández-Camacho and Cooper 1976, p. 53)

Hershkovitz (1987) formalized the taxonomical arrangement, which primatologists accept today (Groves, 2001). However, in proposing the arrangement, Hernández-Camacho and Cooper (1976) assumed that the Humboldt type specimen, which was lost *en route* to Europe, represented the same taxon as the ones they examined from Maturacá, Brazil and the Amazon Federal Territory of Venezuela.

Though Humboldt's painting of *Simia melanocephala* (= *Cacajao melanocephalus*; Fig. 4) suggests an individual with the entire dorsum uniform in color with the 4 limbs, a pattern not observed to date in any form of black uakaris, Humboldt's original description emphasizes the yellowish brown coloration of his specimen:

... the entire body, with the exception of the head and the four hands, is covered by a yellowish brown pelage. The hairs are long, shiny, and a little straight. The chest, the belly, and inner surface of arms and legs are of a paler tinge, of a whitish-yellow. The hands are very thin and black. The extremely long fingers are externally covered with short grey hairs. Collar and nape are nearly bare. Claws are a little flat. The tail is thick, yellowish brown and almost black at the tip. (Humboldt 1811, p. 317)

According to Hershkovitz (1987), Humboldt's "description and figure in color is that of a pale golden brown animal with blackish hands and feet" (p. 28). Considering the general consensus regarding the yellowish brown coloration of *Cacajao melanocephalus ouakary* (Spix 1823; Fig. 4), and its distinctiveness from

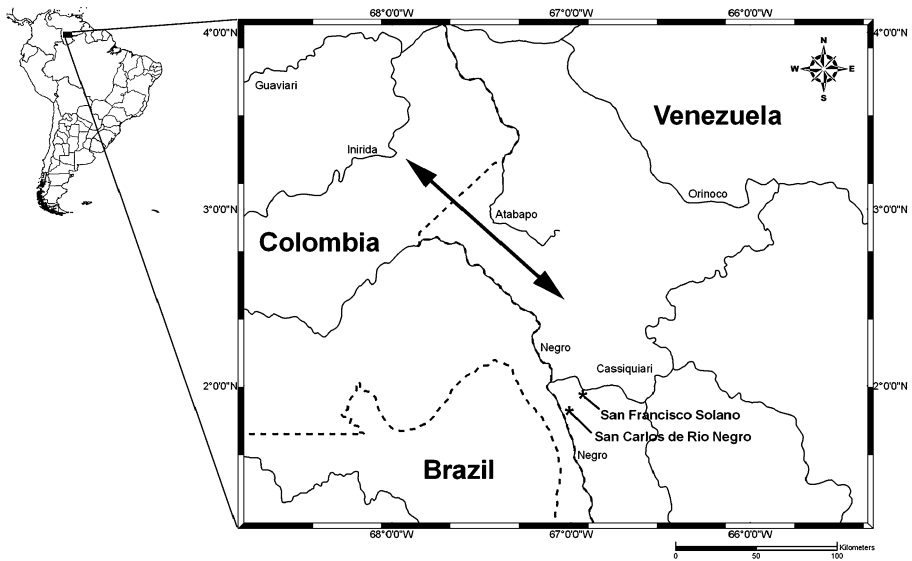


Fig. 5 San Francisco Solano, locality where Humboldt (1811) acquired a pet juvenile black uakari monkey, *Simia melanocephala* (= *Cacajao melanocephalus*). Arrow indicates a natural corridor connecting the Venezuelan Amazonas region north of the Cassiquiare with the Colombian Guaviari/Guainia interfluvium.

the reddish colors of back and flank of the other forms of black uakaris (Fig. 3), we believe that Humboldt's specimen represents the same taxon as Spix's uakari, and as a result we place *ouakary* Spix as a junior synonym of *melanocephalus* Humboldt. This proposition is based on what we now know on the geographical distribution of the different black uakari taxa. The Mission of San Francisco Solano and the neighboring town of San Carlos de Rio Negro are both near the junction of the Canal Cassiquiare and the Rio Negro (Fig. 6). Based on Humboldt's description and painting, it is possible that the specimen he acquired was captured by a local on the right bank of the Rio Negro near San Carlos, *ca.* 15 km from San Francisco Solano, thus within the distribution of golden-backed black uakaris. However, it is more likely that the specimen was captured on the right bank of the Canal Cassiquiare near San Francisco Solano. As shown in Fig. 6, there is no apparent geographical barrier separating the Guaviari region of Colombia and Venezuelan Amazonas north of the Cassiquiare. It is reasonable to expect then that the range of golden-backed black uakaris extends into this area of Venezuela north of the Cassiquiare and that the Cassiquiare marks the boundary between the Neblina and golden-backed uakaris in the region. However, we are unaware of any black uakari museum specimen for the area.

In the following species accounts, we restrict the current use of *Cacajao melanocephalus* to golden brown individuals east and south of the Rio Negro (golden-backed uakaris) and provide new specific names for the remaining forms of black uakaris.

Cacajao melanocephalus (Humboldt 1811)

Golden-brown uakari

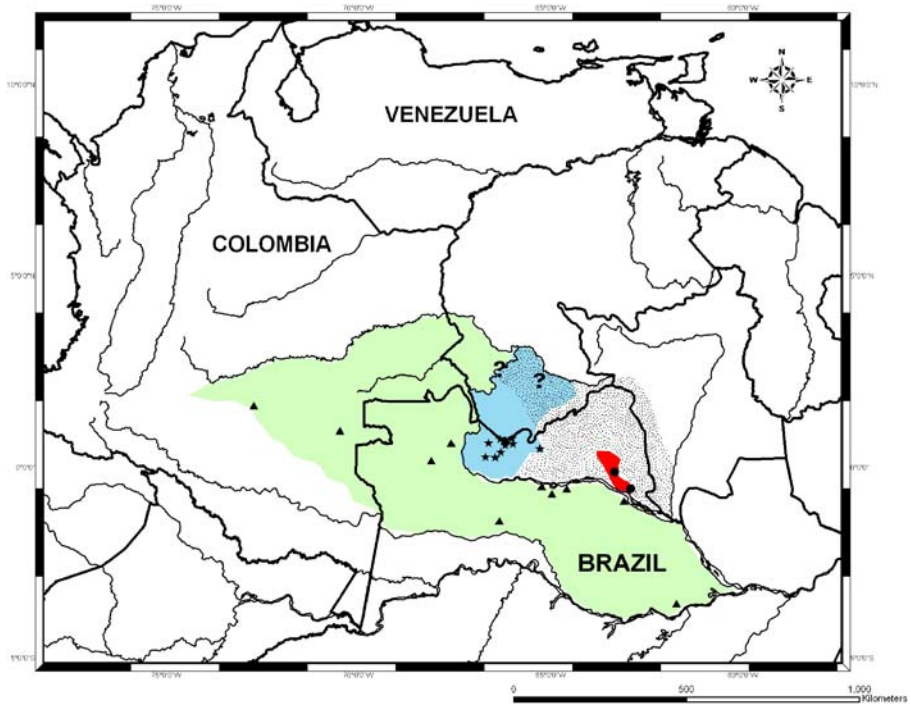


Fig. 6 Suggested geographical distributions of black uakaris. Green area = *Cacajao melanocephalus*, blue area = *C. hosomi*, red area = *C. ayresi*. Sand pattern corresponds to our suggested geographical distribution for *Chiropotes israelita*. Triangles (*C. melanocephalus*), circles (*C. ayresi*), and stars (*C. hosomi*) are localities of observed/collected black uakaris in this study. Two triangles in Colombia correspond to Field Museum specimens (FMNH nos. 88250, 88251, 89468, 89469, 89470, and 89471) and question marks in Venezuela correspond to Smithsonian National Museum specimens (USNM nos. 406423, 406425, 406572, and 406574). See text for details.

Simia melanocephala Humboldt 1811, a pet at San Francisco Solano, Rio Cassiquiare, Venezuela

Brachyurus ouakary Spix 1823, Rio Içá at confluence with Rio Solimões, Brazil (from known distribution, more likely the Rio Japurá on the north bank of its confluence with the Rio Solimões, Hershkovitz 1987)

Ouakaria spixii Gray, 1849. No locality

Holotype A pet not preserved

Type Locality Exact locality unknown, in the region of the Mission of San Francisco Solano on the Canal Cassiquiare, Amazonas, Venezuela

Neotype MN68616 (JPB 110), an adult female, that Boubli collected on December 4, 2003 (original field number JPB 110) at Serraria, right bank of Rio Negro, Amazonas, Brazil 0° 28' 21" S, 65° 10' 14" W. The neotype consists of skin, skull and liver tissue fixed in ethanol.

Type locality Serraria, right bank of Rio Negro, Amazonas, Brazil, 0° 28' 21" S, 65° 10' 14" W, Amazonas, Brazil.

Paraneotypes INPA5240 an adult female that van Roosmalen collected on a lake on the left margin of Rio Solimões, about 1 hour upstream from Manacapuru, Amazonas, Brazil, consisting of skin, skull, liver tissue fixed in ethanol; INPA5238 (original field number MvR 021) a juvenile female, and INPA5239 (original field number MvR 022) a juvenile male that van Roosmalen collected on Rio Solimões, Lago Amanã, ca. 100 km upstream from Manacapuru, Amazonas, Brazil, both consisting of skin, skull, liver tissue fixed in ethanol.

Diagnosis Head, beard, nape, arms, hands and feet are blackish; mantle to shoulders blackish usually with golden hairs showing through, the blackish hairs often extending as a thin overlay to behind mantle but not to midback; lower back slightly redder and darker than yellowish mid back; mid and lower back contrast markedly with bright reddish brown of thighs; nuchal hairs whorled, directed forward on crown, back and nape, the long black hairs sparsely covering shoulders; blackish coronal hairs long, projecting forward beyond brows concealing eyes and ears; coloration of belly reddish brown and of chest blackish with few interspersed golden hairs

Comparisons Differs from the Neblina and Aracá black uakaris by its golden mid and lower back and reddish thighs, legs, and tail that markedly contrast with bright reddish brown coloration of the former and the darker blackish appearance of the latter species; its ventral surface of body is bicolor (blackish in the chest and reddish brown in the belly) as opposed to a more homogeneous blackish ventral surface in the 2 remaining species; its ears and eyes seem more concealed than those of Aracá uakaris but less so than in Neblina uakaris; its pelage seems as long and thick as in Aracá uakaris but less so than in Neblina specimens; tail is chestnut in adults and completely blackish in 2 young individuals (INPA 5238 and 5239) but 1 young male Neblina uakari has a dark reddish brown tail with blackish tip. Hershkovitz (1987) also reported that the type of *Ouakaria spixii* Gray of unknown provenance was a half grown individual with blackish tail.

Specimens Examined ($n=4$) Santa Isabel, 1 female (MN 68616, JPB 110); Manacapuru, 2 females (INPA 5238, MvR 21; original field number by Marc van Roosmalen and INPA 5240, MvR, no number); 1 male (INPA 5239, MvR 22). We saw digital photos kindly provided by Dr. Bruce Patterson of the Field Museum of Natural History of specimens from the Guaviare region of Colombia (FMNH 88250, 88251, 89468, 89469, 89470, 89471) that showed individuals morphologically similar to other *Cacajao melanocephalus* that we examined.

Geographical Distribution We propose a range extension of the known geographical distribution of golden-backed uakaris (Boubli 1993) to include the region between the Canal Cassiquiari and Rio Orinoco in Venezuela. There is no obvious barrier between the head waters of the Rio Negro and the Rio Atabapo along the Colombia-Venezuela border; thus we propose that the golden-backed black uakaris living

between the Rio Guainia and Rio Guaviari in Colombia also occur in Venezuela north of the Cassiquiare Canal (Fig. 6).

Cacajao hosomi sp. nov.

The Neblina Uakari

Etymology From the Yanomami word *hosomi* for uakari monkeys.

Holotype MN 68613, an adult female, that Boubli collected on November 30, 2003 (original field number JPB 106) at Imeri Mountains, Serra do Xamatá, Amazonas, Brazil, 0° 29' 30" S, 65° 16' 18" W. The holotype consists of skin, skull, partial skeleton, and liver tissue fixed in ethanol.

Type locality Imeri Mountains, Serra do Xamatá, Amazonas, Brazil, 0° 29' 30" S, 65° 16' 18" W.

Paratype MN 68611 (JPB 102), an adult male, that Boubli collected on November 30, 2003 (original field number JPB 102) at Imeri Mountains, Serra do Xamatá, Amazonas, Brazil, 0° 29' 30" S, 65° 16' 18" W, consisting of skin, skull, partial skeleton, and liver tissue fixed in ethanol.

Diagnosis Apparently the largest of black uakarids (Table IV); general coloration blackish in mantle to shoulders or beyond; midback bright reddish brown of similar color as lower back, tail and thighs; tip of the tail blackish; head, beard, arms, legs, hands and feet also blackish; pelage very long and thick; hairs of mid-back as long as 90 mm; nuchal hairs whorled, directed forward on crown, back and nape, the long hairs covering shoulders and anterior half of back as a mantle; blackish coronal hairs long, projecting forward beyond brows as a ruff or bangs concealing skin and overlying ears; chest and belly entirely covered by relatively sparse blackish or reddish hair.

Table IV External measurements (mm) and mass (g) of holotype and paratypes of *Cacajao hosomi* sp. nov. and *C. ayresi* sp. nov. and neotype and paraneotypes of *C. melanocephalus*

	Body	Tail	Foot	Ear	Mass
<i>Cacajao hosomi</i> sp. nov.					
MN 68613 (JPB 106) Holotype adult female	418	220	142	27	3100
MN 68611 (JPB 102) Paratype adult male	490	200	150	36	4500
INPA 5242 (JPB 001) Paratype juvenile male	430	140	115	30	1770
<i>Cacajao ayresi</i> sp. nov.					
INPA 5248 (JPB 139) Holotype adult female	380	180	128	30	2450
INPA 5247 (JPB 138) Paratype adult female	395	155	126	30	2250
INPA 5246 (JPB 135) Paratype subadult female	363	180	132	33	2000
<i>Cacajao melanocephalus</i>					
MN 68616 (JPB 110) Neotype adult female	362	139	134	25	2600
INPA 5240 Paraneotype adult female	555	155	122	30	1900
INPA 5238 (MvR 021) Paraneotype juvenile female	420	145	115	26	600
INPA 5239 (MvR 022) Paraneotype juvenile male	395	140	115	26	500

External measurements Table IV.

Comparisons *Cacajao hosomi* sp. nov. specimens present thicker and longer fur with bright reddish brown mid to lower back, thighs and tail, in contrast to Aracá black uakari specimens that have a much darker general coloration and to *C. melanocephalus* as redefined here, which present a golden brown general appearance. Other specimens examined: Male ($n=1$): Maturacá, Neblina National Park, Amazonas, Brazil, 0° 37' N, 66° 7' W; INPA 5242 (JPB 001) juvenile male, that Boubli collected in 1994 consisting of skin, skull and liver tissue fixed in ethanol; sex unknown ($n=4$): (Igarapé Waputa, a tributary of the Canal Maturacá, Pico da Neblina, Amazonas, Brazil) INPA 5249–5251 (JPB 155, 154, 153, respectively) and (Rio Demeti, Pico da Neblina, Amazonas, Brazil) INPA 5252 (JPB 152), all consisting of flat, open skins. We also saw digital photos that Drs. James Whatton and Richard Thorington of the Smithsonian National Museum of Natural History kindly provided of specimens from the upper Orinoco region of Venezuela (USNM 406423, 406425, 406572, 406574). The pictures show individuals that are darker and less red on the back than *Cacajao hosomi* are. Though they are geographically closer to *Cacajao hosomi* than they are to *C. ayresi* sp. nov., only future molecular analysis will be able to indicate the relationship of the population of southeast Venezuela to other black uakaris.

Geographical Distribution *Cacajao hosomi* is limited to the south and west by the Rio Negro, by the Rio Marauíá in the east (Brazil), and by the Canal Cassiquiare and Rio Orinoco to the north (Venezuela; Fig. 6). If specimens in the Smithsonian National Museum of Natural History, from the upper Orinoco region of Venezuela (Rio Mavaca and Upper Canal Cassiquiare) represent a different taxon of black uakari, then the Rio Siapo, a left bank tributary of the Canal Cassiquiare, is a likely eastern limit for *Cacajao hosomi* in Venezuela.

Cacajao ayresi sp. nov.

The Aracá Uakari

Etymology The specific epithet honors the late José Márcio Ayres, in recognition of his work for the conservation of uakaris and their Amazonian forest habitat.

Holotype INPA 5248, an adult female, that Boubli collected on December 2, 2005 (original field number JPB 139) at Rio Aracá, 0° 32' 53.1"S, 62° 54' 40.4" W, Amazonas, Brazil. The holotype consists of skin, skull, and liver tissue fixed in ethanol.

Type Locality Right bank of lower Rio Aracá (0° 32' 53.1"S, 62° 54' 40.4" W).

Paratypes INPA 5246, a subadult female that Boubli collected on March 21, 2005 (original field number JPB 135) at Madixi Igarapé, Rio Aracá, Amazonas, Brazil and INPA 5248, a pregnant female, that Boubli collected on December 2, 2005 (original field number JPB 138) at Rio Aracá, 0° 32' 53.1"S, 62° 54' 40.4" W, Amazonas, Brazil, both consisting of skin, skull, and liver tissue fixed in ethanol.

Diagnosis Small black uakari (Table IV) with overall blackish body coloration; darker mantle does not strongly contrast with midback; midback, lower back, tail and thighs all of similar blackish appearance; tip of the tail black; pelage of body not very long and thick; coronal hairs project forward beyond brows only discretely and do not completely cover the ears; chest and belly entirely covered by relatively sparse uniformly colored black hairs.

External Characters Short-tailed platyrrhine; general coloration blackish; back with reddish hair showing through for most of its length including thighs and tail; individual body hairs on the dorsum more or less uniformly blackish or reddish, with terminal portion usually darker than basal portion that may be pale-yellow; dorsal surface of tail reddish with dark tipped hair for about 3/4 of its length but individual hairs entirely black in its distal end; pelage of body long (but shorter and thinner than in *Neblina black uakaris*); hairs of mid-back ca. 60–70 mm long; head entirely black covered by coronal hairs that are not very long, projecting forward beyond brows only discretely and with ears rather exposed; nuchal hairs whorled, directed forward on crown, back and nape, the longer hairs covering shoulders and anterior half of back as a dark mantle; hands, arms, legs (not thigh) and feet rather black; underparts of body and tail blackish.

External measurements See Table IV.

Comparisons *Cacajao ayresi* sp. nov. has a much darker general appearance, shorter and thinner pelage than that of *C. hosomi* sp. nov.; its pelage is of similar length and thickness to that in *C. melanocephalus* but the latter presents a general yellowish brown coloration, in stark contrast to the reddish tinge of both remaining species; it has coronal hairs that project forward beyond brows only discretely and that do not completely cover the ears as in the other species of black uakaris.

Geographical distribution *Cacajao ayresi* lives in a small area that encompasses the Rio Curuduri basin and adjacent areas (Fig. 6). However, more surveys are needed to understand better the distribution of the species.

Discussion

The primates of Venezuelan Amazonas remain poorly known. In particular, surveys of the region north of the Canal Cassiquiare and South of the Rio Atabapo are needed to determine which species of black uakari occurs there. Further, surveys of the upper Orinoco region, including the Rios Mavaca, Manipitari, and Siapo, are needed to determine if *Cacajao hosomi* occurs there. Four black uakari specimens that the Smithsonian Venezuelan Project collected in the region in 1967 (Handley 1976) and that are now deposited at the Smithsonian National Museum of Natural History are darker, overall less colored and less reddish than *Cacajao hosomi* from Pico da Neblina National Park region of Brazil. Molecular analysis of the specimens should reveal their relationship to other black uakaris.

Given the extremely large geographical distribution of *Cacajao melanocephalus*, a more in-depth phylogeographic analysis is required to determine levels of differentiation between populations occurring at the opposite ends of the specific distribution; it is quite likely that populations from the lower Rio Negro near Manaus, Brazil, have some degree of molecular differentiation from populations from the La Macarena region of Colombia >1000 km to the west. Very little is also known about the distribution of Aracá uakaris (*Cacajao ayresi*). We know they occur in an extremely small area along the Rio Curuduri and parts of the lower Rio Aracá. However, local people report having seen them in other areas in the upper Rio Aracá and in the Igarapé Cuieiras, a right bank tributary of the Rio Demeni.

Of particular interest would be further investigation into the ecology of black uakaris and bearded sakis in the interfluvium of the Rios Branco and Negro. Researchers have long thought that *Cacajao* and *Chiropotes* exclude each other geographically owing to the similarities in their ecology, with *Chiropotes* restricted to the east of Amazonia and *Cacajao* to the west (Ayes 1989). However, brown bearded sakis (*Chiropotes israelita*) occur in several localities on the left bank of Rio Negro in western Amazonia (this study; Bonvicino *et al.* 2003; Boubli 1997, 2002), and thus within the geographic range of *Cacajao hosomi* and *Cacajao ayresi* sp. nov. Because there is no obvious geographical barrier separating these primates, how is their regional coexistence maintained? It is possible that the present distribution of *Cacajao* and *Chiropotes* north of the Rio Negro reflects historical factors instead of present ecological conditions. We suggest that, with the fluctuation in climatic conditions and consequent changes in forest structure and composition in this region of Amazonia during the mid-Pleistocene (Colinvaux *et al.* 1996; Haffer 1997), the ancestral population of *Cacajao hosomi* and *C. ayresi* may have fragmented with *Chiropotes* expanding into the unoccupied area in between. Competitive exclusion now maintains geographic species boundaries. Alternatively, the geographical separation, and thus the driving force for differentiation of *Cacajao hosomi* and *C. ayresi*, may have been again competitive exclusion where the *Chiropotes* appeared as a wedge species displacing *Cacajao* and fragmenting the ancestral species into descendant *C. hosomi* and *C. ayresi*. Although these two scenarios are difficult to differentiate, both regard competition between black uakaris and bearded sakis as an important factor shaping the phylogenetic and geographic distributional patterns of pitheciines north of the Rio Negro.

Though the usually large groups of black uakaris might give the impression that they are abundant, they are relatively rare. Black uakaris are seasonal vagrants, shifting their home ranges in accordance to the availability of preferred foods (Boubli 1999); thus population densities are low at the landscape level. Humboldt (1811) noted that black uakaris were rare and none of the missionaries from the Orinoco knew of them.

Black uakaris are currently classified as Lower Risk by the IUCN (Hilton-Taylor 2000). Such conservation status will need to be reassessed to accommodate the newly described species. Though golden-backed uakaris (*Cacajao melanocephalus*) should remain at lower risk owing to their widespread geographic distribution and lower threat from hunting and habitat destruction, the same is not the case for *C. hosomi* and *C. ayresi*. The latter species have smaller ranges and are heavily hunted by locals; in particular, Yanomami regularly eat *Cacajao hosomi* in Pico da Neblina

National Park (Boubli 1997). The situation for *Cacajao ayresi* is further aggravated by their extremely small geographic distribution and consequently population size, making them susceptible to environmental catastrophes. We suggest that *Cacajao ayresi* and *C. hosomi* be classified as endangered species in the next IUCN assessment for the elaboration of the Red List of Threatened Animals. *Cacajao ayresi* is the only black uakari not protected by a reserve; the first step towards its conservation is a protection area for them.

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