Molecular phylogeny and systematics of bald uakaris, genus *Cacajao* Lesson, 1840 (Primates: Pitheciidae), with the description of a new species

Felipe Ennes Silva[1,2], João Valsecchi do Amaral[3,4,5], Christian Roos[6], Mark Bowler[7], Fabio Röhe[8,9], Ricardo Sampaio[10,11], Mareike Cora Janiak[12], Fabrício Bertuol[9], Marcelo Ismar Santana[13], José de Souza Silva Júnior[14], Anthony B. Rylands[15], Chrysoula Gubili[16], Tomas Hrbek[9], Allan D. McDevitt[12], Jean P. Boubli[12]

[1] Research Group on Primate Biology and Conservation, Mamirauá Institute for Sustainable Development, Estrada da Bexiga 2584, CEP 69553-225, Tefé, Amazonas, Brazil. Email: felipe@mamiraua.org.br, Orcid: https://orcid.org/0000-0002-1315-0847

[2] Department of Evolutionary Biology & Ecology, Université Libre de Brussels, Av. F.D. Roosevelt, 50, Brussels, Belgium

[3] Research Group on Terrestrial Vertebrate Ecology, Mamirauá Institute for Sustainable Development, Tefé, Amazonas, Brazil

[4] Rede de Pesquisa para Estudos sobre Diversidade, Conservação e Uso da Fauna na Amazônia – RedeFauna, Manaus, Amazonas, Brazil

[5] Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica – ComFauna, Iquitos, Loreto, Peru

[6] German Primate Center - Leibniz Institute for Primate Research, Gene Bank of Primates and Primate Genetics Laboratory, Germany

[7] University of Suffolk, Ipswich, Suffolk, UK

[8] Programa de Pós-graduação em Genética, Conservação e Biologia Evolutiva (GCBEv), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil

[9] Departamento de Biologia, Instituto de Ciências Biológicas (ICB), Universidade Federal do Amazonas (UFAM), Manaus, Amazonas, Brazil

[10] Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros (CENAP), Atibaia, São Paulo, Brazil

[11] Programa de Pós-graduação em Biologia Comparada, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP), Universidade de São Paulo (USP), Ribeirão Preto, São Paulo, Brazil

[12] School of Science, Engineering and the Environment, University of Salford, Salford, UK

[13] Universidade de Brasília (UnB), Brazilia, Distrito Federal, Brazil

[14] Museu Paraense Emílio Goeldi, Mastozoology Collection, Belém, Brazil

[15] Re:wild, Austin, TX, USA

[16] Hellenic Agricultural Organisation - DIMITRA, Fisheries Research Institute, Nea Peramos, Kavala, 64007, Greece - Orcid: https://orcid.org/0000-0002-0866-6259

Abstract

Bald uakaris, genus *Cacajao*, are Amazonian primates currently classified as one species and four subspecies based on the patterns of pelage coloration. In this study, we test if their current taxonomy is represented by the phylogenetic relationship of the main lineages retrieved from molecular data. We included, for the first time, all bald uakari taxa in a mitochondrial (cytochrome *b*) and genome-wide (ddRAD) phylogenetic analyses. We also examined the pattern of pelage colouration in specimens from zoological collections. Having determined the number of lineages using Maximum Likelihood and the species tree using coalescent analyses, we test their divergence time using a Bayesian approach. While the cytochrome *b* analysis only recovered two clades, the ddRAD analysis supported the reciprocal monophyly of five lineages of bald uakaris, with all clades including only individuals with distinct and exclusive diagnostic phenotypic characters. We found that species diversification in *Cacajao* occurred during the last 300 Kya and may have been influenced by the formation of rivers and flooded forests in western Amazonia. We propose that the four bald uakari subspecies currently recognised can be upgraded to species level and we describe the white uakaris from the basin of the Rio Tarauacá as a new species.

Keywords: Amazon rainforest – Neotropical primates – Phylogenetic Species Concept – Pitheciinae – species delimitation

1. Introduction

In the last two decades, molecular analyses revolutionized the study of phylogenetics providing a new perspective on the diversity of many groups. It has contributed to the reassessment of taxonomical hypotheses for several taxa for which classification had been based mostly on morphological characters (for example, Outlaw and Voelker 2006; Sánchez-González and Moyle, 2011; Covain et al. 2016; Byrne et al. 2016; McDonough

et al. 2022). Since the species has a pivotal role as a unit of evolution, biodiversity, and conservation, their taxonomic status must be reviewed when new evidence becomes available. The combination of different lines of evidence (e.g., morphology, molecular genetics, ecology) in species delimitation – a practice that some authors refer to as "integrative taxonomy" (Dayrat, 2005; Schlick-Steiner et al., 2010) – provides a solid ground for taxonomic classifications.

In the case of Neotropical primates, the mammalogist Phillip Hershkovitz was impressive in his compilation of information from zoological collections around the world to review the taxonomic classification of several primate genera in the late 1970s, the '80s, and early '90s using morphological data. Molecular analyses combined with the systematic adoption of the Phylogenetic Species Concept (PSC) and new field evidence supported taxonomic reassessments of *Cacajao* (Boubli et al. 2008), *Cebus* (Lynch-Alfaro et al. 2012), *Saguinus* (Buckner et al. 2015; Rylands et al. 2016), *Saimiri* (Mercês et al. 2015), *Callicebus* (Byrne et al. 2016). These studies updated the taxonomic proposals of Hershkovitz, either by supporting the validity of some taxa or rejecting and amending it by presenting new evidence and proposing new classification schemes.

One such genus was *Cacajao* (the uakari monkeys), which Hershkovitz (1987) based his analysis on pelage coloration and morphometry of few available specimens, collected by the 19th and early 20th-century naturalists. *Cacajao* is the largest member of the New World primate family Pitheciidae. It is endemic to the Amazon rainforest and comprises the black-headed uakaris and the bald uakaris; the latter having a bare, red face, a characteristic caused by a complex vascular system in the facial skin (Mayor et al., 2015). The black-headed uakaris occur along the north bank of the Rio Japurá and in the Rio Negro basin, north to the Río Orinoco. The bald uakaris have an unusual distribution of disjunct populations occurring mostly in the forests of the rios Solimões and Juruá in Brazil, and in the Ucayali-Javarí interfluvial in Peru (Silva Jr et al., 2013; Silva et al., 2021).

Hershkovitz (1987) treated the black-headed uakaris as one species with two subspecies (*Cacajao melanocephalus melanocephalus* [Humboldt] in the upper Río Orinoco-Río Cassiquiare basin and *C. m. ouakary* [Spix] in the Rio Negro-Japurá interfluvium, extending west into Colombia), and the bald uakaris as a second species with four subspecies (*Cacajao calvus calvus*, *C. c. ucayali*, *C. c. rubicundus,* and *C. c. novaesi*). The black-headed uakaris were subjected to a taxonomic reappraisal by Boubli et al. (2008). With new information from field surveys, a re-examination of voucher specimens, and molecular phylogenetics using the mitochondrial cytochrome *b* gene, Boubli et al. proposed an arrangement of three species – *Cacajao melanocephalus*, *Cacajao hosomi*, and *Cacajao ayresi*. They argued that *melanocephalus* was the correct epithet for the uakaris along the right bank of the Rio Negro and, *contra* Hershkovitz, not *ouakary*, provided a new name (*hosomi*) for the uakaris north of the Rio Negro that range north to the Orinoco, and described a new, evidently isolated, form (*ayresi*) discovered in the basin of the Rio Aracá, a north (left) bank tributary of the Rio Negro to the east of *hosomi*. This proposal was contested by Ferrari et al. (2014), but see Quintela et al. (2020) for a review of the controversy. Although the new evidence presented by Boubli et al. (2008) stirred up discussion on the taxonomic classification of black-headed uakaris, the phylogenetic relationships and taxonomy of bald uakaris remained overlooked.

1.1. Taxonomic background of bald uakaris

The French naturalist Isidore Geoffroy Saint-Hilaire was the first to describe a bald uakari, the white bald uakari *Brachyurus calvus* I. Geoffroy Saint-Hilaire, 1847. The author's description was based on a specimen donated to the Muséum National d'Histoire Naturelle, Paris, and the type locality was given as "Province de Pará" (I. Geoffroy Saint-Hilaire, 1847, 1852) – a reference to the former province of Grão-Pará, an administrative territory from the colonial period that included today's states of Pará and Amazonas, a vast area in the north of Brazil. Isidore Geoffroy Saint-Hilaire (1852)

examined two other specimens with the same general characteristics of *Brachyurus calvus*, but their locality was also imprecise and described as the upper Rio Amazonas, Peru, near the town of Fonte Boa. A year after the description of the first bald uakari, I. Geoffroy Saint-Hilaire and Deville (1848) described a second species, the red bald uakari *Brachyurus rubicundus*, based on a specimen collected by Castelneau and Deville during their expedition to South America. The type specimen was collected near the territory of São Paulo de Olivença, "*Le Brésil*, *Haut-Amazone*, *près Saint-Paul*" – a municipality in the Amazon State. It is unclear, however, if it was collected on the right (south) or left (north) bank of the Rio Solimões.

Thomas (1928) examined three red uakaris newly collected during the Godman-Thomas Expedition to the Peruvian forests and identified a singular pattern of pelage coloration when compared to the two species described in Brazil (*Brachyurus calvus* and *Brachyurus rubicundus*). The author suggested that the red uakaris from Brazil and Peru would have a zone of intergradation:

*"*The discovery of a member of the remarkable genus *Cacajao* on the Ucayali is of much interest, as the genus had been supposed to have a very restricted distribution in the Teffe-Tonantins region of the Middle Amazon, while the Ucayali is a very long way further up the river. The character of the country is, however, of a sufficiently uniform nature to make it not improbable that examples of the red Uacari will be found in the intervening districts, and I therefore do not distinguish this animal as a separate species." (Thomas, 1928: 253)

The consistency in pelage coloration in the Peruvian uakaris and the supposed existence of an intergradation zone between *rubicundus* and *ucayalii* did, however, motivate Thomas (1928) to describe them as a new subspecies: *Cacajao rubicundus ucayalii* Thomas, 1928. According to the author, the Peruvian uakaris presented a "general coloration as in true *rubicundus*, but the nape instead of being whitish or pale yellowish is bright chestnut-red like the rest of the body" (Thomas, 1928: 252).

Hershkovitz adopted a polytypic species framework, using the subspecies rank – even though he did not specify this as such (Groves, 2014) – to propose that the bald uakaris be classified as one species, *Cacajao calvus*, with four subspecies:

1) *Cacajao c. calvus* (I. Geoffroy Saint-Hilaire, 1847)
2) *Cacajao c. rubicundus* (I. Geoffroy Saint-Hilaire and Deville, 1848)
3) *Cacajao c. ucayalii* (Thomas, 1928)
4) *Cacajao c. novaesi* Hershkovitz, 1987

1.2. Conflicting molecular and morphological information

Boubli and Ditchfield (2000) were the first to use molecular data to shed light on the phylogenetic relationships of the uakaris. They tried to determine the time of divergence among all Pitheciinae to better understand the origin of the adaptation of bald uakaris to flooded forests. They retrieved approximately 10.5 million years for the split between the genus *Pithecia* and the clade composed of *Chiropotes*/*Cacajao*, 2.5 million years for the divergence of *Pithecia albicans* and *P. monachus*, 9 million years for the split between *Chiropotes* and *Cacajao*, and 5 million years for the split between *C. calvus and C. melanocephalus*.

Figueiredo (2006), investigated the phylogenetics of uakaris using the cytochrome *b* gene and mostly museum samples. In a follow-up publication, Figueiredo-Ready et al. (2013) concluded that the four subspecies of bald uakaris are grouped into just two lineages that diverged approximately at 4 million years ago (Mya). In their analysis, the white bald uakaris *C. c. calvus* (from the Mamirauá Sustainable Development Reserve, Mamirauá SDR) grouped with red bald uakaris – *C. c. rubicundus* and *C. c. ucayalii* – in a well-defined clade, comprising individuals distributed on the north bank of the Solimões and the Ucayali-Javari interfluvium, while the white bald uakaris from the Rio Tarauacá and the orange-buff uakari, *C. c. novaesi*, are grouped in another well-defined clade. The populations of white bald uakaris, *C. c. calvus*, from the Mamirauá SDR, north bank of Rio Solimões, would, therefore, be phylogenetically closer to the red bald *C. c.*

rubicundus and *C. c. ucayalii* than to the population of white uakaris found in the Rio Tarauacá basin, way to the south (see Sampaio et al., 2018). The authors concluded, therefore, that the molecular phylogeny contradicts the traditional taxonomic arrangement by Hershkovitz (1987) since the phylogenetic relationship found is "consistent with the geographic distribution but not morphological patterns" (Figueiredo-Ready et al., 2013: 26).

Although the authors urged caution that their analyses included only a few museum samples from few localities and, thus, their interpretations should be considered preliminary, their conclusions could also have been affected by their misidentification of two samples as "*Cacajao calvus novaesi*" (INPA5241 and UFPA-Ccn1). The first, INPA5241 in the mammal collection of Instituto Nacional de Pesquisas da Amazônia (INPA), is an immature male white uakari (*Cacajao* sp.) from the right bank of Rio Tarauacá. This region is near to where Silva-Júnior and Martins (1999) reported an isolated population of white uakaris in the upper Rio Tarauacá basin. For the second sample, UFPA-Ccn1 of the Federal University of Pará, neither skull nor skin is available in any scientific collection. Figueiredo-Ready et al. (2013) assumed, therefore, that this sample would be of *C. c. novaesi*, based on the locality assigned – left bank of Rio Juruá, near the town of Carauari. In this region, however, only white uakaris (*C. c. calvus*) are confirmed and more than 350 km to the north of the known range of *C. c. novaesi* (see Silva et al., 2021).

In our study, we carried out the first comprehensive molecular and morphological investigation of bald uakaris, including samples of the four subspecies (*sensu* Hershkovitz, 1987), and from most of the localities where bald uakaris occur in Brazil besides one locality in Peru. We examined the patterns of pelage coloration of museum voucher specimens – including those collected after Hershkovitz (1987). In an updated dataset from previous publications (Boubli et al., 2008; Figueiredo-Ready et al., 2013), we used the cytochrome *b* gene, including all available sequences from GenBank and newly generated ones. We then generated the first genomic dataset for *Cacajao* (Double Digest Restriction Associated DNA – ddRADseq, Peterson et al., 2012) and applied

different parameter settings for locus and single nucleotide polymorphism (SNP) recovery to build a consensus phylogenomic tree for *Cacajao*, tested two models of species delimitation, and estimated the divergence time of the main lineages identified here. With our results, we propose a new taxonomy for bald-headed uakaris and describe the white uakaris from the Tarauacá-Pauini interfluve as a new species based on morphological analyses and robust genomic data.

2. Material & Methods

2.1. Sample set and Laboratory procedures

We used dried flesh adhering to skulls and skins collected from museum voucher specimens, along with fresh tissue and faeces collected during field surveys carried out by different teams during various mammal inventories in the Amazon rainforest. The cytochrome *b* dataset included 73 (50 newly generated in this study) sequences of all known *Cacajao* taxa (*sensu* Hershkovitz, 1987 and Boubli et al., 2008) as follows: *C. c. calvus* (N=6), *C. c. rubicundus* (N=8), *C. c. ucayalii* (N=14), *C. c. novaesi* (N=5), *Cacajao ayresi* (N=5), *Cacajao hosomi* (N=7), and *Cacajao melanocephalus* (N=18). We also included samples of the white uakaris, *Cacajao* sp. (N=10), from the rios Tarauacá and Pauini (Table S1). We included bearded sakis, *Chiropotes sagulatus* (N=1) as an outgroup for the maximum likelihood inference. *Pithecia irrorata* (N=1) and two titi monkeys – *Plecturocebus cupreus* (N=1) and *Cheracebus purinus* (N=1) – were also used as outgroups for the divergence time estimate (Table S1).

DNA was extracted using the standard phenol-chloroform extraction protocol (Sambrook et al., 1989). The concentration of the extracted DNA was quantified using a Nanodrop 2000 spectrophotometer (Thermo Scientific). After extraction, the genomic DNA was used as a template for polymerase chain reaction (PCR) to amplify the complete cytochrome *b* gene (forward primer: 5'-GCACAACCTACAGCACCACTA-3'; reverse primer: 5'-CAGCTTTGGGTGTTGAYGGTRGAA-3'). Each PCR had a final volume of

25 µl and contained 100 ng of DNA, 2.5 µl of 10X reaction buffer, 0.5 mM of each primer, 0.03 U/µl MyTaq™ HS DNA Polymerase (Bioline), 1.5 mM $MgCl_2$, 0.1 mg/µl Bovine Serum Albumin and 1.25 mM of each dNTP. The amplification cycles were carried out under the following conditions: initial denaturation at 95 °C for 5 min; followed by 35 cycles of denaturing at 94 °C for 1 min, primer annealing of 60 °C for 1 min, and extension at 72 °C for 1 min; a final extension was carried out at 72 °C for 5 min. We analysed the PCR products on 1.5 % agarose gels, and purification and sequencing were performed bidirectionally (Macrogen Inc., Amsterdam).

We also used a subset of 47 samples that were sequenced using the double digest restriction-site-associated DNA sequencing protocol (ddRADseq) (Peterson et al., 2012). For the ddRADseq analyses, we included sequences for the same taxa as in the cytochrome *b* analyses, but in a smaller dataset: *Cacajao ayresi* (N=5), *Cacajao hosomi* (N=2), *Cacajao melanocephalus* (N=10), *C. c. calvus* (N=8), *Cacajao* sp. (N=7), *C. c. rubicundus* (N=6), *C. c. ucayalii* (N=2), and *C. c. novaesi* (N=5). We used the same outgroup in the ddRADseq and cytochrome *b* analyses. The sample set used in the ddRADseq analysis is geographically well-distributed and covers most of the localities where uakaris are known to occur in the Brazilian Amazon (Table S1; Silva et al., 2021;). Library preparation and sequencing were conducted by the LEGAL lab team (https://www.evoamazon.net/) in Manaus, Brazil. The ddRADseq protocol was adapted to allow simultaneous digestion and adapter ligation, and data were generated on the IonTorrent PGM (https://github.com/legalLab/protocols-scripts). In brief, 200 ng of genomic DNA was digested with SdaI and Csp6I restriction enzymes (ThermoFisher), and the IonTorrent P and A adapters were ligated to the digested fragments, all in one step. The fragments were enriched via PCR; the A adapter contains a unique molecular barcode for the identification of individuals and is a divergent "Y" adapter to ensure that only fragments with one P1 and one A adapter are enriched. DNA fragments in the range of 320 to 400 bp were selected using the Pippin Prep (Sage Science), owing to the ability of the IonTorrent PGM to sequence fragments up to 400 bp. The ddRADseq library was

sequenced on an Ion Torrent PGM (ThermoFisher) using the 400-bp PGI 318 Ion PGM sequencing kit following the manufacturer's recommendations. Permits to conduct fieldwork and sample collections were provided by the Brazilian Ministry of the Environment agencies – Chico Mendes Institute for Biodiversity Conservation (ICMBio) (SISBio 55777-2, 42111-1, 42111-2, 42111-3) and Brazilian Institute of Environment and Renewable Natural Resources IBAMA (License N° 005/2005 – CGFAU/LIC).

2.2. Molecular Analysis

We used Geneious Pro 4.8.5 for the cytochrome *b* sequence editing and assembly. For the alignment we used the Mafft online server (Katoh and Standley, 2013; Katoh et al., 2017) under the iterative refinement option (FFT-NS-i Standard), which is known to effectively improve the alignment accuracy for a small number of sequences (Katoh et al., 2002, 2017).

The quality of the raw ddRAD sequences was assessed using FastQC v.0.11.8 (Andrews, 2018) and, trimmed, reads to 250bp using the "process_ratags" component as implemented in the program STACKS v.2.4 (Catchen et al., 2011, 2013; Rochette et al., 2019), and keeping only those reads with PHRED scores > 30 for the subsequent analyses. We used the iPYRAD pipeline (Eaton and Overcast, 2020) to select our ddRAD loci and SNPs from the "de-novo" and "reference" assemblies. We used the available genome of *Pithecia pithecia* (GenBank: PVIP00000000.1) as the reference assembly. Aiming to maximize the loci and SNP recovery in iPYRAD, and test if different parameters settings influence the phylogenetic inference, we combined two key parameters in the iPYRAD pipeline: "cluster threshold" (0.85, 0.90), and "minimum samples per locus" (3, 24 and 36, which represents, approximately 5%, 50%, and 75% of the total samples). The "cluster_threshold" parameter specifies the level of similarity for two sequences to be considered as homologous (Eaton, 2014). If this value is set too high, any polymorphism will hamper homologous sequences to cluster, but if the value is set too low, non-homologous sequences will cluster together (Eaton, 2014; Valencia et al., 2018). The second parameter, "min_samples_locus", specifies the minimum number of samples

required to retain a locus in the final dataset. If this value is set too high, the number of loci will decrease, as loci from divergent sequences probably will not be shared. However, if set too low any locus present in a few samples will be retained and the final matrix will contain a higher number of missing data, which can be computationally infeasible to analyse.

iPYRAD generates a set of output files that can be used for downstream analyses (Eaton and Overcast, 2020). We used the concatenated matrix of loci (.phy file) generated for each assembly method mentioned above to infer the phylogenetic relationship of uakaris. We inferred the phylogeny using a maximum likelihood approach in the program IQTree v.1.6.12 (Nguyen et al., 2015) as implemented in the W-IQ-Tree (http://iqtree.cibiv.univie.ac.at/, Trifinopoulos et al., 2016). The best substitution model was selected using the ModelFinder algorithm (Kalyaanamoorthy et al., 2017), implemented in IQTree. We used the ultrafast bootstrap approach (UFBoot) (Hoang et al., 2018; Minh et al., 2013) with 1,000 bootstrap pseudo-replicates to assess branch support. After assessing the iPYRAD assembly method and parameter settings that retrieved a higher overall bootstrap support value in the phylogenetic inference, we chose the output files from the assembly method with the higher number of loci and SNPs but with no more than approximately 50% of missing data in the concatenated matrix of loci to conduct all subsequent analyses.

We inferred a quartet-based species tree using Tetrad 0.9.13 as implemented in the ipyrad-analysis toolkit (see https://ipyrad.readthedocs.io/). Tetrad is a species tree inference method using the full SNP alignment for each sampled quartet of taxa under the coalescent model based on the SVDQuartets algorithm (https://github.com/eaton-lab/tetrad; see also Chifman and Kubatko, 2014). Tetrad was run with 27,206 SNPs, of which 3,433 were unlinked, which retrieved 178,365 possible quartets among the 47 samples (all *Cacajao* lineages, and two *Chiropotes* as outgroup). To assess node support, we ran 100 non-parametric bootstrap replicates.

For species delimitation, we used a reduced dataset that included two individuals per bald uakari lineage (total 10 individuals) and one *C. melanocephalus* as outgroup in

an SNP matrix of 10,062 SNPs (3,392 unique biallelic SNPs) with less than 8% of missing data to apply the package SNAPP (Bryant et al., 2012) as implemented in Beast 2.6.4 (Bouckaert et al., 2019). SNAPP is a Bayesian multispecies coalescent method for species tree estimation and species delimitation from biallelic markers (Bryant et al., 2012) and it has been used in analysis with RADseq (Nieto-Montes de Oca et al., 2017; Rancilhac et al., 2019; Poelstra et al., 2021). We ran the analyses for 1 million generations after a burn-in of 100,000 generations, sampling every 500 generations. Specifically, we tested if the main lineages retrieved in the phylogenetic inference could be delimited according to the marginal likelihood estimation (MLE) of the following species delimitation model considered here:

- Model 0 (Merge). Two species: *C. calvus* (including both lineages of white uakaris, i.e., *C. calvus* and *Cacajao* sp.) and *C. rubicundus* (including the three lineages of red bald uakaris, i.e., *C. rubicundus*, *C. ucayalii*, and *C. novaesi*)
- Model 1 (Split). Five species: *C. calvus*, *Cacajao* sp., *C. rubicundus*, *C. ucayalii*, *C. novaesi*

The stepping-stone sampling approach was used for the marginal-likelihood estimation (MLE) (Xie et al., 2011) with 20 steps. To evaluate the models, we used a Bayes Factor framework (Kass and Raftery, 1995) calculated as $2*(\ln L_{Split} - \ln L_{Merge})$. A negative Bayes factor value indicates support to model 0 (merge) while a positive value indicates support in favour of model 1 (split), and a Bayes factor greater than six as a strong support to a species delimitation model (Kass and Raftery, 1995).

Finally, we employed Beast 2.6.4 (Bouckaert et al., 2019) to estimate the divergence time between each *Cacajao* lineage from the cytochrome *b* and ddRADseq phylogenetic inferences. In the ddRADseq analysis, we used the reference assembly with approximately 20% missing data. We used the same parameters and outgroup to estimate the divergence time in both datasets (cytochrome *b* and ddRADseq). The molecular clock was set as a lognormal relaxed clock, in which the substitution rates in each branch are independently estimated under a lognormal distribution (Drummond et al., 2006). We used the Coalescent Bayesian Skyline prior (Gernhard et al., 2008) as

a tree model. In simulation studies, this model has performed well to estimate divergence time in datasets with intra and interspecific samples (Ritchie et al. 2017; Mello et al. 2021). To calibrate the tree, we used the age estimated for the fossil genus *Proteropithecia*, the oldest known pitheciin fossil (Kay et al., 1998), timing the divergence between Callicebinae/Pitheciinae. We used a log-normal distribution with an offset of 13.72 (hard minimum), a mean of 1.19, and a standard deviation of 0.8, placing the soft maximum of 26 Ma at the 95% quantile of the prior distribution. We ran the Markov chain for 50,000,000 generations, sampling every 10,000 steps, and visually assessed the convergence, performance, and burn-in using Tracer 1.7.1 (Rambaut et al., 2018).

2.3. Taxonomic reassessment

For the taxonomic classification of bald uakaris, we first assessed if the clusters retrieved from the molecular analysis included only individuals with the same pattern of pelage coloration and geographically structured; looking, therefore, for consistency between molecular, morphological, and geographic information. We examined 101 voucher specimens from six scientific collections (see Supplementary Material - Appendix I). We followed the diagnostic characters used by Hershkovitz (1987) to assess the pattern of pelage coloration in each population of bald uakaris. We then provide a taxonomic account with a review of the general characters, type series and type localities, and geographic distribution of each species considered here. For the synonymy, we provide the first use of the name, aiming to clarify misidentifications in the literature (Supplementary Material - Appendix II). This list, therefore, is not exhaustive but aims to rectify any possible errors in the literature and support the species list in the management plans of protected areas of the states of Amazonas and Acre. Hershkovitz (1987) provided a historical perspective of the names used before the 1980s.

3. Results

3.1. Molecular Analysis

In total, we obtained 1092 bp for the cytochrome *b* dataset. In the phylogenetic inference using cytochrome *b*, bald uakaris are well separated from black-headed uakaris, as found in previous studies (Boubli and Dietchfield, 2000; Figueiredo-Ready et al., 2013). In black-headed uakaris, the primary split occurs between species from the north and south bank of Rio Negro. Accordingly, *C. melanocephalus* is in one clade, and *C. ayresi* and *C. hosomi* are sister species, each one in well-defined clades (Fig. 1). Two clades were also recovered for bald uakaris. The first solely consists of the white uakaris (*C. c. calvus* and *Cacajao* sp.), and the second clade includes all red bald uakaris (*C. c. rubicundus*, *C. c. ucayalii*, and *C. c. novaesi*) (Fig. 1).

In the ddRADseq analysis, the use of the reference mapped data resulted in higher SNP and locus recovery when compared to the *de novo* assembly (Table 1). In both assembly methods, the higher the values of "min_samples_locus", the lower the number of SNPs and loci recovered and the lower the percentage of missing data in the final matrices (Table 1). The two values of "cluster_threshold" tested retrieved a similar number of SNPs and loci, with the 0.90 threshold recovering a slightly higher number (Table 1). This affects the phylogenomic analysis only when using the more stringent parameters – probably by removing polymorphic and informative loci (Crotti et al., 2019; Huang and Lacey Knowles, 2016). The global bootstrap support in our phylogenetic inferences is, therefore, higher for those trees with more permissive "minimum samples per locus". Considering, therefore, the parameters tested here, the main impact in the phylogenetic inference is identified in the most restrictive values of "min_samples_locus", which influence the tree resolution when using only the loci present in > 75% of the samples (Supporting Information, Figs. S1 – S9).

The ddRAD phylogenetic inference is effective in recovering the relationships within the red and the white uakaris. Five clades were recovered – two of white uakaris (*C. c. calvus* and *Cacajao* sp.), and three of red uakaris (*C. c. rubicundus*, *C. c. ucayalii*, and *C. c. novaesi*) (Fig. 2). The white uakaris (*C. c. calvus*) from the Rio Solimões basin – i.e., from the Mamirauá SDR and from the right bank of the lower Rio Jutaí – form a clade

that is clearly separated from the white uakaris (*Cacajao* sp.) from the rios Tarauacá and Pauiní. This separation is found in all analyses and with 100% bootstrap support.

The red uakaris are organized into three main clades, with *C. c. novaesi* as sister group to *C. c. rubicundus* and *C. c. ucayalii*, with 100% of bootstrap support. *Cacajao c. ucayalii* is a sister to *C. c. rubicundus*, although we only got two samples of *C. c. ucayalii* for the genomic analysis from a single locality (Serra do Divisor National Park, Brazil). This relationship is consistent with what has been found for black-headed uakaris: the individuals from the south bank of the Rio Negro (*C. melanocephalus*) are grouped in one clade, while the individuals from the north bank are grouped into two, corresponding to *C. hosomi* and *C. ayresi* (*sensu* Boubli et al., 2008). The topology of the quartet-based species tree was consistent with the concatenated maximum-likelihood tree: five lineages of bald uakaris and three lineages of black-headed uakaris. These lineages are defined here with 100% bootstrap support, except for the position of *C. c. ucayalii* (62%) which shows some variation over the bootstrap replication (Fig. 3). In the SNAPP Bayes factor analysis, the alternative model 1 (split) is the one with the highest marginal-likelihood score and a decisive Bayes factor, supporting, therefore, five species of bald uakaris (Table S2).

We recovered similar divergence times in both datasets. From the ddRADseq dataset, Pitheciinae – *Cacajao*, *Chiropotes*, and *Pithecia* – diverged from Callicebinae – *Plecturocebus*, *Cheracebus*, and *Callicebus* – in the Early Miocene, about 17.01 Mya (95% HPD: 13.98–22.03) (Fig. 4, Table 2, Suppporting Information, Fig. S10). The divergence time between *Pithecia* and *Chiropotes/Cacajao* was in the Mid-Miocene, about 10.12 Mya (95% HPD: 6.37–14.49 Mya), and the split between *Chiropotes* and *Cacajao* occurred in the Early Pliocene, about 5.1 Mya (95% HPD: 2.91–7.68 Mya). Black-headed and bald uakaris diverged about 1.13 Mya (95% HPD: 0.67–1.72 Mya). The black-headed uakaris from the north (*C. ayresi* and *C. hosomi*) and south bank of Rio Negro (*C. melanocephalus*) diverged about 0.48 Mya (95% HPD: 0.27–0.78 Mya) and the former separated about 0.20 Mya (95% HPD: 0.11-0.29 Mya). The splits between the bald uakaris are on a similar time scale. White (*calvus* and *Cacajao* sp.) and red (*rubicundus*,

ucayalii and *novaesi*) uakaris diverged about 0.46 Mya (95% HPD: 0.29–0.7 Mya). *Cacajao c. novaesi* diverged from *C. c. rubicundus* + *C. c. ucayalii* about 0.31 Mya (95% HPD: 0.18–0.44 Mya), while the latter two splits about 0.26 Mya (95% HPD: 0.16–0.38 Mya). *Cacajao c. calvus* and *Cacajao* sp. separated about 0.31 Mya (95% HPD: 0.20–0.43 Mya).

We also dated the phylogeny using the cytochrome *b* dataset and recovered similar divergence times between the following clades: Pitheciinae and Callicebinae (17.18 Mya, 95% HPD: 14.01–22.48); *Pithecia* and the clade that includes *Chiropotes* and *Cacajao* (9.73 Mya, 95% HPD: 6.26–14.09 Mya); and between *Chiropotes* and *Cacajao* (5.74 Mya, 95% HPD: 3.34–8.45 Mya) (Table 2, Supporting Information, Fig. S10). The divergence time between black-headed and bald uakaris is estimated at 2.38 Mya (95% HPD: 1.3–3.58 Mya). Black-headed uakaris from the north (*C. ayresi* and *C. hosomi*) and south bank of Rio Negro (*C. melanocephalus*) diverged about 0.99 Mya (95% HPD: 0.5–1.56 Mya), while white uakaris (*calvus* and *Cacajao* sp.) diverged from red uakaris (*rubicundus*, *ucayalii* and *novaesi*) about 0.91 Mya (95% HPD: 0.5–1.42 Mya). While we estimated the divergence time between *C. ayresi* and *C. hosomi* (0.17 Mya, 95% HPD: 0.07-0.31 Mya), we have no resolution within the clades of red and white uakaris in the cytochrome *b* time-tree (Table 2, Supporting Information, Fig. S10).

3.2. Taxonomic implications

In his taxonomic revision of *Cacajao*, Hershkovitz (1987) suggested a zone of intergradation between *calvus* and *rubicundus* based on the pelage coloration of the reddish uakaris from the Auati-Paraná (a *paraná* is a channel) in the west portion of Mamirauá SDR.

“A total of 8 specimens from Auati-Paraná range in coloration from nearly uniformly reddish orange except for pale buffy nuchal whorl and small of back, to pale orange or buffy on entire dorsum as in extremely saturate samples of *C. c. calvus*.” (Hershkovitz, 1987: 37).

"Another seeming anomaly is that the Auati-Paraná *rubicundus* are widely separated from their nearest relatives in the area between the lower Rio Içá and Solimões. Until the problem can be resolved, perhaps by closer scrutiny of available data or possibly with more material, the Auati-Paraná series is regarded as intermediate between *calvus* and *rubicundus* but with the Auati-Paraná region tentatively excluded from the range of either subspecies." (Hershkovitz, 1987: 36).

Indeed, a contact zone between *C. c. calvus* and *C. c. rubicundus* was reported in the Aiupiá channel, a south bank tributary of the Auati-Paraná (Vieira et al., 2008), but unfortunately, we did not get any samples from this area to include in the ddRADseq analysis to investigate gene flow between *C. calvus* and *C. rubicundus*. The only *C. rubicundus* sequences from Auati-Paraná channel were retrieved from GenBank (FJ531652 and FJ531653; see also Figueiredo-Ready et al., 2013) and were used in our cytochrome *b* tree. These sequences were extracted from museum skins.

Contrary to what Thomas (1928) suggested, however, contact zones between reddish uakaris were never reported. *Cacajao c. rubicundus* has a disjunct distribution occurring in three areas in the flooded forests of the Solimões basin: 1) the Auati-Paraná channel; 2) the left bank of the Rio Jutaí; and 3) the Jacurapá channel, near the mouth of Rio Içá (Silva et al., 2021). These areas are well separated from where *C. c. novaesi* and *C. c. ucayalii* occur (Silva et al., 2021).

Therefore, we found that the four subspecies considered by Hershkovitz (1987) are monophyletic, geographically well-separated and include only individuals with consistent patterns of pelage coloration considered to be diagnostic for each of them. When Hershkovitz (1987) reviewed the taxonomic classification of *Cacajao*, he did not have available specimens from the rios Tarauacá, Pauini and Jurupari (Silva-Júnior and Martins 1999; Sampaio et al., 2018; Silva et al., 2021). Our genomic analyses consistently revealed that the white uakaris from these areas are an independent lineage separated from the white uakaris of the Rio Jutaí and the Mamirauá SDR. Under the Phylogenetic Species Concept (PSC) (monophyly + diagnosability, see Mayden et al., 1997; Groves, 2012), the bald uakaris can be classified at the species level and we suggest here this

classification scheme since, in our view, it better represents the diversity of *Cacajao* (Fig. 5). We, therefore, suggest the following taxonomic arrangement for bald uakaris:

3.2.1. *Cacajao calvus* (I. Geoffroy Saint-Hilaire, 1847) – White Bald Uakari

Brachyurus calvus: C. R. Acad. Sci. Paris, 24: 576.

Holotype

The holotype is an adult male, mounted, and stored in the mammal collection of the Muséum national d'Histoire naturelle, Paris – Catalogue number MNHN-ZM-MO-1847-1667a (Fig. 6).

Type locality

The precise location is unknown. The holotype was a donation by M. d' Alcantara Lisboa in 1807, and the origin of this specimen was considered as "Pará" (I. Geoffroy Saint-Hilaire, 1851: 57). Castelnau and Deville sent four other specimens that were mentioned in I. Geoffroy Saint-Hilaire (1852): "*C'est du Para*, *comme je l' ai dit plus haut*, *qu' est venu le type de cette espèce. Les individus que le Muséum a reçus*, *quelques mois plus tard*, *de MM. de Castelnau et Deville*, *viennent du Pérou*, *Haut-Amazone*, *environs de Fonteboa. Malgré la différence des localités*, *les mêmes caractères se retrouvent presque exactement chez tous.*" (I. Geoffroy Saint-Hilaire, 1852: 564). Translation: *"*It is Pará, as I said above, that the type of this species has come. The individuals which the Museum received a few months later from MM. de Castelnau and Deville, come from Peru, upper Amazon, near Fonte Boa. In spite of the difference of the localities, the same characters are found almost exactly in all." (I. Geoffroy Saint-Hilaire, 1852: 564).

Hershkovitz (1987) restricted the type locality: "'Para' where the species does not occur; the Castelnau Expedition specimens recorded by I. Geoffroy (1852: 560) are from the vicinity of Fonte Boa but must have originated on the left bank of the Solimões opposite Fonte Boa. This has generally been regarded as the type locality and is here so restricted." (Hershkovitz, 1987: 44).

The Mamirauá SDR falls within this region, on the north bank of the Solimões, near the Paraná do Maiana, opposite the town of Fonte Boa, where indeed white uakaris occur (Ayres, 1986; Cardoso et al., 2014; Silva et al., 2021). Two considerations are important here. First, there is no evidence for the occurrence of uakaris on the south bank of the Solimões near the mouth of the Rio Juruá. Surveys have been conducted in that region, but uakaris were never reported (for example, Cardoso et al., 2014; Silva et al., 2021). The holotype, therefore, was probably collected on the left (north) bank of Solimões, as Hershkovitz (1987) suggested, in the Paraná do Maiana channel. Second, we include in the molecular analysis samples from Mamirauá SDR and analyse the MUZUSP and MNRJ series of skins from the Auatí-Paraná and Paraná do Maiana, therefore, nearby the type locality.

General characters

Two populations were examined here and considered as *C. calvus*. The variation in the overall pelage coloration is geographically consistent in both populations. The series from the north bank of the Rio Solimões includes the specimens from the mouth of the Japurá and the Auatí-Paraná channel in the Mamirauá SDR. The males from the Mamirauá SDR have a yellowish and greyish white pattern on the nape, dorsum, and sides of the trunk due to the presence of yellowish hairs with a blackish terminal portion or the presence of some sparse greyish hairs (Supporting Information, Fig. S11). This characteristic of the dorsum contrasts with the orange or golden orange pattern of the ventral region, especially on the chest and limbs (Supporting Information, Fig. S11). Some adult females from the Auatí-Paraná have the same contrast, while others have a more uniform buffy yellowish or whitish pattern on the dorsum (Supporting Information, Fig. S12). The beard is dark reddish-brown in both males and females.

Although in our analyses the white uakaris from the Rio Jutaí (right bank) are nested in the clade of *C. calvus*, we identified a remarkable greyish pattern in the nape, dorsum, and sides of the trunk contrasting to the whitish (or yellowish-white) in some individuals. This aspect is due to the higher frequency of hairs entirely greyish or blackish interspersed with whitish hairs (but not orange as in the Mamirauá SDR series) with the

terminal portion blackish or greyish (Supporting Information, Fig. S13). The specimens from the Rio Jutaí series have the ventral region and the inner parts of the limbs with whitish or yellowish-orange hairs (Supporting Information, Fig. S13).

Geographic distribution

Cacajao calvus occurs in two isolated areas: 1) the Mamirauá SDR – limited by the rios Solimões and Japurá, and by the Auati-Paraná channel to the west; 2) on the left bank of the middle Rio Juruá, throughout the right bank of the Rio Riozinho and the lower Rio Jutaí (Fig. 7) (see also Silva et al., 2021).

3.2.2. *Cacajao rubicundus* (I. Geoffroy Saint-Hilaire and Deville, 1848) – Red Bald Uakari

Brachyurus rubicundus: C. R. Acad. Sci. Paris, 27: 498.

Type series of *Cacajao rubicundus*

When I. Geoffroy Saint-Hilaire and Deville (1848) reported the new species of uakari, *Brachyurus rubicundus*, they did not attribute a holotype. In his 1852 publication, I. Geoffroy Saint-Hilaire gave a more detailed descriptions of both *B. calvus* and *B. rubicundus* and mentioned that the specimens were sent to the Muséum National d'Histoire Naturelle, Paris (NMNH-Paris), by Castelnau and Deville in 1847:

"*C'est en mars 1847 que ce don précieux nous a été fait*, *et*, *en avril*, *que j' ai fait connaître le* Brachyurus calvus*. J' étais loin alors de me douter que*, *dans la même année*, *le Muséum allait recevoir*, *par MM. de Castelnau et Deville*, *une belle suite d' individus de cette espèce*, *et*, *avec eux*, *plusieurs représentants d' une espèce voisine*, *plus curieuse*, *ou*, *pour mieux dire*, *plus étrange encore*, *celle qui va être décrite ci-après sous le nom de* Brachyurus rubicundus*.*" (I. Geoffroy Saint Hilaire, 1852: 561). Translation: "It was in March 1847 that this precious gift was sent to us, and in April, that I reported the *Brachyurus calvus*. I was far from suspecting that in the same year the museum would receive, from MM. de Castelnau and Deville, a succession of individuals of this species

and, with them, several representatives of a sister species, which will be described hereinafter under the name of *Brachyurus rubicundus*." (I. Geoffroy Saint Hilaire, 1852: 561).

Hershkovitz (1987) reported on the two males and three females sent to the NMNH-Paris by Castelnau and Deville that are considered syntypes. The lectotype is a mounted, adult male (Catalogue number MNHN-ZM-2005-898), collected in the Village de Saint-Paul, Brazil (São Paulo de Olivença, Brazil) (Fig. 8).

Type locality

Isidore Geoffroy Saint-Hilaire and Deville (1948: 498) indicated São Paulo de Olivença, state of Amazonas, as the origin of the specimens used to describe *C. rubicundus*: "*Du Brésil*, *village de Saint-Paul*". Some years later, I. Geoffroy Saint-Hilaire (1852: 567) provided more details on the occurrence of *C. rubicundus*, according to what had been reported by Castelnau:

"*Ainsi*, *l' espèce à poils roux habite assez communément les bois qui s' étendent en face d' Olivença*, *et ne paraît pas dépasser le Putumayo*." Translation: "Thus, the species with red hair inhabits the forests, which extend from opposite Olivença and does not seem to pass the Putumayo." (I. Geoffroy Saint-Hilaire, 1852: 567). Based on these reports and new field evidence (Silva et al., 2021), we restrict the type locality to the flooded forest of the Jacurapá channel, north (left) bank of Rio Solimões, opposite São Paulo de Olivença, Amazonas, Brazil.

General characters

We identified three patterns of pelage coloration in *C. rubicundus*, which are consistent with the geographic distribution of each population. The individuals from the type locality (north bank of Rio Solimões, flooded forests of Jacurapá channel) have a nape with whitish hairs contrasting with the reddish-orange of the mid-back, rump, and sides of the trunk and limbs. In some individuals, the whitish hairs of the nape are gradually replaced by light orange hairs in the mantle (Supporting Information, Fig. S14). Specimens from the Rio Jutaí (left bank) have whitish hairs on the nape extending to the

mantle that is gradually replaced by the reddish-chestnut hairs of the saddle while the pattern of the mid-back, rump, and sides of the trunk and limbs is entirely reddish-chestnut (Supporting Information, Fig. S15). The overall pattern of these individuals is reddish-chestnut that differs from the reddish-orange of the series from the Jacurapá channel. The specimens of the Auatí-Paraná have a similar reddish-chestnut colouring to those of the series from the Rio Jutaí on the sides of the trunk and limbs, but with an evident whitish or pale buffy colour throughout the dorsum, from the nape to the tail in the male and to the saddle in the one female examined (Supporting Information, Fig. S16). The arms, legs, and sides of the trunk in the adult males are reddish-chestnut interspersed with hairs entirely yellowish or with the basal portion reddish-orange, becoming more whitish-yellow in the terminal and subterminal portions (Supporting Information, Fig. S16).

Geographic distribution

Cacajao rubicundus is restricted to three disjunct populations in the middle Rio Solimões: 1) the flooded forests delimited by the Jacurapá channel and Rio Solimões (the type locality); 2) the left bank of the Rio Jutaí, a south bank tributary of Rio Solimões; and 3) along the Auati-Paraná, which connects the rios Solimões and Japurá (Fig. 7) (see also Silva et al., 2021).

3.2.3. *Cacajao ucayalii* Thomas, 1928 – Ucayali Bald Uakari

Cacajao rubicundus ucayalii: Ann. Mag. Nat. Hist. ser. 10, 2: 252.

Holotype

Adult male, skin and skull, collected on 29 October 1927 and kept in the British Museum (Natural History), London (number 1928.5.2.41) (Napier, 1976).

Type locality

Cerro Azul, Contamana, Peru (Thomas, 1928), altitude about 609.6 m (2000 ft) a.s.l.

General characters

An overall reddish-chestnut or reddish-orange without the contrasting whitish or yellowish coloration of the dorsum, as found in *C. rubicundus* and *C. novaesi*. Hershkovitz (1987) mentioned a "north-to-south bleaching gradient" in the Peruvian bald uakaris. Although we identified some differences in the overall tone of reddish coat colour between the populations, we did not identify this north-south cline variation in the specimens we examined. Kalinowski's series from the FMNH, for example, was collected along the Río Javari-Mirim (Loreto District in Peru) and presents an overall reddish-chestnut pelage coloration with some dark-reddish or blackish hairs on the limbs and dorsal surface of the tail (Supporting Information, Fig. S17). The series from the MPEG (collected along the Río Amazonas, right bank, opposite the mouth of the Río Napo), however, presents a lighter tone with an overall reddish-orange and some yellowish hairs on the dorsum (Supporting Information, Fig. S18). The adult males also present a lighter tone of reddish-orange on the dorsum, which is more evident in juveniles (Supporting Information, Fig. S18).

Geographic distribution

Cacajao ucayalii occurs mainly in the Ucayali-Javari interfluve (Fig. 7), with isolated populations reported beyond this area (Vermeer et al., 2013). This taxon was confirmed in Brazil only along the Rio Moa, Serra do Divisor National Park (SDNP) (Silva et al., 2021).

3.2.4. *Cacajao novaesi* Hershkovitz, 1987 – Novaes' Bald Uakari

Cacajao calvus novaesi: Am. J. Primatol. 12: 27.

Holotype

Adult male, skin and skull, Royal Natural History Museum, Stockholm, catalogue number 612508 (see also Hershkovitz, 1987, for the type series).

Type locality

Santo Antônio, Rio Eiru, Amazonas, Brazil.

General Characters

Overall coloration is reddish-orange or reddish-chestnut in some individuals with the contrasting colour of the dorsum, from the nape to the rump or tail. The whitish and yellowish pattern of the dorsum is gradually replaced by light orange hairs on the saddle, limbs, and flanks. The arms and legs are reddish-orange, interspersed with entirely yellowish hairs or with the basal portion reddish-orange and yellowish in the terminal portion (Supporting Information, Fig. S19).

Geographic distribution

Cacajao novaesi is confirmed only in the Gregório and Tarauacá interfluve. The southern limit of its occurrence is unknown (Fig. 7) (Silva et al., 2021).

3.2.5. *Cacajao amuna* sp. n.

Holotype

IDSM03676, field number FES095, skin, skull, skeleton, adult male in the Mammal collection of the Mamirauá Institute for Sustainable Development, Amazonas, Brazil (Fig. 9A), collected by Felipe Ennes Silva on 25 January 2017.

Type locality

Lago Itucumã, seasonally flooded forest (*várzea*) of the right bank of the lower Rio Tarauacá, a right-bank tributary of the Rio Juruá, state of Amazonas, Brazil (6°56'06" S, 69°44'16" W).

Description

Most of the hairs of the dorsum are entirely white or whitish, with a few having a greyish terminal portion or entirely greyish. This characteristic gives a light greyish white appearance throughout the dorsum, which contrasts slightly with the nape and the posterior portion of the tail where the hairs are entirely white. The flanks have hairs that are entirely white or whitish with the terminal portion greyish. The sparse hairs on the chest and belly are whitish. The arms are yellowish-white, paler on the forearms. The

legs are whitish on the external surface, but cream-coloured on the internal. The tail is whitish on the upper surface but cream-coloured underneath. The hands and feet have short orange hairs interspersed with greyish white hairs. The beard is reddish-orange and the face essentially bare.

Paratypes

- INPA7276, field number RS063, skin, skull, skeleton, adult male collected by Ricardo Sampaio in February 2014 in a flooded forest along the Rio Moaco, a right-bank tributary of the Rio Pauini, state of Amazonas, Brazil (8°02'02" S, 69°14'53" W). Mammal collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil (Fig. 9B).
- INPA7280, field number RS064, skin, skull, skeleton, adult female collected by Ricardo Sampaio in February 2014 in a flooded forest along the Rio Moaco, a right-bank tributary of the Rio Pauini, state of Amazonas, Brazil (7°36'21.27" S, 69°07'55.35" W). Mammal collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil (Fig. 9C).
- IDSM03668, field number FES064, skin, skull, skeleton, adult female collected by Felipe Ennes Silva on 19 January 2017 in a flooded forest of the right bank of the Rio Tarauacá, Igarapé Grande, near the community of São Romão, state of Amazonas, Brazil (6°40'14" S, 69°40'02" W). Mammal collection of the Mamirauá Institute for Sustainable Development, Brazil (Fig. 9D).
- IDSM03674, field number FES070, skin, skull, skeleton, adult female collected by Felipe Ennes Silva on 28 January 2017 in a flooded forest on the right bank of the Rio Tarauacá, Igarapé Grande, near the community of São Romão , state of Amazonas, Brazil (6°40'14" S, 69°40'02" W). Mammal collection of the Mamirauá Institute for Sustainable Development, Brazil (Fig. 9E).
- IDSM03671, field number FES071, skin, skull, skeleton, subadult female collected by Felipe Ennes Silva on 28 January 2017 in a flooded forest on the right bank of the Rio Tarauacá, Igarapé Grande, nearby the community of São Romão, state of

Amazonas, Brazil (6°40'14" S, 69°40'02" W). Mammal collection of the Mamirauá Institute for Sustainable Development, Brazil (Fig. 9F).

Description of the paratypes

The type series of *Cacajao amuna* sp. n. is composed of the holotype and five paratypes. There is minor intraspecific variation in the paratypes, but each differs consistently from all other *Cacajao* species. The paratype male INPA7276 has a whiter dorsum due to the fewer greyish hairs when compared to the holotype, and the beard is reddish-chestnut rather than reddish-orange. Hairs on the flanks are entirely white or whitish, interposed with hairs distally yellowish. The arms and legs are cream-coloured, on the external and internal surfaces. The female IDSM03674 is overall cream-coloured, but slightly yellowish to orange on the insides of the legs. The nape has some hairs with a greyish terminal and subterminal portion. The female IDSM03668 and subadult female IDSM03671 have greyish mantles, due to hairs with a greyish terminal and subterminal band. This pattern contrasts slightly with the whiter saddle. The legs and arms are yellowish-white in the posterior portion but whiter on the anterior. Also, the tail is whitish-cream in the posterior portion and yellowish-orange in the anterior portion. The beard is reddish-orange as in the holotype. The dorsal hairs of the adult female INPA7280 are entirely white or whitish, with the terminal and subterminal portion greyish interposed with sparse greyish hairs, producing a light greyish-white aspect as described for the holotype. The arms, legs, tail and sides of the trunk are predominantly white. The beard is reddish-chestnut. All of the type series specimens have sparse white or yellowish-white hairs on the chest and belly (Fig. 9).

Type Locality

Lago Itucumã (6°56'06" S, 69°44'16" W), right bank of the Rio Tarauacá, state of Amazonas, Brazil.

Diagnosis

Cacajao amuna sp. n. is a bald uakari that differs from all others by a pattern of pelage coloration that is consistently found in the specimens from the Rio Taruacá basin. The chest and abdomen have sparse white hairs without the hirsute reddish-orange or

reddish-chestnut chest found in *C. calvus* from Mamirauá SDR. The dorsum and flanks are whitish, especially in males. The forelimbs are yellowish-white, with slightly paler (whiter) forearms. The legs and tail are whitish.

Comparisons with *Cacajao calvus*

Cacajao amuna sp. n. differs from its sister species, *Cacajao calvus*, by the overall whitish coloration of the dorsum and flanks, without the marked contrast with the orange hairs of the underparts that is typical of the uakaris from the Mamirauá SDR (Fig. 10). The uakaris of Mamirauá SDR have a more hirsute reddish-orange or reddish-chestnut chest that is not found in *Cacajao amuna* sp. n. (Fig. 10). Uakaris from the Jutaí basin, here also considered to be *C. calvus*, have a darker grey dorsum, not found in the *C. amuna* sp. n. specimens that we have examined. *Cacajao amuna* sp. n. has a reddish-orange or reddish-chestnut beard, generally paler than the reddish-brown beard typical of *C. calvus*.

Geographic Distribution

Cacajao amuna sp. n. occurs in the forests of the right bank of the Rio Tarauacá, extending to the rios Envira and Jurupari, where white uakaris were recorded by Silva-Júnior and Martins (1999) (Fig. 7). The species is also found in the headwaters of the rios Pauini and Moaco, affluents of the upper Rio Purus to the east (Sampaio et al., 2018). We estimated a distribution of at least 30,028 km^2. Its southern limit is unknown and we have no information from the upper Tarauacá. Two hundred kilometers separate their range from that of the white uakaris of the left bank of the Rio Juruá, 400 km from the populations of the Rio Jutaí, and about 700 km from the populations of the Mamirauá SDR.

Habitat

Cacajao amuna sp. n. occurs in the white-water flooded forests (*várzeas*) of the right bank of the Rio Tarauacá and headwaters of the Rio Pauini.

Etymology

The new species is named in tribute to the Amuna-dyapas, a Kanamari subgroup of the Kanamaris do Rio Juruá Indigenous Territory (TI Kanamaris do Rio Juruá), on the right

bank of the Rio Taraucá. “Amuna” is a Katukina vocative that means “uakari monkey”. We suggest the common name “the Kanamari white uakari”.

4. Discussion

The phylogenetic analysis presented here is concordant with the pelage differences in *Cacajao*. For the bald uakaris, the phylogenetic inference using cytochrome *b* and ddRADseq separates the white and red bald uakaris into two well-defined groups. The genome-wide representation also retrieved a structure within these two clades showing that the four subspecies considered by Hershkovitz (1987) are reciprocally monophyletic, in addition to having unique diagnostic characters. The ddRADseq analysis also revealed two well-defined clades of white uakaris – the first includes the populations from the Mamirauá SDR and the Rio Jutaí (*C. calvus*), and the second includes individuals from the rios Tarauacá and Pauini (described here as *C. amuna* sp. n.), both species are separated by about 500 km (Fig. 7). The three lineages of red uakaris retrieved from the ddRADseq dataset correspond to *C. rubicundus*, *C. ucayalii*, and *C. novaesi*. Bald-headed uakaris lineages diverged in the Mid-Pleistocene (approximately 0.3 Mya).

In our understanding, this calls for a classification of the bald uakaris, including the newly described form from the Tarauacá river basin – *Cacajao amuna* sp. n. – at the species level. The use of different characters is essential to support a classification scheme. The taxonomic scheme proposed here adheres to the Phylogenetic Species Concept (PSC) since each taxon is monophyletic and they accrue differences in pelage coloration that are geographically consistent (i.e., monophyletic and diagnosable, see Mayden, 1997; Groves, 2012).

When looking into the clades of the red uakaris (*C. rubicundus*, *C. ucayalii*, *C. novaesi*) and white bald uakaris (*C. calvus*, *C. amuna* sp. n.), the phylogenetic relationships within them were overshadowed when using only one locus. If the low resolution in the cytochrome *b* tree is caused by introgression and/or incomplete lineage sorting – which

are processes that may influence the phylogenetic inference and result in different tree topologies when comparing nuclear and mitochondrial datasets (Heckman *et al*., 2007; Artyushin et al., 2018; Dias et al., 2018; Kutschera et al., 2014; Wang et al., 2018) – remains to be elucidated.

The divergence time estimated here with both datasets differs from what was estimated in previous studies (Boubli and Ditchfield, 2000; Figueiredo-Ready et al., 2013). For example, the divergence time between black-headed and bald uakaris was estimated at around 5-5.8 Mya using cytochrome *b* (Boubli and Ditchfield, 2000, Figueiredo-Ready et al., 2013), while in our cytochrome *b* tree these groups diverged around 2.38 Mya, with the main split within both clades only occurring at approximately 0.91-0.99 Mya. We believe that these differences lay mainly in the methodological approaches used by these authors. For example, the divergence time estimated by Figueiredo-Ready et al. (2013) was based on the confidence interval of 6.3-12.9 Mya for the split of *Cacajao* and *Chiropotes* estimated by previous authors (i.e. secondary calibration); while Boubli and Ditchfield (2000) used the standard vertebrate molecular clock rate estimate for the cytochrome *b* gene of approximately 2% sequence divergence per million years (i.e. strict clock; Irwin et al., 1991).

Divergence times dating to the late Pleistocene have also been found in other primates (Lynch-Alfaro et al., 2012; Poelstra et al., 2021) that may have their diversification influenced by the Pleistocene climatic oscillations and geomorphological changes. Indeed, western Amazonia underwent recent and dynamic sedimentological and geomorphological activity that caused changes in the rivers as seen, for example, in the major avulsions and paleochannels of the rios Juruá and Japurá (Ruokolainen et al., 2020). The bald uakaris' evident preference for riparian flooded forests would make them particularly susceptible to the fluvial dynamics related to climatic and geomorphological changes in the late Pleistocene, with episodes of isolation and contact promoting and/or hindering gene flow over the last 500 thousand years, producing this unusual patchwork of the various species, including isolated populations reported in

upland forests at > 600 m a.s.l. (Vermeer et al., 2013; McHugh et al., 2012; Silva et al., 2021).

5. Conclusions

For the first time since Hershkovitz's (1987) revision, we have another view of the taxonomic classification of bald uakaris, with the main lineages identified using a robust molecular analysis. The findings presented here also have implications for conservation by providing an updated view of the diversity of uakaris. The bald uakaris were categorized as Vulnerable in the previous IUCN Red List assessment (Aquino et al., 2021), but all as subspecies of *C. calvus*. Widely, but patchily distributed through western Amazonia, each taxon has different priorities in terms of research and conservation measures – especially concerning habitat loss by deforestation and anthropogenic climate change. *Cacajao calvus* and *C. rubicundus*, for example, are not hunted (Pereira et al., 2019) and have significant portions of their ranges legally protected by various categories of protected areas, in an area where extensive deforestation is not imminent (Trancoso et al., 2010). The deforestation rate is much higher, however, for the populations of *C. amuna* sp. n. and *C. novaesi*, due to their proximity to expanding urban centres (for example, Eirunepé, Envira, Tarauacá, and Feijó). The BR-364 cuts through the main rivers where both taxa occur (i.e., the rios Gregório, Envira, Eiru, and Tarauacá) and there is a hotspot of deforestation in the state Acre connecting the largest cities in the state (Cruzeiro do Sul and Rio Branco) to the state of Rondônia – where the deforestation rate is among the highest throughout Amazonia.

Bald uakaris are a flagship species for conservation in Brazil and Peru. The Mamirauá Sustainable Development Reserve (Mamirauá SDR), for example, was created to protect bald uakaris in an initiative that included researchers, local communities, governmental and non-governmental agencies in the political and social context of the 1980s (Ayres and Johns, 1987; Alves, 2011; Queiroz, 2011). The Mamirauá SDR was the first of its kind, and a model for protected areas subsequently established elsewhere in Brazil and in the

world, both marine and terrestrial, having a scientific basis for the management of natural resources while promoting improvements in the social conditions and well-being of local communities. The unique red face, striking reddish or whitish coat colour, and the evolutionary uniqueness of the bald uakaris' ecology and behaviour (their use of space, group size, and adaptation for seed predation) make them remarkable primates that are easily recognized by locals in any forest. Bridging evolutionary and ecological studies with actions for the conservation of primates with this appeal is essential during the current challenging times for biodiversity in the Amazon rainforest. What seems to be a utopian goal in the current political scenario in Brazil (year-base: 2022) is, actually, an urgent priority for researchers and conservationists alike.

CRediT authorship contribution statement

Felipe Ennes Silva: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review and editing, Visualization, Supervision, Project administration, Funding acquisition. **João Valsecchi do Amaral**: Conceptualization, Resources, Funding acquisition. **Christian Roos**: Conceptualization, Methodology, Resources, Writing – review and editing. **Mark Bowler**: Conceptualization, Methodology, Resources, Writing – review and editing. **Fabio Röhe**: Conceptualization, Investigation, Methodology, Resources. **Ricardo Sampaio**: Conceptualization, Investigation, Methodology, Resources, Funding acquisition. **Mareike Cora Janiak**: Methodology, Formal analysis, Writing – review and editing. **Fabrício Bertuol**: Methodology, Formal analysis. **Marcelo Ismar Santana**: Conceptualization, Investigation, Writing – review and editing. **José de Souza Silva Júnior**: Conceptualization, Resources. **Anthony B. Rylands**: Conceptualization, Validation, Writing – review and editing. **Chrysoula Gubili**: Methodology, Validation, Formal analysis, Resources, Writing – review and editing. **Tomas Hrbek**: Conceptualization, Methodology, Validation, Resources, Funding acquisition. **Allan D. McDevitt**: Methodology, Validation, Resources, Writing – review and editing. **Jean P.**

Boubli: Conceptualization, Methodology, Validation, Formal analysis, Resources, Writing – review and editing, Visualization, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

ddRAD raw sequences are available in the NCBI BioProject PRJNA830637. Accession numbers for Cytochrome *b* and ddRAD sequences are available in the Table S1 – Supplementary Material

Acknowledgements

We thank the curators and staff of the following zoological collections: Museu Paraense Emílio Goeldi, Instituto de Desenvolvimento Sustentável Mamirauá, Instituto Nacional de Pesquisas da Amazônia, Museu de Zoologia da Universidade de São Paulo, Museu Nacional do Rio de Janeiro, Field Museum of Natural History, Muséum national d'Histoire naturelle. Funds were granted by the following institutions: Brazilian National Council for Scientific and Technological Development (CNPq) (Process nos.: 303286/2014-8, 303579/2014-5, 200502/2015-8, 302140/2020-4, 300365/2021-7, 301407/2021-5, 301925/2021-6); International Primatological Society for the Conservation grant; The Rufford Foundation (14861-1, 23117-2), the Margot Marsh Biodiversity Foundation (SMA-CCO-G0000000023, SMA-CCO-G0000000037), Primate Conservation Inc. (#1713 and #1689), and the American Society of Mammalogists for a Latin American Fellowship. The Pauini river expedition was part of the project: “Primates in Amazonian Protected Areas” financed by the Brazilian government’s Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). Permits to conduct fieldwork and sample collections were provided by the Brazilian Ministry of the Environment agencies – Chico Mendes Institute for Biodiversity Conservation (ICMBio) (SISBio 55777-2, 42111-

1, 42111-2, 42111-3) and Brazilian Institute of Environment and Renewable Natural Resources IBAMA (License N° 005/2005 – CGFAU/LIC). We are grateful to Dr. Cécile Callou for the pictures of the holotypes from the Muséum national d'Histoire naturelle, and to Dr Stephen Nash for the drawings of bald uakaris. FES, JVA, MIS, FR, RS are also grateful for the support of local people during the field research. The authors have no conflict of interest.

References

Alves, A.R.P., 2011. A tribute to José Márcio Ayres. In: Pinedo-Vasquez, M., Ruffino, M.L., Padoch, C., Brondízio, E.S., (Eds.). The Amazon Várzea: the decade past and the decade ahead. The Amazon várzea. Springer, Dordrecht, pp. 297–299.

Andrews, S., 2018. FASTQC. A quality control tool for high throughput sequence data. http://www.bioinformatics.babraham.ac.uk/projects/fastqc/. (accessed 30 May 2019).

Aquino, R., Queiroz, H.L., Paim, F.P., Boubli, J.P., Mittermeier, R.A., Ravetta, A.L., Shanee, S., Urbani, B., de Azevedo, R.B., Calouro, A.M., Cornejo, F.M., 2021. *Cacajao calvus*. The IUCN Red List Threat Species (amended version of 2020 assessment). <https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T3416A191694447.en> Downloaded 31 May 2021.

Artyushin, I.V, Kruskop, S.V., Lebedev, V.S., Bannikova, A.A., 2018. Molecular phylogeny of serotines (Mammalia, Chiroptera, *Eptesicus*): evolutionary and taxonomical aspects of the *E. serotinus* species group. Biol Bull 45, 469–477.

Ayres, J.M., 1986. Uakaris and Amazonian flooded forest. Unpublished D. Phil. Thesis, University of Cambridge, Cambridge.

Ayres, J.M., Johns, A.D., 1987. Conservation of white uacaries in Amazonian várzea. Oryx 21(2), 74–80.

Boubli, J.P., Ditchfield, A.D., 2000. The time of divergence between the two species of uacari monkeys: *Cacajao calvus* and *Cacajao melanocephalus*. Folia Primatol 71(6), 387–391.

Boubli, J.P., da Silva, M.N.F., Amado, M.V., Hrbek, T., Pontual, F.B., Farias, I.P., 2008. A taxonomic reassessment of *Cacajao melanocephalus* Humboldt (1811), with the description of two new species. Int J Primatol 29(3), 723–741.

Bouckaert, R., Vaughan, T.G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Müller, N.F., Ogilvie, H.A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M.A., Wu, C.H., Xie, D., Zhang, C., Stadler, T., Drummond, A.J., 2019. BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. Plos Comput Biol 15(4), e1006650.

Bryant, D., Bouckaert, R., Felsenstein, J., Rosenberg, N.A., Roychoudhury, A., 2012. Inferring species trees directly from biallelic genetic markers: bypassing gene trees in a full coalescent analysis. Mol Biol Evol 29(8), 1917–1932.

Cardoso, N.A., Valsecchi, J.A., Vieira, T., Queiroz, H.L., 2014. New records and range expansion of the white bald uakari (*Cacajao calvus calvus*, I. Geoffroy, 1847) in central Brazilian Amazonia. Primates 55(2), 199–206.

Catchen, J.M., Amores, A., Hohenlohe, P., Cresko, W., Postlethwait, J.H., 2011. Stacks: building and genotyping loci *de novo* from short-read sequences. G3: Genes, Genomes, Genetics 1(3), 171–182.

Catchen, J., Hohenlohe, P.A., Bassham, S., Amores, A., Cresko, W.A. 2013. Stacks: an analysis tool set for population genomics. Mol Ecol 22(11), 3124–3140.

Chifman, J., Kubatko, L., 2014. Quartet inference from SNP data under the coalescent model. Bioinformatics 30(23), 3317–3324.

Covain, R., Fisch-Muller, S., Oliveira, C., Mol, J.H., Montoya-Burgos, J.I., Dray, S., 2016. Molecular phylogeny of the highly diversified catfish subfamily Loricariinae (Siluriformes, Loricariidae) reveals incongruences with morphological classification. Mol Phylogenet Evol 94, 492–517.

Crotti M, Barratt CD, Loader SP, Gower DJ, Streicher JW. 2019. Causes and analytical impacts of missing data in RADseq phylogenetics: insights from an African frog (*Afrixalus*). Zool Scr 48(2), 157–67.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol 4(5), 699–710.

Dayrat, B., 2005. Towards integrative taxonomy. Biol J Linn Soc 85, 407–415.

Dias, C., de Araújo Lima, K., Araripe, J., Aleixo, A., Vallinoto, M., Sampaio, I., Schneider, H., do Rêgo, P.S., 2018. Mitochondrial introgression obscures phylogenetic relationships among manakins of the genus *Lepidothrix* (Aves: Pipridae). Mol Phylogenet Evol 126, 314–320.

Eaton, D.A.R., 2014. PyRAD: assembly of *de novo* RADseq loci for phylogenetic analyses, Bioinformatics 30(13), 1844–1849.

Eaton, D.A.R., Overcast, I., 2020. IPYRAD: interactive assembly and analysis of RADseq datasets. Bioinformatics 36(8), 2592–2594.

Ferrari, S.F., Guedes, P.G., Figueiredo-Ready, W.M.B., Barnett, A.A., 2014. Reconsidering the taxonomy of the black-faced uacaris, *Cacajao melanocephalus* group (Mammalia: Pitheciidae), from the northern Amazon Basin. Zootaxa 3866(3), 353–370.

Figueiredo, W.M.B., 2006. Estimativas de tempos de divergência em platirrinos e filogenia molecular e filogeografia dos uacaris, parauacus e cuxiús. Unpublished D. Phil. thesis, Universidade Federal do Pará, Belém.

Figueiredo-Ready, W.M.B., Schneider, H., Ferrari, S.F., Harada, M.L., Silva, J.M.C., Silva-Júnior, J.S., Bates, J.M., 2013. A molecular phylogeography of the uacaris (*Cacajao*). In: Veiga, L., Barnett, A.A., Ferrari, S.F., Norconk, M.A. (Eds.), Evolutionary biology and conservation of titis, sakis and uacaris. Cambridge University Press, Cambridge, pp. 23–30.

Geoffroy Saint-Hilaire, I., 1847. Note sur un singe americain appartenant au genre. *Brachyure*, Comptes Rendus des Seances hebdomadaires de l'academie des Sciences 24, 576–577.

Geoffroy Saint-Hilaire, I., 1851. Catalogue méthodique de la collection de mammifères Part 1. Mammifères, Introduction et Catalogue des Primates du Muséum d'histoire naturelle, Paris 96(xi).

Geoffroy Saint-Hilaire, I., 1852. Description des mammifères nouveau ou imparfaitement connus de la collection du Muséum d'Histoire naturelle et remarques sur la classification et les caractères des mammifères: Troisieme memoir. Archive du Muséum d'Histoire naturelle, Paris (5), 529–584.

Geoffroy Saint-Hilaire, I., Deville, E., 1848. Note sur huit especies nouvelles de singes americaines, faitent parties des collections de M. de Castelnau et Emile Deville, Comptes Rendus hebdomadaires des Seances de l'academie des Sciences 27, 497–499.

Gernhard, T., Hartmann, K., Steel, M., 2008. Stochastic properties of generalised Yule models, with biodiversity applications. J Math Biol 57(5), 713–735.

Groves, C.P., 2012. Species concept in primates. Am J Primatol 74, 687-691.

Groves, C.P., 2014. Primate taxonomy: inflation or real? Annu Rev Anthropol 43, 27–36.

Heckman, K.L., Mariani, C.L., Rasoloarison, R., Yoder, A.D., 2007. Multiple nuclear loci reveal patterns of incomplete lineage sorting and complex species history within western mouse lemurs (*Microcebus*). Mol Phylogenet Evol 43(2), 353–367.

Hershkovitz, P., 1987. Uacaries, new world monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): a preliminary taxonomic review with the description of a new subspecies. Am J Primatol 12, 1–53.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q., Vinh, L.S., 2018. UFBoot2: improving the ultrafast bootstrap approximation. Mol Biol Evol 35(2), 518–522.

Huang, H., Knowles, L., 2016. Unforeseen consequences of excluding missing data from next-generation sequences: simulation study of rad sequences. Syst Biol 65: 357–365.

Irwin, D.M., Kocher, T.D., Wilson, A.C., 1991. Evolution of the cytochrome *b* gene of mammals. J Mol Evol 32(2), 128–144.

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., Von Haeseler, A., Jermiin LS. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimate. Nat Methods 14(6), 587–589.

Kass, R.E., Raftery, A.E., 1995. Bayes factors. J Am Stat Assoc 90, 773–795.

Katoh, K., Misawa, K., Kuma, K., Miyata, T., 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acid Res 30(14), 3059–3066.

Katoh, K., Rozewicki, J., Yamada, K.D., 2017. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Brief Bioinform 20(4), 1160–1166.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30, 772–780.

Kay, R.F., Johnson, D.J., Meldrum, D.J., 1998. A new pitheciin primate from the middle Miocene of Argentina. Am J Primatol 45, 317–336.

Kutschera, V.E., Bidon, T., Hailer, F., Rodi, J.L., Fain, S.R., Janke, A., 2014. Bears in a forest of gene trees: phylogenetic inference is complicated by incomplete lineage sorting and gene flow. Mol Biol Evol 31(8), 2004–2017.

Lynch-Alfaro, J.W., Boubli, J.P., Paim, F.P., Ribas, C.C., Silva, M.N.F., Messias, M.R., Röhe, F., Mercês, M.P., Silva Júnior, J.S., Silva, C.R., Pinho, G.M., Koshkarian, G., Nguyen, M.T.T., Harada, M.L., Rabelo, R.M., Queiroz, H.L., Alfaro, M.E., Farias, I.P., 2015. Biogeography of squirrel monkeys (genus *Saimiri*): south-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. Mol Phylogenet Evol 82, 436–454.

Mayden, R.L., 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge, M.F., Dawah, H.A., Wilson, M.R. (Eds.), Species. The units of biodiversity. Chapman and Hall, CRC Press, London, pp. 381–423.

Mayor, P., Mamani, J., Montes, D., González-Crespo, C., Sebastián, M.A., Bowler, M., 2015. Proximate causes of the red face of the bald uakari monkey (*Cacajao calvus*). Roy Soc Open Sci 2(7), 1–7.

McDonough, M. M., Ferguson, A.W., Dowler, R.C, Gompper, M.E., Maldonado, J.E., 2022. Phylogenomic systematics of the spotted skunks (Carnivora, Mephitidae, Spilogale): additional species diversity and Pleistocene climate change as a major driver of diversification.” Mol Phylogenet Evol, 107266.

McHugh, S., Cornejo, F., McKibben, J., Zarate, M., Tello, C., Jiménez, C., Schmitt, C., 2020. First record of the Peruvian yellow-tailed woolly monkey *Lagothrix flavicauda* in the Región Junín, Peru. Oryx 54(6), 814–818.

Mello, B., Tao, Q., Barba-Montoya, J., Kumar, S., 2021. Molecular dating for phylogenies containing a mix of populations and species by using Bayesian and RelTime approaches. Mol Ecol Resour. 21, 122–136.

Minh, B.Q., Nguyen, M.A.T., Von Haeseler, A., 2013. Ultrafast approximation for phylogenetic bootstrap Mol Biol Evol 30(5), 1188–1195.

Napier, P.H., 1976. Catalogue of Primates in the British Museum (Natural History). Part 1: Families Callitrichidae and Cebidae. British Museum (Natural History), London.

Nieto-Montes de Oca, A., Barley, A.J., Meza-Lázaro, R.N., García-Vázquez, U.O., Zamora-Abrego, J.G., Thomson, R.C., Leaché, A.D., 2017. Phylogenomics and species delimitation in the knob-scaled lizards of the genus *Xenosaurus* (Squamata: Xenosauridae) using ddRADseq data reveal a substantial underestimation of diversity. Mol Phylogenet Evol 106, 241–253.

Nguyen, L.T., Schmidt, H.A., Von Haeseler, A., Minh, B.Q., 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol Biol Evol 32(1), 268–274.

Outlaw, D.C., Voelker, G., 2006. Systematics of *Ficedula flycatchers* (Muscicapidae): A molecular reassessment of a taxonomic enigma. Mol Phylogenet Evol 41, 118–126.

Pereira, P.M., Valsecchi, J., Queiroz, H., 2019. Spatial patterns of primate hunting in riverine communities in Central Amazonia. Oryx 53(1), 165–173.

Peterson, B.K., Weber, J.N., Kay, E.H., Fisher, H.S., Hoekstra, H.E., 2012. Double digest RADseq: An inexpensive method for *de novo* SNP discovery and genotyping in model and non-model species. PLoS One 7(5), 1–11.

Poelstra, J.W., Salmona, J., Tiley, G.P., Schüßler, D., Blanco, M.B., Andriambeloson, J.B., Bouchez, O., Campbell, C.R., Etter, P.D., Hohenlohe, P.A., Hunnicutt, K.E., Iribar, A., Johnson, E.A., Kappeler, P.M., Larsen, P.A., Manzi, S., Ralison, J.M., Randrianambinina, B., Rasoloarison, R.M., Rasolofoson, D.W., Stahlke, A.R., Weisrock, D.W., Williams, R.C., Chikhi, L., Louis Jr, E.E., Radespiel, U., Yoder, A.D., 2021. Cryptic patterns of speciation in cryptic primates: microendemic mouse lemurs and the multispecies coalescent. Syst Biol 70(2), 203–218.

Queiroz, H.L., 2011. Protected areas of sustainable use, involvement of social actors, and biodiversity conservation in the várzea: the case of the Mamirauá Reserve-sharing conservation benefits in Central Amazonia, Brazil. In: Pinedo-Vasquez, M., Ruffino, M., Padoch, C., Brondízio, E. (Eds.), The Amazon Várzea. Springer, Dordrecht, pp. 239–257.

Quintela, F.M., Rosa, C.A., Feijó, A., 2020. Updated and annotated checklist of recent mammals from Brazil. An Acad Bras Ciênc 92, 1–57.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst Biol 67, 901–904.

Rancilhac, L., Goudarzi, F., Gehara, M., Hemami, M.R., Elmer, K.R., Vences, M., Steinfarz, S., 2019. Phylogeny and species delimitation of near Eastern *Neurergus* newts (Salamandridae) based on genome-wide RADseq data analysis. Mol Phylogenet Evol 133, 189–197.

Ritchie, A.M., Lo, N., Ho, S.Y.W., 2017. The Impact of the tree prior on molecular dating of data sets containing a mixture of inter and intraspecies sampling. Syst Biol 66 (3), 413–425.

Rochette, N.C., Rivera-Colón, A.G., Catchen, J.M., 2019. STACKS 2: analytical methods for paired-end sequencing improve RADseq-based population genomics. Mol Ecol 28(21), 4737–4754.

Ruokolainen, K., Moulatlet, G.M., Zuquim, G., Hoorn, C., Tuomisto, H., 2019. Geologically recent rearrangements in central Amazonian river network and their importance for the riverine barrier hypothesis. Front Biogeogr 11(3), e45046

Sambrook, J., Fritsch, E.R., Maniatis, T., 1989. Molecular cloning: a laboratory manual. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press.

Sampaio, R., Röhe, F., Rylands, A.B., 2018. Diversity of primates and other mammals in the middle Purus basin in the Brazilian Amazon. Mammalia 82, 565–579.

Sánchez-González, L.A., Moyle, R.G., 2011. Molecular systematics and species limits in the Philippine fantails (Aves: Rhipidura). Mol Phylogenet Evol, 61(2), 290–299.

Schlick-Steiner, B.C., Steiner, F.M., Seifert, B., Stauffer, C., Christian, E., Crozier, R.H., 2010. Integrative Taxonomy: a multisource approach to exploring biodiversity. Annu Rev Entomol 55, 421–438.

Silva Júnior, J.S., Martins, E.S., 1999. On a new white bald uakari population in southwestern Brazilian Amazonia. Neotrop Prim 7(4), 120–121.

Silva-Júnior, J.S., Figueiredo-Ready, W.M.B., Ferrari, S.F., 2013. Taxonomy and geographic distribution of the Pitheciidae. In: Veiga, L., Barnett, A.A., Ferrari, S.F., Ma, N., (Eds.), Evolutionary biology and conservation of titis, sakis and uacaris. Cambridge University Press, Cambridge, pp. 31–42.

Silva, F.E., Lemos, L.P., Ravetta, A.L., Röhe, F., Sampaio, R., Franco, C.L.P., Santos, P.M.R.S., Santana, M.I., Valsecchi, J.A., Endo, W., Haugaasen, T., Peres, C.A., Boubli, J.P., 2021. On the geographic distribution of the bald uakaris (*Cacajao calvus* ssp.) in Brazilian Amazonia, Primate Conserv (35), 18pp.

Thomas, O., 1928. The Godman-Thomas Expedition to Peru. VII. The mammals of the Rio Ucayali. Ann Mag Nat Hist 2(10), 249–265.

Trancoso, R., Carneiro Filho, A., Tomasella, J., Schietti, J., Forsberg, B., Miller, R., 2009. Deforestation and conservation in major watersheds of the Brazilian Amazon. Environ Conserv 36(4), 277–288.

Trifinopoulos, J., Nguyen, L.T., von Haeseler, A., Minh, B.Q., 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acid Res 44, W232–W235.

Valencia, L.M., Martins, A., Ortiz, E.M., Di Fiore, A., 2018. A RAD-sequencing approach to genome-wide marker discovery, genotyping, and phylogenetic inference in a diverse radiation of primates. PloS One 13(8), e0201254.

Vermeer, J., Tello-Alvarado, J.C., Villacis del Castillo, J.T., Bóveda-Penalba, A.J., 2013. A new population of red uakaris (*Cacajao calvus* spp.) in the mountains of north-eastern Peru. Neotrop Prim 20, 12–17.

Vieira, T., Oliveira, M., Queiroz, H., 2008. Novas informações sobre a distribuição de *Cacajao calvus* na Reserva de Desenvolvimento Sustentável Mamirauá. Uakari 4(2), 41–51.

Wang, K., Lenstra, J.A., Liu, L., Hu, Q., Ma, T., Qiu, Q., Liu, J., 2018. Incomplete lineage sorting rather than hybridization explains the inconsistent phylogeny of the wisent. Commun Biol 1(1), 1–9.

Xie, W., Lewis, P.O., Fan, Y., Kuo, L., Chen, M.H., 2011. Improving marginal likelihood estimation for Bayesian phylogenetic model selection. Syst Biol 60(2), 150–60.

Figure legends

Fig. 1. Maximum likelihood tree retrieved from the cytochrome *b* dataset. Numbers refer to bootstrap values of the main nodes.

Fig. 2. Maximum likelihood tree retrieved from the ddRAD concatenated matrix of loci using the reference assembly method with the minimum samples per locus set to 24 (~50%). The coloured bars delimit two lineages of white uakaris – *C. calvus* (light grey) and *Cacajao* sp. (yellow) – and three lineages of red uakaris – *C. rubicundus* (brown), *C. ucayalii* (red), and *C. novaesi* (orange).

Fig. 3. ddRAD species tree retrieved from Tetrad analysis with 100 non-parametric bootstrap replicates. The coloured bars represent two lineages of white uakaris – *C. calvus* (light grey) and *Cacajao* sp. (yellow) – and three lineages of red uakaris – *C. rubicundus* (brown), *C. ucayalii* (red), and *C. novaesi* (orange). The main lineages were defined with 100% of bootstrap support, except by *C. ucayalii* (red bar), which received a support of 62%.

Fig. 4. ddRAD nuclear time-calibrated phylogeny for *Cacajao*. Nodes with mean divergence times received full support (PP=1.00). Node bars indicate the 95% highest posterior density (HPD) (See Table 2). The coloured bars indicate the following lineages: *C. calvus* (light grey bar), *Cacajao* sp. (yellow bar), *C. rubicundus* (brown bar), *C. ucayalii* (red bar), and *C. novaesi* (orange bar).

Fig. 5. The five species of bald uakaris. A – *Cacajao amuna*. B – *Cacajao calvus*. C – *Cacajao novaesi*. D – *Cacajao rubicundus*. E – *Cacajao ucayalii*. Drawing by Stephen Nash, used with permission.

Fig. 6. *Brachyurus calvus* (=*Cacajao calvus*) specimens from the Paris National Museum of Natural History. A -Holotype: MNHN-ZM-MO-1847-1667a, male. B - MNHN-ZM-MO-1847-1667b, female; and C – MNHN-ZM-MO-1847-1667c, unknown sex. Specimens B and C were collected by Castelnau and Deville and assessed by I. Geoffroy Saint-Hilaire

(1952) to provide more details of the first bald uakari species. Photographs by Dr. Cecile Callou.

Fig. 7. The geographic distribution of *Cacajao* taxa (sensu Hershkovitz, 1987; Boubli et al., 2008).

Fig. 8. Lectotype of *Brachyurus rubicundus* (=*Cacajao rubicundus*), an adult male stored in the Paris National Museum of Natural History (Catalogue number MNHN-ZM-2005-898), collected in the Village de Saint-Paul, Brazil (= São Paulo de Olivença, Brazil). Photographs by Dr. Cecile Callou.

Fig. 9. Dorsal and ventral views of voucher specimens of *Cacajao amuna* sp. n. from the rios Tarauacá and Pauini stored in the Mamirauá Institute for Sustainable Development (IDSM) and National Institute of Amazonian Research (INPA). A) The holotype, adult male IDSM03676; B) Adult male INPA7276; C) Adult female INPA7280; D) Adult female IDSM03668; E) Adult female IDSM03674; F) Subadult female IDSM03671.

Fig. 10. The patterns of pelage colouration in *C. amuna* sp. n. (top row) and *C. calvus* (bottom row).

Table legends

Table 1. Loci and SNP recovering, parsimony-informative sites, and overall bootstrap support of the Maximum Likelihood analysis according to each parameter setting and assembly method.

Table 2. Estimated divergence times inferred from the cytochrome *b* and ddRADseq datasets for *Cacajao*. N/A = Not Applicable are the clades without resolution in the cytochrome *b* tree.

Supplementary material legends

Table S1. Samples used in the molecular analyses and their origin. Collection codes refers to the following zoological collections: Museu Paraense Emílio Goeldi (MPEG), Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Instituto Nacional de Pesquisas da Amazônia (INPA), Museu de Zoologia da Universidade de São Paulo (MUZUSP), Field Museum of Natural History (FMNH), Museum of Vertebrate Zoology at UC-Berkeley (MVZ), Universidade Federal do Pará (UFPA), Universidade Federal do Amazonas - Laboratório de Evolução e Genética Animal (CTGAM).

Table S2. The Marginal Maximum Likelihood Estimation (MLE) for each model and the Bayes factor (BF) calculated as 2*(lnLSplit – lnLMerge).

Figure S1. Consensus tree of the de-novo assembly using the minimum samples per locus parameter as 10 (~20% of the samples) and the cluster threshold as 0.90.

Figure S2. Consensus tree of the de-novo assembly using the minimum samples per locus parameter as 24 (~50% of the samples) and the cluster threshold as 0.90.

Figure S3. Consensus tree of the de-novo assembly using the minimum samples per locus parameter as 36 (~75% of the samples) and the cluster threshold as 0.90.

Figure S4. Consensus tree of the de-novo assembly using the minimum samples per locus parameter as 10 (~20% of the samples) and the cluster threshold as 0.85.

Figure S5. Consensus tree of the de-novo assembly using the minimum samples per locus parameter as 24 (~50% of the samples) and the cluster threshold as 0.85.

Figure S6. Consensus tree of the de-novo assembly using the minimum samples per locus parameter as 36 (~75% of the samples) and the cluster threshold as 0.85.

Figure S7. Consensus tree of the reference assembly using the minimum samples per locus parameter as 10 (~20% of the samples).

Figure S8. Consensus tree of the reference assembly using the minimum samples per locus parameter as 24 (~50% of the samples).

Figure S9. Consensus tree of the reference assembly using the minimum samples per locus parameter as 24 (~75% of the samples).

Figure S10 – Cytochrome b time-calibrated phylogeny for *Cacajao*. Nodes with mean divergence times received full support (PP=1.00). Node bars indicate the 95% highest posterior density (HPD) (See Table 2).

Figure S11. Dorsal and ventral views of adult males of *Cacajao calvus* from Mamirauá SDR series stored in the Museum of Zoology of the University of São Paulo (MUZUSP) and National Museum of Rio de Janeiro (MNRJ). A) MUZUSP 17535, B) MNRJ 1706, C) MNRJ 1705.

Figure S12. Dorsal and ventral views of adult females of *Cacajao calvus* from Mamirauá SDR series stored in the Museum of Zoology of the University of São Paulo (MUZUSP) and National Museum of Rio de Janeiro (MNRJ). A) MUZUSP 17537; B) MNRJ 2447; C) MNRJ 2452.

Figure S13. Dorsal and ventral views of voucher specimens of *Cacajao calvus* from the right bank of Rio Jutaí stored in the Mamirauá Institute for Sustainable Development. A) Adult male IDSM00787; B) Adult male IDSM00040; C) Subadult male IDSM00786; D) Subadult female IDSM00784.

Figure S14. Dorsal and ventral views of voucher specimens of *Cacajao rubicundus* from nearby the type locality – opposite to São Paulo de Olivença, várzea forests from Jacurapá channel – stored in the Mamirauá Institute for Sustainable Development. A) Adult male IDSM03665; B) Adult female IDSM03666.

Figure S15. Dorsal and ventral views of voucher specimens of *Cacajao rubicundus* from the left bank of Rio Jutaí stored in the Mamirauá Institute for Sustainable Development. A) Adult male IDSM00082; B) Adult female IDSM00083.

Figure S16. Dorsal view of voucher specimens of *Cacajao rubicundus* from Auati-Paraná channel, north bank of Rio Solimões stored in the Emílio Goeldi Museum (MPEG). A) Adult male MPEG17552; B) Adult female MPEG17553.

Figure S17. Dorsal view of *Cacajao ucayalii* from Rio Javari Mirim stored in the Field Museum of Natural History (FMNH). Adult males: A) FMNH 88821; B) FMNH 88822; C) FMNH 88824. Adult females: D) FMNH 88816; E) FMNH 88817; F) FMNH 88819.

Figure S18. Dorsal and ventral view of voucher specimens of *Cacajao ucayalii* from Amazon River, opposite the mouth of Rio Napo, stored in the Emílio Goeldi Museum (MPEG). A) Immature male MPEG 468; B) Adult male MPEG049; C) Adult male MPEG511.

Figure S19. Dorsal view of voucher specimens of *Cacajao novaesi* from Rio Eiru stored in the Museum of Zoology of the University of São Paulo (MUZUSP) and in the Mamirauá Institute for Sustainable Development. Adult males: A) MUZUSP 5496; B) MUZUSP 4339; C) MUZUSP 4333; D) IDSM03672. Adult females: E) MUZUSP 4331; F) MUZUSP 19359; G) MUZUSP 4149; H) IDSM03670.

Appendix I - Scientific Collections

Appendix II - Synonymy

Table 1. Loci and SNP recovering, parsimony-informative sites, and overall bootstrap support of the Maximum Likelihood analysis according to each parameter setting and assembly method.

Cluster threshold	Minimum samples per locus	SNPs Matrix Size	Missing sites (%)	Sequence Matrix Size	Missing sites (%)	Loci	Parsimony informative sites (IQTree)	Mean Bootstrap Support
0.90	10	55415	51.18	1943103	51.20	7915	13625	86,95
0.90	24	28323	36.15	881375	34.07	3589	7608	88,75
0.90	36	6708	20.64	195662	18.13	798	2198	84,00
0.85	10	54183	51.66	1903051	51.51	7751	13408	87,70
0.85	24	27206	36.40	851707	34.29	3468	7328	88,27
0.85	36	6317	20.69	186323	18.23	760	2059	83,02
na	10	62780	31.04	2392150	34.88	9732	19126	90,55
na	24	45352	18.26	1540356	18.31	6251	14793	89,91
na	36	32553	10.11	1080448	9.74	4382	11104	89,32

Table 2. Estimated divergence times inferred from the cytochrome *b* and ddRADseq datasets for *Cacajao*. N/A = Not Applicable are the clades without resolution in the cytochrome *b* tree.

Clade or Split	Cytochrome *b* dataset			ddRAD dataset		
	Mean Age (Mya)	Lower 95 % HPD	Upper 95 % HPD	Mean Age (Mya)	Lower 95 % HPD	Upper 95 % HPD
Pitheciinae vs. Callicebinae	17.18	14.01	22.48	17.01	13.98	22.03
Pithecia vs. *Chiropotes* + *Cacajao*	9.73	6.26	14.09	10.12	6.37	14.49
Chiropotes vs. *Cacajao*	5.74	3.34	8.45	5.1	2.91	7.68
Black-headed vs. Bald uakaris	2.38	1.3	3.58	1.13	0.67	1.72
Red bald uakaris (*C. rubicundus* + *C. ucayalii* + *C. novaesi*) vs. White bald uakaris (*C. calvus* + *C. amuna*)	0.91	0.5	1.42	0.46	0.29	0.7
North bank of Rio Negro (*C. hosomi* + *C. ayresi*) vs. South bank of Rio Negro (*C. melanocephalus)*	0.99	0.5	1.56	0.48	0.27	0.78
C. rubicundus + *C. ucayalii* vs. *C. novaesi*	N/A	N/A	N/A	0.31	0.18	0.44
C. calvus vs. *C. amuna*	N/A	N/A	N/A	0.31	0.20	0.43
C. rubicundus vs. *C. ucayalii*	N/A	N/A	N/A	0.26	0.16	0.38
C. hosomi vs. *C. ayresi*	0.17	0.07	0.31	0.20	0.11	0.29

Fig. 1.

Click here to access/download;Figure;Cytb_tree.jpg

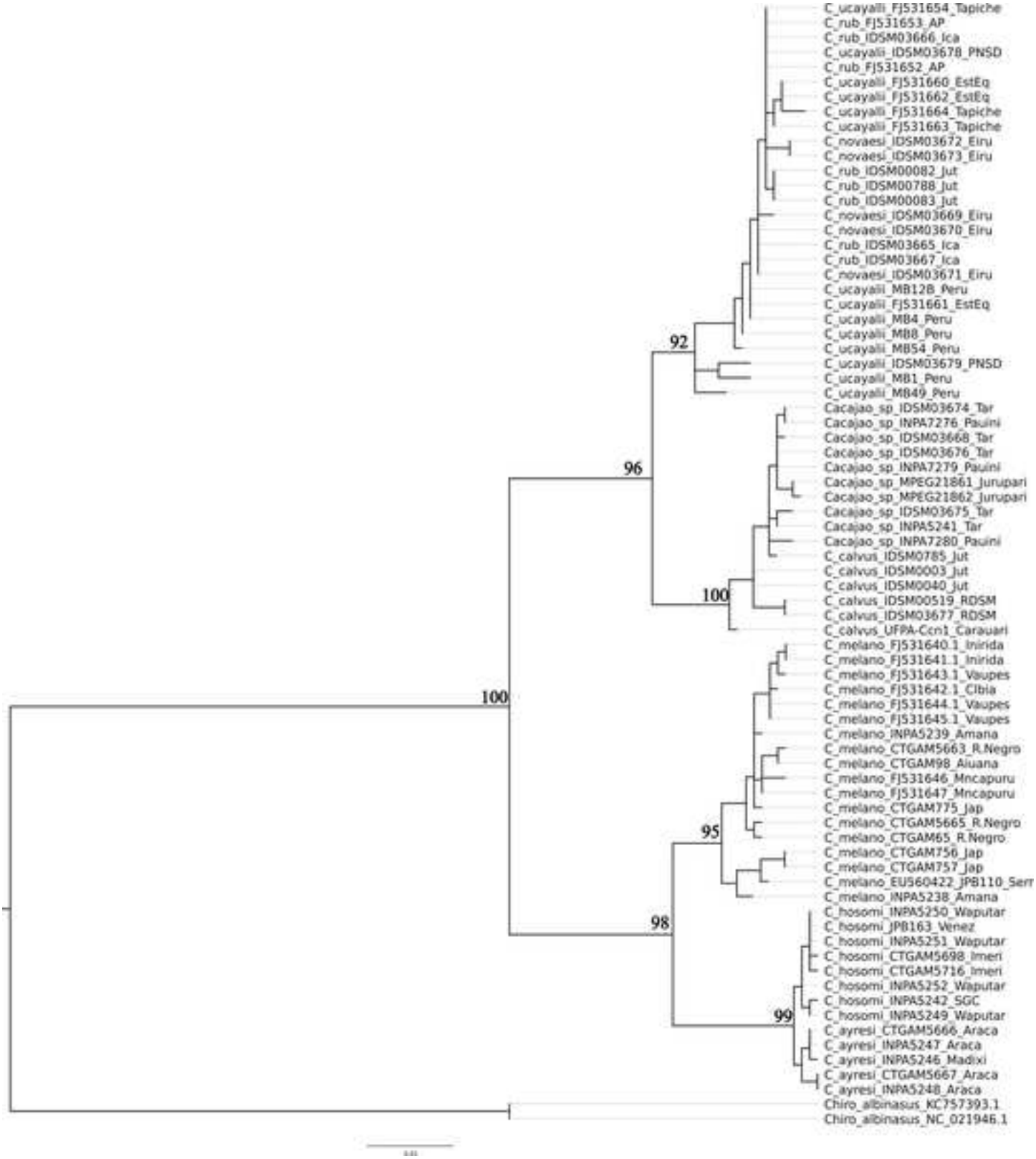


Fig. 2.

Click here to access/download;Figure;ddRAD_tree.jpg

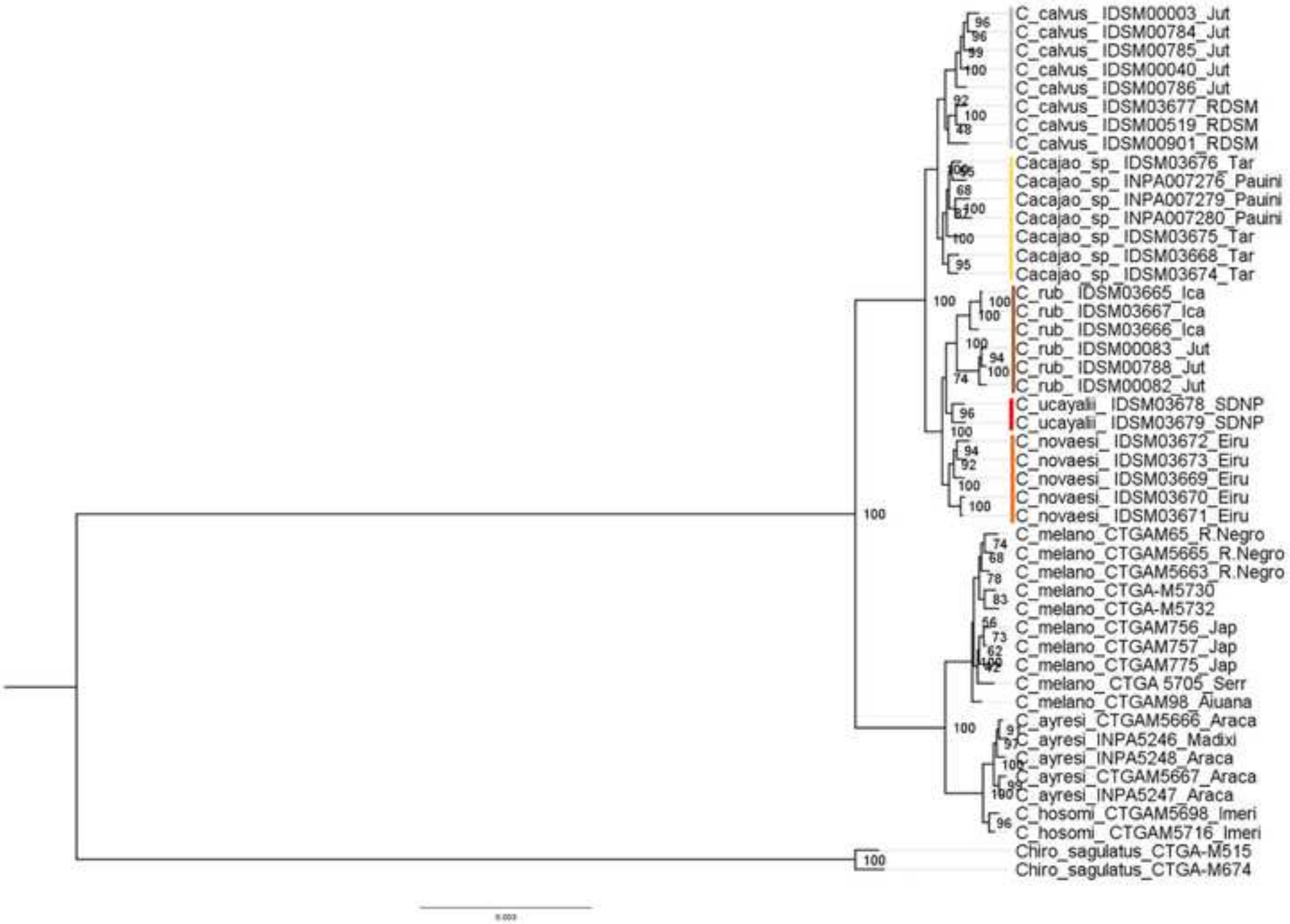


Fig. 3.

Click here to access/download;Figure;Species_tree.png

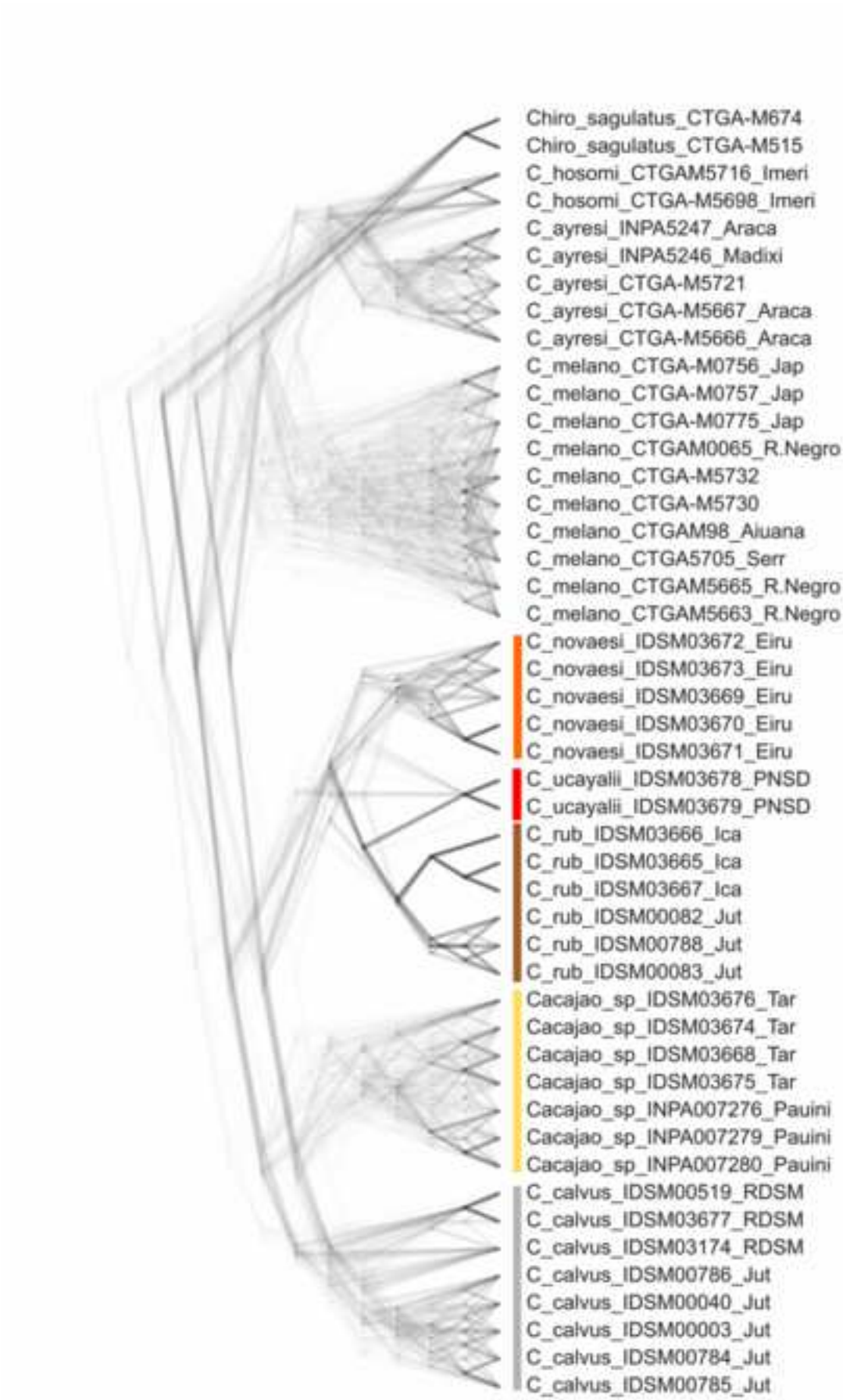


Fig. 4.

Click here to access/download;Figure;time_tree.jpg

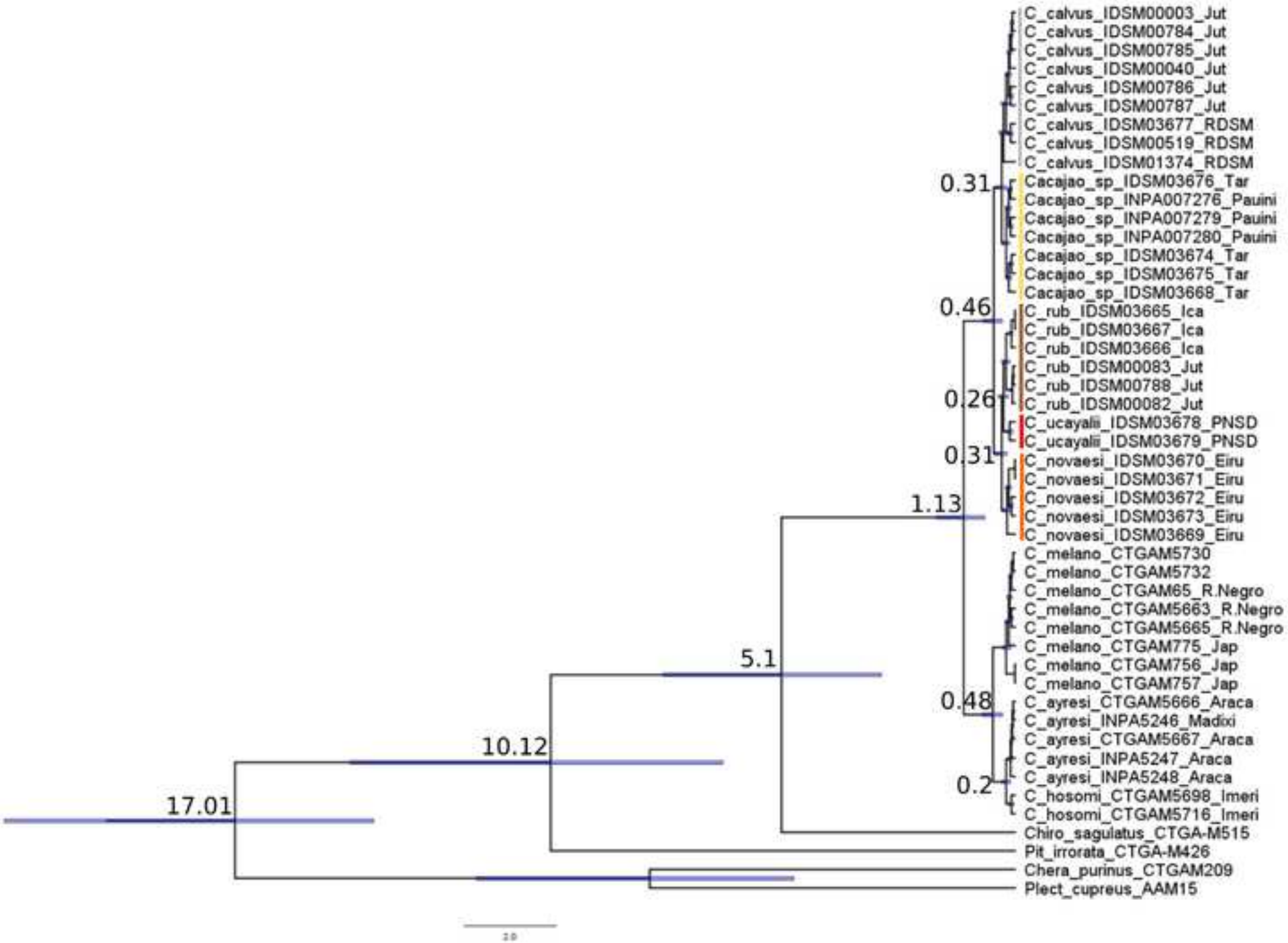


Fig. 5

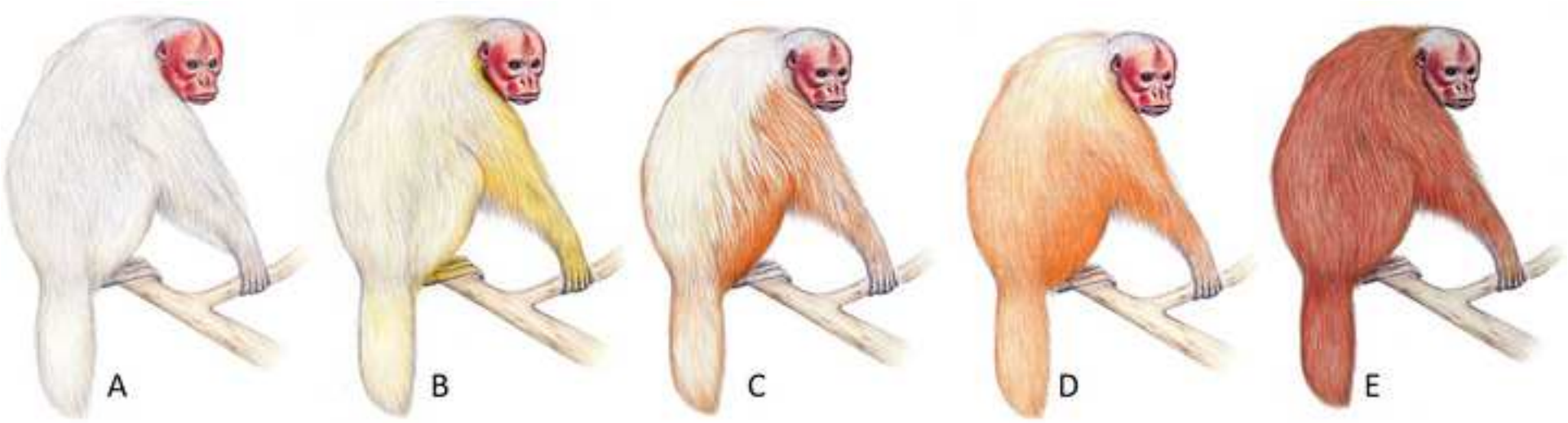


Fig. 6

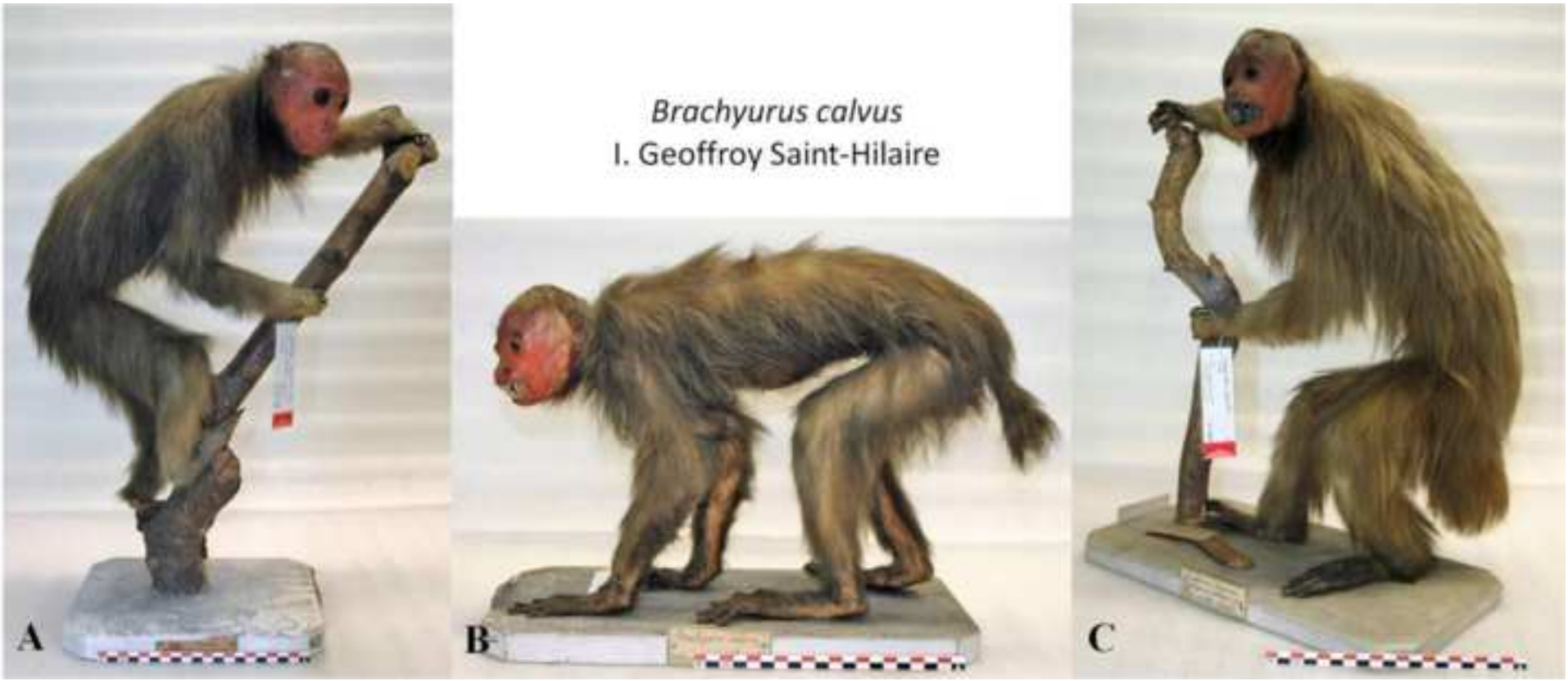


Fig. 7

Click here to access/download;Figure;Map.jpg

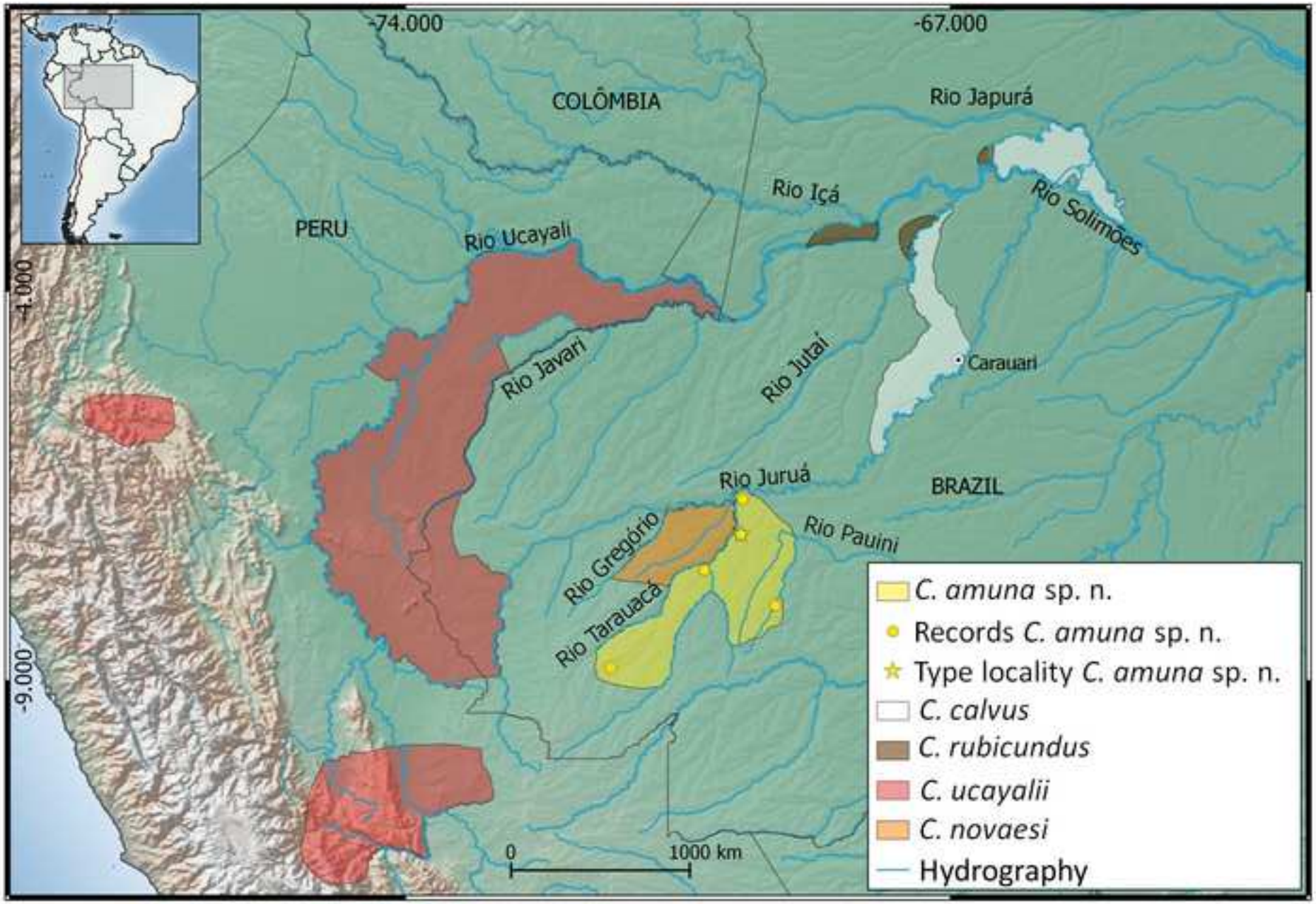


Fig. 8

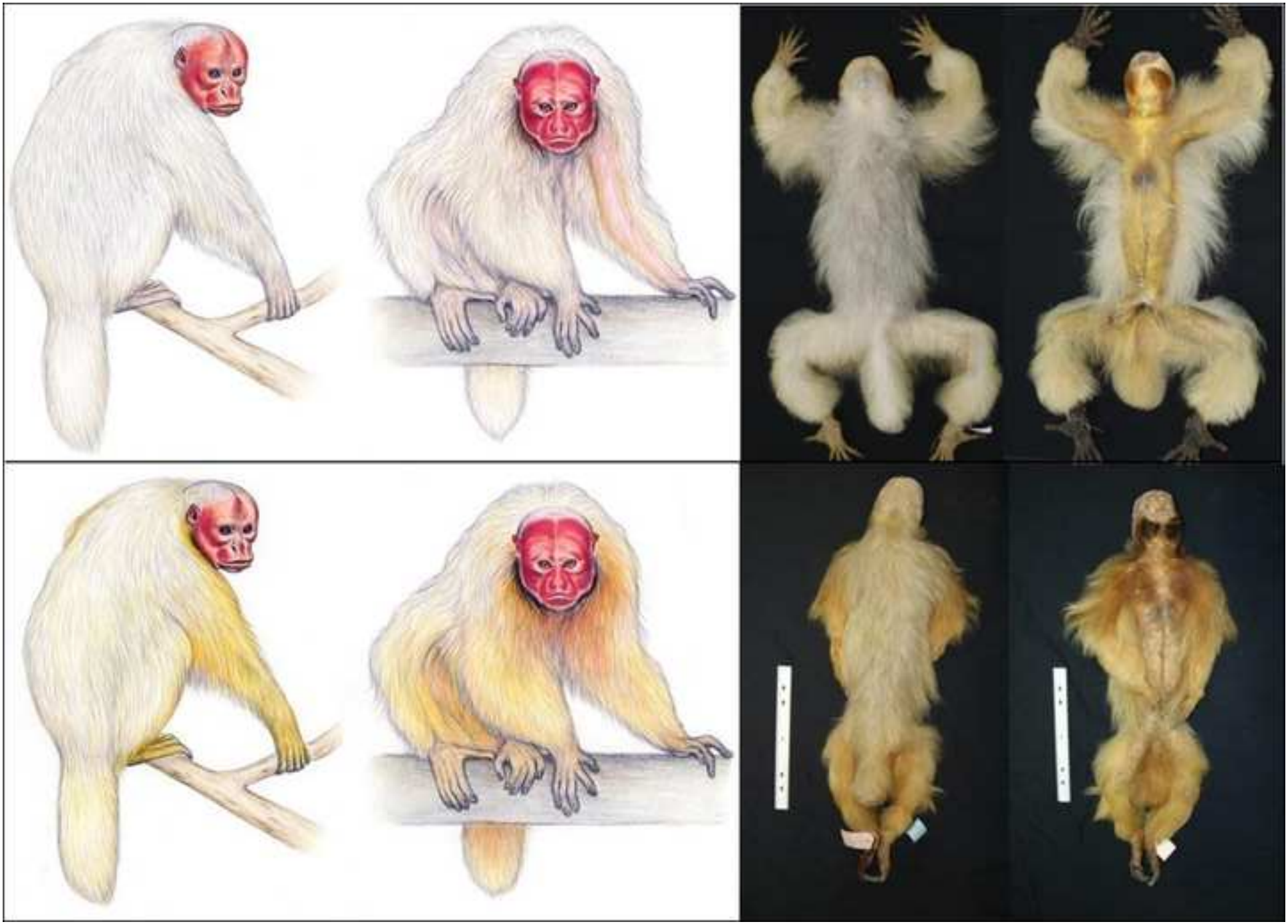
Click here to access/download;Figure;C. rubicundus.jpg

Fig. 9

Click here to access/download;Figure;C. amuna.jpg

Fig. 10

Click here to access/download;Figure;White_uakaris.jpg



CRediT authorship contribution statement

Felipe Ennes Silva: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **João Valsecchi do Amaral**: Conceptualization, Resources, Funding acquisition. **Christian Roos**: Conceptualization, Methodology, Resources, Writing – review & editing. **Mark Bowler**: Conceptualization, Methodology, Resources, Writing – review & editing. **Fabio Röhe**: Conceptualization, Investigation, Methodology, Resources. **Ricardo Sampaio**: Conceptualization, Investigation, Methodology, Resources, Funding acquisition. **Mareike Cora Janiak**: Methodology, Formal analysis, Writing – review & editing. **Fabrício Bertuol**: Methodology, Formal analysis. **Marcelo Ismar Santana**: Conceptualization, Investigation, Writing – review & editing. **José de Souza Silva Júnior**: Conceptualization, Resources. **Anthony B. Rylands**: Conceptualization, Validation, Writing – review & editing. **Chrysoula Gubili**: Methodology, Validation, Formal analysis, Resources, Writing – review & editing. **Tomas Hrbek**: Conceptualization, Methodology, Validation, Resources, Funding acquisition. **Allan D. McDevitt**: Methodology, Validation, Resources, Writing – review & editing. **Jean P. Boubli**: Conceptualization, Methodology, Validation, Formal analysis, Resources, Writing – review & editing, Visualization, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.