# THE TRUE IDENTITY AND CHARACTERISTICS OF *SIMIA ALBIFRONS* HUMBOLDT, 1812: DESCRIPTION OF NEOTYPE

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## Abstract

The historic holotypic description of Alexander von Humboldt for the primate *Simia albifrons* contains obvious errors which have created various taxonomic problems, since it has been impossible to compare descriptions of subspecies with an original holotype, which was never preserved. An historic taxonomic error was the recognition of *Cebus albifrons unicolor* as a different taxon from *Cebus albifrons albifrons*, which we correct in this paper by the recognition of *Cebus albifrons unicolor* as a synonym for *Cebus albifrons albifrons*. We describe *Cebus albifrons albifrons* for the first time, based on a neotype collected by us close to the type locality. Additionally, confusions about the type locality are discussed and clarified. Maypures is established as the correct type locality. General information on the geographic distribution and natural history of the species and subspecies is also provided.

**Key Words -** Primates, Cebidae, pale-fronted capuchin monkey, *Cebus albifrons albifrons, Simia albifrons* Humboldt, 1812 (type locality, characters, neotype), distribution, natural history.

## Resumen

La descripción holotípica e histórica de Alexander von Humboldt para el primate *Simia albifrons* contiene obvios errores que han creado varios problemas taxonómicos, dado que ha sido imposible comparar descripciones de subespecies con un holotipo original, el cual nunca se preservó. Un error histórico es el reconocimiento de *Cebus albifrons unicolor* como un taxon distinto de *Cebus albifrons albifrons,* el cual corregimos en este articulo por el reconocimiento de *Cebus albifrons unicolor* como sinónimo para *Cebus albifrons albifrons*. Describimos *Cebus albifrons albifrons* adecuadamente en este artículo por la primer vez, basado en un neotipo colectado por nosotros cerca a la localidad típica. Adicionalmente, se discute y se clarifica confusiones sobre la localidad típica, indicando Maypures como la localidad típica correcta. Adicionalmente, se presenta información general sobre la distribución geográfica y la historia natural de la especie y la subespecie nominal.

**Palabras Claves –** Primates, Cebidae, capucino de frente blanca, *Cebus albifrons albifrons, Simia albifrons* Humboldt, 1812 (localidad típica, caracteres, neotipo), distribución, historia natural.

## Introduction

During the years 1799-1804, on an extensive biological and geographical reconnaissance of Colombia, Venezuela, Ecuador, Peru, Cuba and Mexico, including the Orinoco and Magdalena rivers and the Colombian and Ecuadorian Andes, Baron Alexander von Humboldt and his companion Aimé Bonpland explored isolated and little-known regions of South America, studying geographical, climatological and geophysical aspects of the countryside, local customs, archaeology and the innumerable plants and animals native to those parts. As fruit of their explorations, many organisms were described for the first time in the thirty volumes which were published, complemented with numerous articles in scientific journals. This was surely the most extensive project of its kind ever published by one individual, given that Humboldt's friend Aimé Bonpland, except for the botanical part, contributed very little to the actual writing of the results of the voyage of these two scientists. Even with the botanical work, Bonpland prevaricated until Humboldt was forced to search for other collaborators such as Karl Sigesmund Kunth in the preparation of the seven volume *Nova genera et species plantarum* (Botting, 1973: 205) [1].

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† It is with great sadness that I inform the primatology and conservation community of the untimely death of Professor Jorge Ignacio Hernández-Camacho on September 15, 2001. Professor Hernández or "El Mono" was my friend, colleague and teacher for over 25 years. My knowledge of Colombian primatology and other vertebrate fauna was greatly enriched by having known and worked with him. His human qualities were considerable, and he will be missed by many. (TRD)

While in the Orinoco region, Humboldt (1812a: 305-363) discovered and described five new taxa of primates: *Aotus trivirgatus* [= *Simia trivirgata* Humboldt], *Callicebus torquatus lugens* [= *Simia lugens* Humboldt], *Lagothrix lagothricha* [= *Simia lagothricha* Humboldt], *Cacajao melanocephalus* [= *Simia melanocephala* Humboldt], *Chiropotes satanas chiropotes* [= *Simia chiropotes* Humboldt] and *Cebus albifrons* [= *Simia albifrons* Humboldt] [2].

This article discusses the characteristics of *Simia albifrons*, the species' taxonomy, its authentic type locality, the fixation of a neotype for the taxon, the status of *Cebus gracilis* Spix, 1823, the synonymy of *Cebus albifrons unicolor* with *Cebus albifrons albifrons*, the geographic distribution of *C. albifrons*, and aspects of the species' natural history.

## Methods

Color terminology for pelage descriptions follows Ridgway ("1912" = 1913). Measurements are expressed in millimeters, unless otherwise noted. Head and body length were obtained by subtracting the tail length from total length. For this article we examined all specimens of *Cebus albifrons albifrons* and *Cebus albifrons unicolor* deposited in Colombian collections (11 specimens), comparing them to our knowledge of Venezuelan and Brazilian specimens of *Cebus albifrons unicolor*. Additionally we reviewed specimens of other *Cebus albifrons* subspecies deposited in Colombia (21 specimens), and we cursorily examined specimens in the United States National Museum (68 specimens, including holotypes for *Cebus albifrons cesarae* and *Cebus albifrons pleei*). There are no specimens of Colombian *Cebus albifrons albifrons* (= *C. a. unicolor*) held in collections outside of Colombia except for a series collected from the right bank of the río Arauca and deposited in the Field Museum of Natural History (FMNH), Chicago.

The following acronyms are used:

AMNH - The American Museum of Natural History, New York, USA.
FMNH - Field Museum of Natural History, Chicago, USA.
ICN - Collection of mammals in the Instituto de Ciencias Naturales, Museo de Historia Natural, Facultad de Ciencias, Universidad Nacional de Colombia, Santa Fe de Bogotá, Colombia.
IVH - Instituto de Recursos Biológicos Alexander von Humboldt, Ministerio del Medio Ambiente, Villa de Leíva, Boyacá, Colombia.
MNHNP - Muséum National d'Histoire Naturelle, Paris, France.
UNIFEM - mammal collection, Unidad de Investigaciones Federic Medem, Instituto Nacional de Recursos Naturales y Protección al Medio Ambiente (INDERENA), Santa Fe de Bogotá, Colombia. This collection is now deposited in IVH.
USNM - Natural History Museum, Smithsonian Institution, Washington, DC, USA.

### *Simia albifrons* Humboldt, 1812

**The original description of *Simia albifrons*.** As von Humboldt and Bonpland entered the world of the "Upper Orinoco" [3] they began to see individuals of species of "Matchís" [4]. They were already acquainted with both *Cebus apella*, the "Sajou" [5], and the "saï" [6] from earlier collections. Humboldt named this new monkey *Simia albifrons*: "Face bluish gray with the exception of orbits and forehead, which are pure white. The contrast of these two colors distinguishes the "Ouavapavi", which I name *Simia albifrons*, from the "Saï" and from the ordinary "Sajou" (translation from the French) (Humboldt, 1812a: 324).

Humboldt (1812a: 324-325) described *Simia albifrons* as follows:

> "Le Matchi du Haut-Orénoque, que les Indiens Guarekens [7] appellent *Ouavapavi* a $0^{m}$,378 (14 pouces) de long du sommet de la tête à l'origine de la queue: il a la face gris-bleuâtre, à l'exception des orbites et du front qui sont d'un blanc pur. Le contraste de ces deux couleurs fait distinguer au premier abord l'*Ouavapavi*, que je désigne sous le nom de *Simia albifrons*, du Saï et du Sajou ordinaire. La tête est un ovale très-alongé. Le pelage du corps est grisâtre, plus clair vers la poitrine et le ventre, plus obscur vers les extrémités que son d'un brun-jaunâtre. Le sommet de la tête est d'un gris tirant sur le noir: une strie cendrée se prolonge longitudinalemente de la calotte par le milieu de front vers le nez: les sourcils sont de même d'un gris très-obscur. Les yeux son grands, bruns et très-vifs. Les oreilles ont un rebord et sont couvertes de poils. La queue est prenante, mais toute couverte de poils, et par conséquent sans callosité: elle est à peu près de la longueur de corps, cendrée par dessus, blanchâtre par dessous, et d'un brun-noir à l'extrémité. Les ongles son tous arrondis et très-peu convexes. Une strie d'un gris foncé obscur descend le long de dos.
> *SIMIA ALBIFRONS, imberbis, cauda prehensili, ex albo cinerascens, vertice nigro, facie coerulea, fronte et orbitis niveis, cruribus et brachiis fuscescentibus."*

Further on in the above publication, Humboldt lists *Simia albifrons* in his *Tableau Synoptique des Singes de l'Amérique* as follows:

> "19. *Simia albifrons, ex albo cinerascens, vertice nigro, facie caerulea, fronte et orbitis niveis, cruribus et brachiis fuscescentibus.*" (Humboldt, 1812b: 356).

**Type specimen and type locality.** Humboldt did not specifically designate a type specimen nor a type locality, although he added the following comment:

> "Les *Ouavapavis* sont très-laids, mais extrêmement doux, agiles et moins criards que les Singes pleureurs [*Cebus nigrivitattus*]. Ils habitent, par troupeaux, les forêts qui avoisinent les cataractes de l'Orénoque [8] et la mission de Santa Barbara [9]. Nous en avons trouvé un individu à Maypures [10] qui, tous

> les matins, saisissoit un cuchon sur lequel il resoit monté toute la journée en parcourant la savane qui environne les cabanes de Indiens [Maypures]. Nous l'avons même vu souvent sur le dos d'un chat qui avoit été élevé avec le Singe dans la maison du missionnaire, et qui souffroit patiemment les effets de la pétulance de l'*Ouavapavi*."(Humboldt, 1812a: 324–325).

The original description was based exclusively on a captive individual that Humboldt (1812a: 325) first reported he saw at Maipures, on the left bank of the río Orinoco, but added that he had observed wild individuals around the Mission of La Esmeralda (Estado Amazonas, Venezuela), on the upper río Orinoco (right bank) and in the forests on both sides of the Orinoco between La Esmeralda and Maipures. Later, Humboldt (1824a: 98-99, [1]) wrote in his *Relation Historique* of the journey to the río Orinoco where he had supposedly observed *Simia albifrons* in the Atures Mission [11], 50 km north of Maipures on the opposite side of the river, directly contradicting his original statement in Humboldt (1812a: 325).

This new account (Humboldt, 1824a: 98-99) [12] is entirely based on the original one, including the Latin diagnosis, but no mention of Maipures is made nor a clarifying explanation. Under such circumstances, von Humboldt certainly created a source of confusion twelve years after the original description was published, since there is no evidence of the presence of *Cebus albifrons* in the vicinity of Atures on the right bank (Venezuelan bank) of the Orinoco, where *Cebus nigrivittatus* occurs instead (see Bodini and Pérez-Hernández, 1987; Bodini, 1989) [13].

One of us (TRD) studied the distribution of *Cebus albifrons* and *Cebus apella* in the Maipures region and was not able to confirm the presence of *Cebus albifrons* in the inmediate location of Maipures, south of the río Tuparro (Defler, 1985). The site that Maipures formerly occupied is in an extensive natural savanna with isolated forest patches that contain some *Cebus apella* as well as *Alouatta seniculus* and *Aotus* sp. (perhaps *A. trivirgatus*)[14]. However, *C. albifrons* is common (and replaces *C. apella*) immediately 3 km north (on the northern bank of the lower río Tuparro) where there are nearby extensive gallery forests (Fig. 1).

As such, this argues against the possibility that the specimen upon which Humboldt based the original description of *Simia albifrons* was obtained at the Atures mission or any other locality in Venezuela and suggests that it was captured in the neighborhood of Maipures mission, Vichada, Colombia, where *Cebus albifrons* (as currently understood) is known to occur close by.

Possible doubts for the occurrence of *Cebus albifrons* on the Colombian bank of the río Orinoco that could eventually arise were definitively resolved with the findings of the above survey and of the additional collection of the species in the río Bita (Vita), further to the north of the survey area.

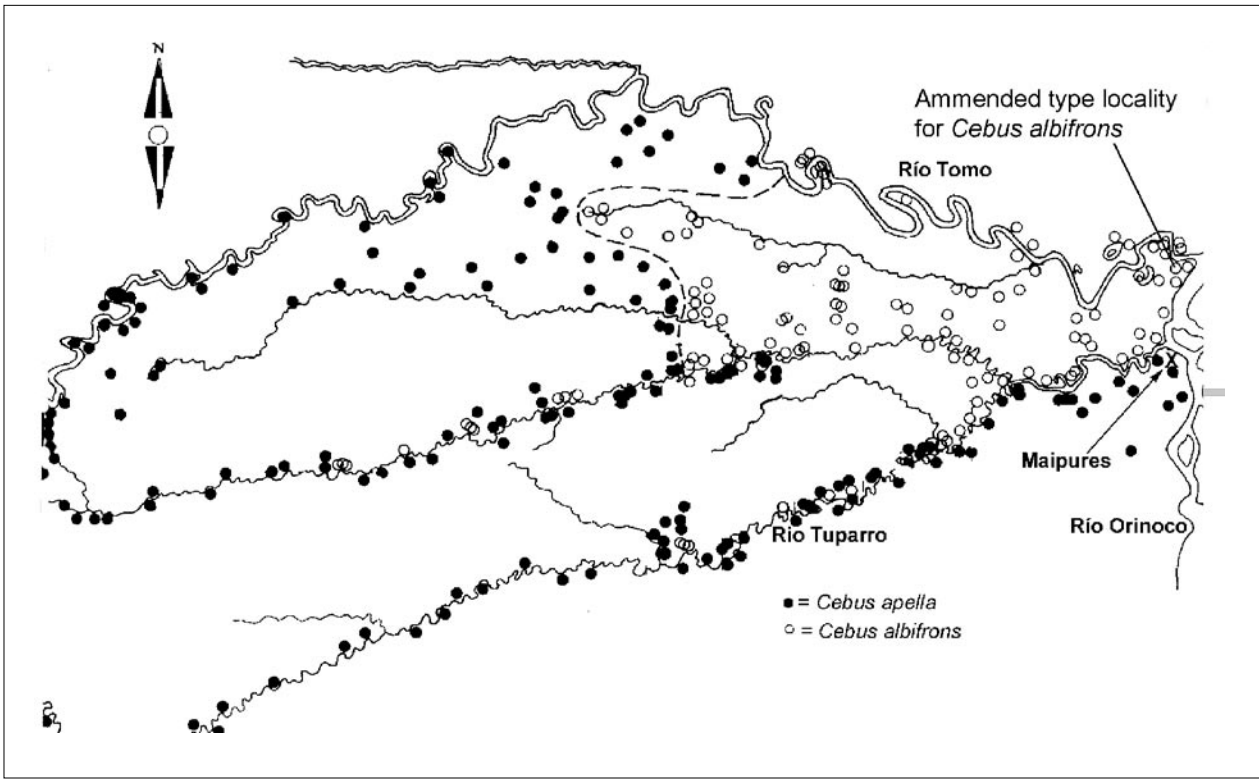


**Figure 1.** Map of Maipures region north to the río Tomo showing the distribution of *Cebus albifrons* and *Cebus apella*, and including the amended type locality for *Cebus albifrons* (based on Defler, 1985).

**Fixation of a neotype for *Simia albifrons*.** The fixation of a neotype is justified because: It is desirable to establish the neotype to secure nomenclatural stability; the holotype was not preserved; and it is convenient to clarify the type locality of the species and suppress any ambiguity that could lead to confusion or controversial interpretations.

**The identity and the proper characterization of *Simia albifrons* Humboldt**. There can be no doubt the original description of *Simia albifrons* was based upon the specimen kept in the mission at Maipures, since it was obviously handled in order to take accurate measurements of head and body length (taken from the crown). However, Humboldt did not publish a figure of it, neither did he record its sex or relative age, and unfortunately it was not preserved. The specimen was possibly a juvenile, since it rode about on the back of a pig, and piggy-back riding is typical of the young (when pigs or other species are available).

*Simia albifrons* must unquestionably be considered as belonging to the genus *Cebus* Erxleben, 1777, following É. Geoffroy Saint-Hilaire (1812) and the current usage of subsequent authors. The only species of non-tufted capuchin approaching the original description is undoubtedly *Cebus albifrons*, as interpreted by Hershkovitz (1949: 371). There are discrepancies in the original description of the coloration, as shown above, but there is no doubt that the chromatic pattern of the species is the same in the Department of Vichada population in Colombia as well as the Amazonas state population in Venezuela. There are some differences in the presence of eumelanin in the pelage, which can be interpreted as individual variation. The dark color of the hair of the tip of the tail described by von Humboldt (1812a: 325) is a color pattern that the authors have not detected in other individuals. This allows us to hypothesize that the dark tail tip was an individual variant and the general color of the "grayish" pelage may suggest that the holotype was a young animal in which the color was lighter than in adults, or that the captive animal had been exposed to so much sunlight that depigmentation (fading) had occurred and the yellowish-red tones had been lost. We have noticed that captive specimens, when exposed to too much sun tend to lose their natural color, such that tonalities become duller towards gray.

However, as previously noted, no type or syntype of this species was preserved. It has also been established here that the type locality is fairly clearly the former site of the Maipures mission, although only *Cebus apella* exists in the immediate vicinity of Maipures (south of the río Tuparro), as established by Defler (1985). The species of *Cebus* can be identified as *Cebus albifrons* due to the white color of the orbits and the forehead indicated by von Humboldt (1812a: 324-325) in the original description of *Simia albifrons*.

Hershkovitz (1949: 371) rightly indicated that the original description (and Latin diagnosis) of *Simia albifrons* "refers to a monkey with some characters that have never been found [observed] until now in any of the specimens [in other populations of the species]". Having now available topotypes of *Simia albifrons*, in addition to a considerable number of preserved and live specimens examined from most of the geographic range of the species, we fully agree with Hershkovitz' remarks.

The distinctive chromatic characters used by Humboldt to define *Simia albifrons* are:
—*Face bluish gray ("facie caerulea") except for the orbital regions and the forehead which are white* ("*niveis*"). Comments: The usual condition in this species for all specimens examined is a depigmented facial skin, including the forehead, instead of a pigmented facial skin, with unpigmented orbits and forehead. However, a certain grade of facial pigmentation as blotches of eumelanin over a light pinkish skin color has been observed in the populations of the río Matavén (s. Vichada) and in the río Apaporis (s. Vaupés) region (T. R. Defler, pers. obs.). It is conceivable that a general pale bluish gray color could appear in the facial skin (excluding the orbits and the forehead), due to small amounts of scattered eumelanin as an individual variation.
—*Eyebrows very dark gray* ("*gris très-obscur*"). Comment: Von Humboldt undoubtedly referred to the presence of very dark hairs ("*sourcils*") in the eyebrows, as in *Cebus albifrons*, and not to a dark superciliary stripe.
—*Crown gray tending to black* ("*vertice nigro*"), *anteriorly continued as a grayish narrow stripe* ("*strie cendrée*") *that descends towards the nose.* Comments: The basic contrasting dark design of the crown occurs in all the various subspecies of *Cebus albifrons*, but its color can change, varying from a medium brown to a dark brown (almost blackish), but never with gray tonalities. Possibly the dark gray almost black color might be due to some degree of bleaching due to excessive exposure to sunlight.
—*Underparts grayish* ("*grisâtre*"; "*albocinerascens*" in the Latin diagnosis), *darker in the extremities* ("*cruribus et brachiis*") *which are yellowish brown* ("*fuscescentibus*") *with a darker middorsal stripe* ("*gris foncé obscur*"). Comments: The "*grisâtre*" coloration can be translated as "grayish" or "grayish brown" that would be closer to the tonalities present in the topotypes of *Simia albifrons* (in any case, not tending to ashy gray), and the middorsal stripe is not darker gray. The color of the extremities, including hands and feet, can be interpreted as yellowish brown, not duller ("*fuscescentibus*").
—*Tail above ashy gray* ("*cendrée*"), *whitish underneath* ("*blanchâtre par dessous*") *blackish brown* ("*brun-noir*") *towards the tip.* Comments: In the topotypes of *Simia albifrons* the tail is more richly colored and not strikingly darker (brownish black) towards the tip. In none of the specimens of *Cebus albifrons* does the tail tip approach a very dark brown color; on the contrary, a tendency towards a lighter tail tip is frequent.
—*Breast and belly whitish.* Comment: The breast and belly are brighter colored in the topotypes. Some individuals, however, have a very white ventrum.

To summarize: the coloration described for the middorsal area, the proximal dorsal surface of the tail and the sides of

the body in the type specimen of *Simia albifrons* is rather duller and decidedly more grayish than in the topotypes, and with a unique feature; the brownish black tip of the tail. These discrepancies cannot be entirely attributed to a process of bleaching or fading due to excessive exposure to sunlight. It is well-known that black (eumelanin) hairs bleach or fade to reddish brown instead of deep gray due to excessive exposure to sunlight, unlike the case here. Under these circumstances we can conclude that either the type of *Simia albifrons* was abnormally colored, or the published chromatic description was affected by inaccuracies in the terminology used, or the description was at least in part subject to defective perception of the tonalities involved. Otherwise we should expect a close similarity or even identity in chromatic characters between the type and the topotypes.

A strict interpretation of the original description of *Simia albifrons* leads us to the conclusion that *Cebus albifrons* cannot be satisfactorily identifiable and should be replaced by *Cebus unicolor* Von Spix, 1823. The obvious alternative is to preserve the use of *Simia albifrons,* based on the characters of the topotypes now available and the acceptance of Maipures as the type locality for this binomen. As this procedure essentially is in accordance with the taxonomic and nomenclatural treatment of Hershkovitz (1949) that has generally been followed since then, and in order to consolidate nomenclatural stability, in this article we fix one of the specimens collected by us a few kilometers north of Maipures as a neotype for *Simia albifrons.*

There are no arguments to suggest that the populations subsequently observed by us in the wild nearby are not of the same population as the holotype. Since the species is polytypic with a wide geographic range, the taxonomic identity needs to be consolidated according to Article 75 of the International Code of Zoological Nomenclature. It is important to designate a neotype for the species with the object of establishing a nomenclature and taxonomic base for the species and genus.

***Cebus albifrons albifrons* (Humboldt, 1812)**

## Synonymic history

*Simia albifrons* Humboldt, 1812a: (original description and Latin diagnosis).
- Humboldt, 1812b: 563 (Latin diagnosis; "Habite les environs de Maypures et d'Atures, sur les bords de l'Orénoque").
- Humboldt, 1824a: 98-99, footnote 1 (citation in the text of the footnote; Latin diagnosis; characters; recorded among the primates seen "à la mission de Atures", not Maypures!).

*Cebus albifrons* É. Geoffroy Saint-Hilaire, 1812: 111 (nomenclatorial transference to *Cebus*).
- Goeldi & Hagmann, 1904: 48 (including *Cebus chrysopus* and *C. gracilis* in synonymy).
- Elliot, 1913: 88 (*partim*; synonymy including *C. gracilis* and *C. leucocephalus* as synonyms; characters).
- Cruz Lima, 1945: 149 (characters based on the original description; erroneous citation of type locality as "Santa Barbara Mission, cataracts of río Orinoco").
- Napier, P. 1976: (*partim*; catalogue of specimens in the British Museum [Natural History]).
- Handley, 1976: 42 (*partim*; Río Mavaca, 108 km SSE of Esmeralda, 140 km and Tamacama, Río Orinoco, 135 m., T[erritorio] F[ederal] Amazonas [= Estado Amazonas], Venezuela).
- Groves & Pulido, 1982: 228 (erroneous citation of type locality as "Venezuela, Orinoco River").
- Cuervo-Díaz, Hernández-Camacho & Cadena [Gómez], 1986: (*partim*; actual distribution and synonymy with *C. a. unicolor*).
- Bodini & Pérez-Hernández, 1987: (*partim*; distribuction in Venezuela).
- Bodini, 1989: 105–106 (distribution of species in Venezuela).
- Groves, 1993: 259 (erroneous citation of type locality as "Venezuela, Orinoco River").
- Uribe Hurtado & Ortiz Von Halle, 1993: fig. s.n. (Caño Limón, Department of Arauca, Colombia).
- Alberico, Cadena, Hernández-Camacho & Muñoz-Saba, 2000: 58 (Department of Putumayo and Vichada, Colombia).

*C[ebus] c[apucinus] gracilis* Pusch, 1941: 192 (*partim*: including records from the Amazonian region as well as *"Cebus gracilis* Hellsternig" described by Lönnb*erg* [1939]).

*C[ebus] c[apucinus] versicolor* Pusch, 1941: 193 (*partim*: including the records from the Amazonian region and "*Cebus flavus* Geoffroy", non *Cebus versicolor* Pucheran, 1945 [=*Cebus albifrons versicolor*]).

*C[ebus] cuscinus cuscinus* Pusch, 1941: 196 (*partim*: "*Cebus gracilis* dunkelstirning" described by Lönnberg [1939] and a female from Chicosa, eastern Perú; non *Cebus flavescens cuscinus* Thomas, 1901 [=*Cebus albifrons cuscinus*]).

*Cebus flavus* É. Geoffroy Saint-Hilaire, 1812: 111 (original description; holotype MNHNP, no. 562 (type specimen catalogue) and 458 (general collection); unsexed adult (?) collected by Alexandre Rodrigues Ferreira in Brazil) [15].

*Cebus unicolor* Spix, 1823: 7, pl. 4 (original description; holotype: Zoologische Staatssamlung München, adult male, skin and skull, collect by the expedition of Jean Baptist Ritter von Spix and Carl Friedrich von Martius in Brazil). Type locality: forests of Río Tefé, near its junction with the Amazon River near Ega [= Tefé], Amazonas, Brazil).

*Cebus gracilis* Spix, 1823:8, pl. 5 (original description; holotype: Zoologische Staatssamlung, München, skin and skull collected by the expedition of Johann Baptist Ritter von Spix and Carl Friedrich von Martius in Brazil; type locality: Tefé, mouth of Tefé River on the Amazon River, Amazonas,

Brazil; distribution forests of the Solimões from "la ville de rio Negro [=Manaus, Amazonas, Brazil] vers le Peru").
- Cruz Lima, 1945: 149-150 (pl. xxiv (characters based on the original description).

"*Sajou à pieds dorée au chrysope"* F. Cuvier, 1825: 2pp., pl. (description of a living menagerie specimen from "l'Amerique septentrionale").

*Cebus chrysopus* Lesson, 1827: 55 (based on the original description of the "sajou a pieds dorées de F. Cuvier in 1825; type not preserved).

"Machín (*nuova vapari*; [*sic.* = *ouavapavi* ?]: Codazzi, 1841: 156 ("tiene pelo gris y cara azulada con las órbitas y la frente como la nieve; Venezuela, without definite locality).

*S[imia] albifrons*: Vergara & Velasco, 1902: 190 (cited in the text; Colombia without precise locality; common name "machín").

*C[ebus] albifrons* Pittier & Tate, 1932: 278 ("Raudales del Orinoco", Venezuela).

*Cebus albifrons* [*albifrons*] Defler, 1979a: 475, 487, 488 (ecological aspects of topotypical population).
- Defler, 1979b, 1979: 491, 501 (behavioral aspects of topotypic population).

*Cebus unicolor unicolor*: Cruz Lima, 1945:150 (characters based on the original description).

*Cebus gracilis* Spix (*vel C. albifrons* Humboldt ?): Lönnberg, 1939: 17 *et seq. q.* (Codajáz, rio Solimões, Amazonas, Brazil; Irocanga, rio Tapajós, Pará, Brazil; Jaburú, rio Purús, Amazonas; Igarapé do Gordão, rio Juruá, Amazonas; João Pessoa, rio Juruá, Amazonas; Lago Grande, rio Juruá, Amazonas, Brazil; San Antônio, rio Eirú, Amazonas, Brazil).

*Cebus albifrons albifrons*: Hershkovitz, 1949: 370–372, fig. 54 (taxonomic revision; characters transcribed from the original description).
- Cabrera, 1958: 160 (type locality: "selvas próximas a los raudales del Orinoco"; distribution "alto Orinoco").
- Hill, 1960: 450–451 (characters translated from the original description; type locality and distribution after Humboldt [1812b]).
- Pusch, 1941 (*partim*: original description only?, as synonyms included belonging to the *Cebus apella* group and geographical distribution is given as "Rio de Janeiro and São Paulo", Brazil.
- Rylands, Mittermeier & Rodríguez-Luna, 1995: 120, 128, 137, 13 (Colombia; IUCN classification LR = Lower Risk).

*C[ebus] a[lbifrons] albifrons*: Hernández-Camacho & Cooper, 1976: 58, fig. 10 (characters taken from Humboldt compared with topotypical population; "eastern Vichada").
- Hernández-Camacho & Defler, 1989: 91–92 (basic characteristics; conservation status).
- Rylands, Schneider, Langguth, Mittermeier, Groves & Rodríguez-Luna, 2000:68 (tab. 5) 76, 78–79 (*C. a. unicolor* included as a junior synonym of *C. a. albifrons*).

*C[ebus] a[lbifrons] unicolor*: Hernández-Camacho & Cooper, 1976: 58, fig. 10 (possible junior synonym of *C. a. albifrons*; range in Colombia: Vaupés and south of the río Caquetá (except for the interfluvium between the río Guamués and río San Miguel or Sucumbíos, Department of Putumayo, inhabited by *C. a. yuracus*, Hershkovitz, 1949).

*C[ebus] a[lbifrons]* [subsp.]: Hernández-Camacho & Cooper, 1976: 58, fig. 10 ("pale and dull colored population" in western Arauca, northern Boyacá and southwestern and southeastern Norte de Santander; somewhat similar to *C. a. adustus* Hershkovitz, 1949).

*Cebus albifrons unicolor*: Hershkovitz, 1949: 372–375, fig. 54 (revision; characters; Marimonda, río Orinoco, Amazonas, Venezuela; Solano, río Cassiquiare, Amazonas, Venezuela; Yavanari, rio Negro, Amazonas, Brazil; Casas Pereira Igarapé, rio Negro, Amazonas, Brazil; Puerto Victoria, río Pachitea, Huanuco, Perú; Tingo María, Huanuco, Perú; no locality, Perú).
- Cabrera, 1958: 161–162 (distribution, including southeastern Colombia).
- Hill, 1960: 451–453 (characters essentially based on Hershkovitz [1949]; distribution).
- Rylands, Mittermeier & Rodríguez-Luna, 1995:120, 128, 135, 137, Perú and Venezuela; IUCN classification LR = Lower Risk).

**Neotype.** Young adult male in fresh pelage, skin and skull (Table 1), UNIFEM (Unidad Investigativa Federico Medem - INDERENA) now deposited in the collection of the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IVH), Villa de Leyva, Boyacá, Colombia, No. 2844, collected by T. R. Defler on 30 January, 1978 (Figs. 2 & 3).

**Amended type locality.** About 10 km north of Maypures, 200 m north of the Cerro Rocoso, El Tuparro National Park, Department of Vichada, Colombia (5°20'N, 67°45'W) (Fig. 1).

**Topotypes.** Young adult male, skin and skull, UNIFEM, No. 2843 by T. R. Defler on 30 January, 1978. Adult female, skin and skull, UNIFEM, No. 2839 by T. R. Defler on 30 January, 1978, all specimens collected from the same group as the neotype and now deposited in the collection of the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IVH), Villa de Leyva, Boyacá, Colombia.

**Coloration of neotype.** Alae nasi with dark brown pigmentation with sparse light *Cartridge Buff* hairs over

Table 1. *Cebus albifrons albifrons:* Measurements in millimeters of neotype and topotype.

| Collection number | Head & body | Tail | Hind foot | Ear | Greatest skull length | Condylobasal length | Zygomatic width | Palatilar length | Palatal length | Occipital -nasal length |
|---|---|---|---|---|---|---|---|---|---|---|
| 2844 | 385 | 430 | 90 | 40 | 91.1 | 68.8 | 57.6 | 24.3 | 31.8 | 84.4 |
| 2843 | 365 | 425 | 83 | 30 | 87.0 | 67.0 | 55.1 | 26.6 | 27.6 | 78.8 |
| 2839 | 338 | 412 | 85 | 30 | 84.1 | 60.2 | 55.2 | 22.0 | 24.6 | 76.1 |

| Collection number | Biorbital breadth | Postorbital Constriction | Braincase Width | Braincase Length | Mastoid Breadth | Basion Length | Basilar Length | Interorbital Breadth | Rostral Breadth | Bulla Length |
|---|---|---|---|---|---|---|---|---|---|---|
| 2844 | 51.4 | 41.4 | 50.2 | 70.1 | 47.8 | 63.3 | 64.0 | 4.8 | 24.5 | 19.5 |
| 2843 | 47.4 | 40.2 | 49.0 | 67.0 | 46.2 | 61.9 | 59.3 | 4.7 | 20.4 | 19.3 |
| 2839 | 48.9 | 39.1 | 49.6 | 67.7 | 44.3 | 54.4 | 50.0 | 3.7 | 21.0 | 19.2 |

| Collection number | Condilobasilar | $I^1$-$M^3$ | C-$M^3$ | $PM^1$-$PM^3$ | $I^{1-1}$ | $I^{2-2}$ | $M^1$-$M^1$ | C-$M_1$ | Mandible Length | |
|---|---|---|---|---|---|---|---|---|---|---|
| 2844 | 62.0 | 35.0 | 27.2 | 22.0 | 9.3 | 14.4 | 28.6 | 29. | 55.6 | |
| 2843 | 65.3 | 32.2 | 26.5 | 20.3 | -- | 15.0 | 26.8 | 28.2 | 59.9 | |
| 2839 | 53.0 | 30.3 | 23.3 | 19.6 | 8.4 | 13.6 | 27.3 | 26.4 | 53.7 | |

| Collection number | Coronoidal Height (min.) | Coronoidal Height (plano) | Weight (g) |
|---|---|---|---|
| 2844 | 27.8 | 30.5 | 2650 |
| 2843 | 26.4 | 27.9 | 2156 |
| 2839 | 26.0 | 27.1 | 2228 |

frontal region; dark blackish narrow line extends from nose up, crossing supra-orbital band and ending in superciliary hairs *Hair Brown* above center of forehead; supra-orbital blackish band above and lateral to the orbits with *Hair Brown* superciliary hairs; crown *Sepia* with bases of hairs more pallid than *Cartridge Brown*; lightest parts of ears close to *Cartridge Buff* but slightly lighter and yellower; back at mid-dorsal line *Snuff Brown* x *Pale Pinkish Buff*; sides lighter with less brown, lateral fringe slightly lighter than *Cinnamon Buff*; no whitish patch in front of shoulders; scapular region and shoulder *Pinkish Buff* x *Pale Pinkish Buff*; chest and belly *Ochraceous Buff* x *Ochraceous Orange*; forearm and thighs *Ochraceous Buff* x *Zinc Orange* contrasting with dark lining of back; wrists and ankles *Mikado Brown* but fingers with much less hair and contrasting with blackish skin; feet dorsally same color as thighs; diminished hair on digits shows blackish skin. Palmar and plantar surfaces including digits dull pink; tail bicolored with broad dorsal stripe *Saccardo Umber* with grizzled effect due to *Ochraceous Buff* hair tips throughout to tail tip; distal dorsal part of tail slightly lighter *Xanthine Orange* x *Zinc Orange*, with tail ventrum lighter than *Cartridge Buff*.

**Coloration of topotypes.** UNIFEM No. 2843; similar to the neotype but crown *Warm Sepia* with bases of hairs more pallid than *Cartridge Buff*; back at middorsal line *Buckthorn Brown*, anterior parts darkening to *Russet* over hips; sides lighter with less brown; forearm and thighs *Ocraceous Buff* x *Ochraceous Orange*; tail bicolored with broad dorsal stripe *Saccardo Umber* proximal to the body, lightening considerably over middle and distal parts to *Cinnamon Buff*. UNIFEM No. 2839; essentially similar to the neotype except for the color of the chest and belly which appear slightly brighter *Ochraceous Buff* x *Zinc Orange*.

**Comparison with *Cebus albifrons unicolor*.** Spix (1823: 7) described *Cebus unicolor* (= *Cebus gracilis* Spix, 1823: 8) from near the mouth of Tefé (formerly Ega), Amazonas, Brazil. His animal has been identified throughout a wide area of the middle and upper Amazon, including Colombia, Peru and Bolivia, as well as part of the upper Orinoco in southern Venezuela. Elliot (1913) included *Cebus unicolor* Spix as a synonym of *Cebus albifrons*, and treated *C. gracilis* as a distinct species. *Cebus gracilis* Spix was based on an adult female collected in the same locality as the type male of *C. unicolor* Spix, and the alleged differences between those nominal species fall in the individual and sexual dichromatism known in other populations of *C. albifrons*. As a result, Hershkovitz (1949: 372-373) regarded *unicolor* and *gracilis* as synonyms. The characters, as published by Hershkovitz (1949:


**Figure 2.** Color plate of neotype of *Cebus albifrons albifrons* Humboldt, 1812. By Margarita Nieto.

372-375), based on the original description of material and upon color plates of *unicolor*, are as follows: "Most uniformly brightly colored race of *albifrons*, Cap Snuff Brown to Bister, frontal region buffy to ochraceous; back Ochraceous-Buff to Ochraceous-Orange or Tawny more or less lined with dark brown; sides with less brown, lateral fringe Ochraceous-Buff to Ochraceous-Orange; forearm and foreleg Ochraceous-Buff to Tawny contrasting with dark lining of black; hairs of belly Ochraceous-Buff to Ochraceous-Orange, of chest like belly or white; whitish patch obsolete on front of shoulder."

***Cebus albifrons unicolor* is a synonym of *Cebus albifrons albifrons*.** Hershkovitz' (1949: 372-374) description of *Cebus albifrons unicolor* seems very similar to the population north of Maipures. One of us (JHC) examined specimens from southern Venezuela (Amazonas State) in the AMNH and the USNM also ascribed to *C. a. unicolor*, and found them to be virtually identical to *C. a. albifrons* as represented by its neotype. Specimens examined by us from the area between the riós Amazonas and Vichada (Amazonia, Colombia) usually ascribed to *C. a. unicolor* also seem indistinguishable from *C. a. albifrons* as described here. This leads us to the conclusion that *unicolor* is a synonym of *albifrons*.

**Other specimens examined.** UNIFEM 3022 adult male, Miritί-Paraná, Amazonas, Colombia; UNIFEM 3023 adult male, Miritί-Paraná, Amazonas, Colombia; UNIFEM 3029 juvenile male, Miritί-Paraná, Amazonas, Colombia; UNIFEM 2843 adult female; UNIFEM (uncatalogued) adult female, Caño Brava, río Cotuhé, Amazonas, Colombia; UNIFEM 0206, río Arauca, 65 km upriver from the town of Arauca, Colombia; UNIFEM 1523, San José de Ocuné ("30 miles" [45 km] to the south), Vichada, Colombia; UNIFEM 2667, río Peneya, Caquetá, Colombia.

**Distribution of *Cebus albifrons albifrons* as previously recognized.** The geographic range of this apparently isolated population of *C. a. albifrons* is mapped in Defler (1985) and is reproduced in Figure 1. The range includes the lower ríos Tuparro (left bank), Tuparrito, Tomo, Bita and Meta (right bank) in Vichada. On the upper parts of these rivers *C. albifrons* is replaced by *C. apella* (Hernández Camacho and Cooper, 1976; Defler, 1985). Another apparently isolated population is found in Arauca, Colombia; though the limits of this population are not clearly defined and possibly reach into western Venezuela (Apure State). Because of the lack of specimens in many areas, it is not possible to define securely the limits of *C. a. albifrons* outside of Colombia.

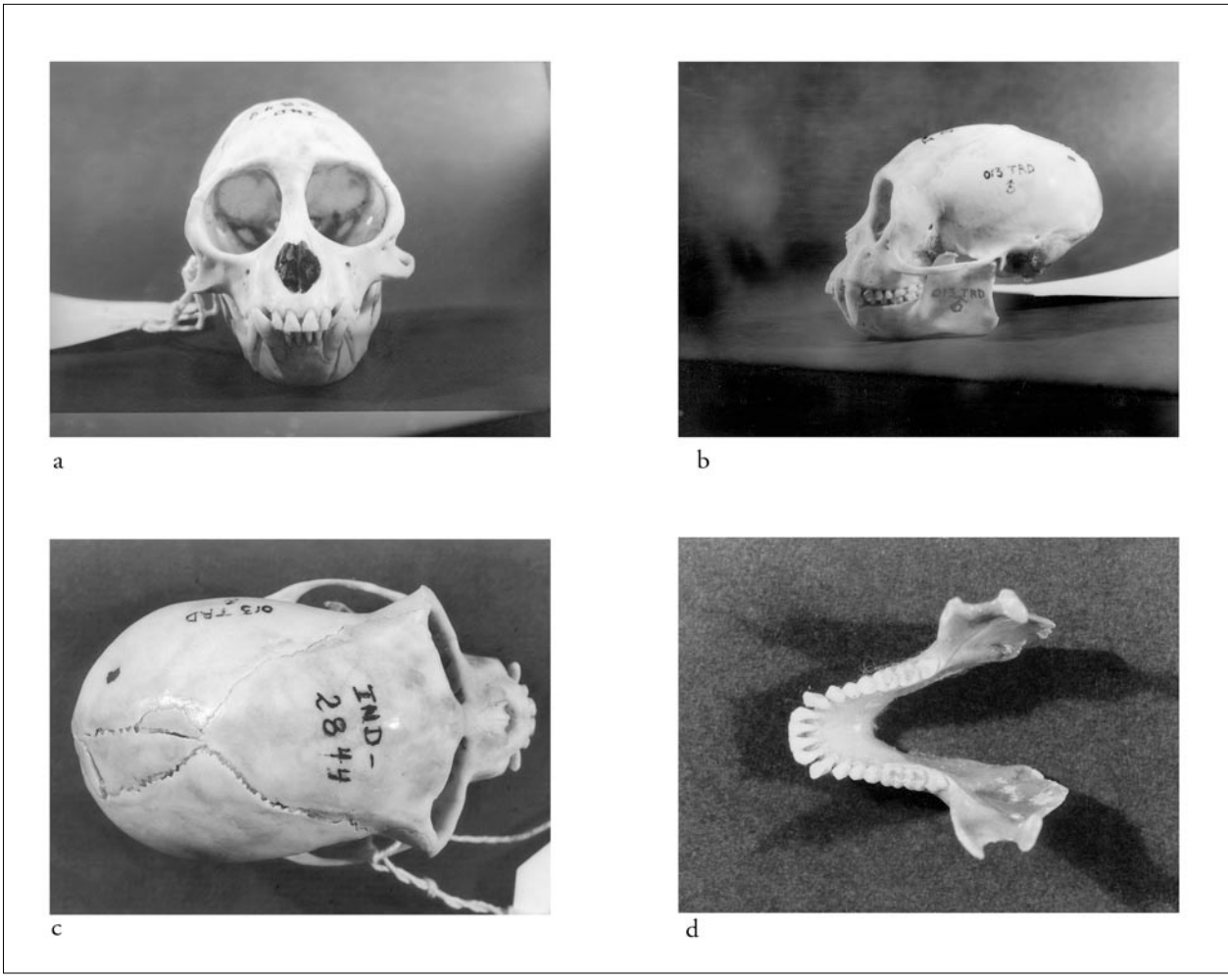


**Figure 3.** Photograph of skull of neotype: a. Frontal view; b. Lateral view; c. Dorsal view; d. Inferior mandible.

**Expanded geographic range of *Cebus albifrons albifrons*.** Accepting *C. a. unicolor* as a synonym for *C. a. albifrons* extends the range to a huge area in the upper Amazon of Brazil, Colombia, Peru and Bolivia from the right bank of the Marañon River in the south, but also crossing the Amazon and including much of southeast Colombia and southern Venezuela (Fig. 4). A gazetteer of Colombian specimens and observations by TRD of *Cebus albifrons* and *C. a. albifrons* is given in Defler (in press). Limits for the species are still imperfectly known.

**Variation.** Some specimens have an admixture more yellowish than reddish on the arms and legs. One male specimen collected at Puerto Rastrojo in the Miritií-Paraná of the Colombian Amazon weighed 4135 g (INDERENA No. 3033) and another male from the same locality (INDERENA No. 3022) weighed 3490 g. These specimens have a darker, buffy-brown forehead as compared to the neotype and topotypes, and the dorsal brown is darker. In general these animals also have a more reddish cast than the neotype, while the neotype and topotypes are lighter and more buffy. A juvenile male specimen from the same site (INDERENA No. 3029) is much lighter than INDERENA No. 3033 and 3022, approximating the neotype in most respects but without the grizzled effect on the tail. A young male specimen (INDERENA No. 0206) from Arauca Department (Colombia) was the lightest specimen examined. Fur on the forehead and shoulders is almost white, while the ventrum of the belly and tail is very light buff. Another young specimen (INDERENA No 1794) of about the same age as INDERENA No. 0206 is similar in coloration, although the forehead is slightly darker buff and the dorsal coloring over the hips is a darker brown. The most anomalous specimen examined is INDERENA No. 2667 from the río Peneya, Caquetá department (Colombia). This poorly preserved skin is the darkest brown of all specimens examined although, like the other specimens, the darker crown does contrast with the brown back, and there are tonalities of chestnut red on the arms, legs and hips. The forehead of this specimen is a buffy-gray.

**Natural history and ecology of *Cebus albifrons*.** The natural history and ecology of this species has been studied


**Figure 4.** The geographic distribution of *Cebus albifrons*. The revised range of *C. a. albifrons* is indicated in dark grey. Sources: Aquino and Encarnación (1994), Bodini and Pérez-Hernández (1987), Encarnación *et al.* (1990), Hernández-Camacho and Cooper (1976), Hershkovitz (1949), Linares (1998).

in Colombia by Defler (1979a, 1979b, 1980, 1985) and in two sites in Peru by Soini (1983) and Terborgh (1983). Currently it is being studied in Trinidad by K. A. Phillips (1998; in prog.). This review of the species' natural history and ecology has been summarized from Defler (in press).

**Habitat preferences.** Defler (1985) showed that in the region of the type locality the species prefers a slightly more xeromorphic habitat than does *C. apella*. Such habitats include *Bactris* palm forests in seasonally dry riverbeds, and rocky forests around the bases of inselbergs. *C. albifrons* commonly crosses open tracts of rock and savanna from forest patch to forest patch. In most areas studied it is also commonly found in flooded forest, which *C. apella* tends to avoid. Flooded forests, then, tend to be part of the habitat used by *C. albifrons* where *C. apella* is sympatric on *terra firme.* On the upper río Cahuinarí, Amazonas, Colombia, there is a population of *C. albifrons* in forests growing on white sand, where *C. apella* is apparently absent. However, both species are sympatric in very low numbers in white-sand caatinga forest on the upper Guacayasi Creek in Guainía, Colombia. *C. albifrons* is widely syntopic with *C. apella.*

**Group size.** In eastern Vichada, Colombia, near the type locality, *C. a. albifrons* is found in very large groups of around 35 animals. A study group at this site contained 10 adult females, four adult males, three subadult males, five juvenile females, four juvenile males, one unclassified juvenile, four infant females, three infant males and one unclassified infant (Defler, 1979a). To the south, in the closed rainforest of Peru, *C. albifrons* groups are smaller, with an average of about eight members at one site, and 15 per group at another (Soini, 1986; Terborgh, 1983), perhaps because of competition from *C. apella*. The groups are multi-male and multi-female. In Vichada the sex ratio is 2.5 females per male.

*C. albifrons* has been seen to form large transient congregations when seasonal conditions of food availability are favorable. Hernández-Camacho and Cooper (1976: 59) reported an instance in August, 1956 where a congregation of several hundred monkeys was observed in a few hectares along a newly opened road through a secondary forest association of "guamo" or "guamera" (*Inga* sp.) with a rather dense 8–12 m canopy connected to two areas of primary forest. This was on the road from El Centro to Quebrada Lísama (Antioquia). There were also, along a distance of about 300 m on both sides of the road, considerable numbers of parrots (*Amazona amazonica*, *A. ochrocephala* and *A. farinosa*).

**Density.** At the type locality, the species is present in gallery and isolated small forests surrounding local inselbergs, at densities of about 30 individuals/km² (Defler, 1979a). Where *C. albifrons* is sympatric with *C. apella* it often occurs in greatly reduced densities, making its detection difficult. North of the lower río Apaporis in the Colombian Department of Vaupés around the Estación Biológica Caparú (1º5'33"S, 69º30'48"W), for example, the density is around 1 or less individuals/km² (Defler, unpublished data). In the Pacaya-Samiria National Park in Peru, densities are 4.2–6.2 individuals/km² (Soini, 1986) and in the Manu National Park, Peru, densities are much higher, around 35 individuals/km² (Terborgh, 1983).

**Home range.** A group home range of more than 150 ha was calculated in the Manu study (Terborgh, 1983), while at least 120 ha were used in the study area in northern Colombia (Defler, 1979a).

**Day range.** An average day range of 1820 m was calculated in the Manu study (Terborgh, 1983).

**Activity (time) budget.** Terborgh (1983) estimated a time budget for the species as follows: 18% resting, 21% traveling, 22% feeding on plant material, and 38% foraging and feeding on insect material (total feeding time 61%).

**Diet.** The diet of *C. albifrons* includes fruits, small invertebrates, their eggs and larvae, small mammals, lizards, and bird's eggs. They especially like to eat ant and wasp larvae, and are adept at robbing beehives for honey. Defler (1979a) observed them hunting frogs (*Hyla* sp.) in the interstices of the large fleshy plant *Phenakospermum guianense*, which forms a water reservoir between the leaf bases and the main stem. This water reserve shelters frogs, and is also used by the monkeys for drinking when other sources are scarce. The monkeys obtain these resources by biting out chunks of the plant tissues that cover the water reservoir.

During the dry season, when there are few fruits, they spend more than half the day on the forest floor, searching for live prey. Terborgh (1983) observed *C. albifrons* exploiting 73 species of plants from 33 families, of which by far the most important was Moraceae, with 17 species included in the diet. Near the type locality, the palm species *Maximiliana (Attalea) regia* is a key species, being used more than any other plant resource. The palm nuts provide a nutritious food during the dry season when little other plant food is available. At the Manu National Park, *Astrocaryum* and *Scheelea* palms are the most important plants for these monkeys. Ants, ant eggs and small beetles are searched for incessantly in rolled leaves and around the leaf bases of palms.

**Reproductive behavior.** Copulation by the dominant male lasts several minutes with the male mounting the female, grasping her hind legs with his hind feet. The gestation time is unknown, but it is probably similar to *Cebus apella,* at about 160 days.

**Infant development.** Usually one infant is born. During the first 1–2 days it tries various positions for holding onto the mother, including clasping the tail, hind leg, and arms, until it discovers a position over the neck and shoulders that is typical for the species. After some weeks of riding

oriented crossways over the shoulders the baby is able to ride lengthwise on her back as do most primate babies. All members of the group are interested in the newborn infant and wish to be close to it. The genitals are of particular interest to the other females in the group. As the infant matures, various group members try to entice the baby onto them for carrying, and, eventually, the mother allows others, including adults and young monkeys, males and females, to help carry the baby. Even the alpha male carries infants.

**Social behavior.** Males are very friendly to each other and seem very unassertive. Nevertheless, the sub-alpha males are constantly aware of the position and activities of the alpha. Males are very aggressive towards males of neighboring groups, and aggressive chasing bouts occur where two territories overlap. All members of the group, and especially the alpha male, break branches over predators or over perceived danger, causing noisy crashes through the forest vegetation and much excitement. Near the type locality, boas (*Boa constrictor*) and tayras (*Eira barbara*) have been observed stalking the capuchins, but these predators were usually detected and then ignored. *Cebus albifrons* showed great fear towards a raptor, *Spizaetus ornatus*, which attempted to attack them, causing all troop members to drop to the ground and flee.

White-fronted capuchins are sometimes associated with squirrel monkeys, *Saimiri sciureus*, brown capuchins, *Cebus apella*, and woolly monkeys, *Lagothrix lagothricha*. They can feed in trees occupied by red howling monkeys, *Alouatta seniculus* (Defler, 1979a). The general condition of sympatry between *C. albifrons* and *C. apella* is evidenced by the observation of both capuchin monkeys in 15 inventories of mammal species carried out in Amazonia (Voss and Emmons, 1996: 103–114).

**Ecological niche.** Terborgh (1983) studied the strategy of this species in closed-canopy forest when in sympatry with *C. apella*. *Cebus albifrons* travels widely, searching for patchy resources such as *Ficus*, which it exploits exhaustively before moving on. It seems probable that the strategy they use in the gallery forests near the type locality may be different, however, from the food-rich study site on the río Manu in southern Peru.

## Acknowledgements

We are particularly grateful to the personnel of the collections at the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (Fernando Gast and Yaneth Muñoz), Instituto de Ciencias Naturales of the Colombian National University (Alberto Cadena), and the US National Museum (Richard Thorington III) for permission to work with material in these collections. We are grateful also to the American Museum of Natural History for permission to work there. We thank INDERENA, the American Peace Corps, the Universidad Nacional de Colombia, Conservation International, and the Margot Marsh Biodiversity Foundation for support for various facets of this work, and Margarita Nieto for the color plate in this article.

## Notes

[1] Von Humboldt and Bonpland's itinerary has often been described with the claim that they arrived for the first time on Colombian territory on 2 April, 1801 at Puerto del Zapote in the Bahía of Cispata, Córdova (formerly Córdoba) on the Caribbean coast of Colombia, The two scientists stayed there for three days before continuing their journey to Cartagena de Indias. However, the first day that von Humboldt arrived on Colombian territory was not the above date, but rather on 13 April, 1800, when they landed on the Playa de Guaripo or Guaripa (*ca.* 5º56'N, 67º30'W), above the Raudal de San Borja, Vichada (Dugand,1954: 210).

[2] Hershkovitz (1987a: 54) published the following pertinent remarks on von Humboldt's activities during his trip to tropical America: "Monkeys, however, absorbed more of Humboldt's attention than other animals. He carried with him a number of live simians captured in the upper Río Orinoco region for shipment to the Jardin des Plantes in Paris, via the Antillean island of Guadeloupe. The newly discovered bearded saki (*Chiropotes satanas chiropotes* Humboldt [= *Simia chiropotes* von Humboldt, 1812]…) died before transshipment, but its skin was saved and arrived in Paris. The type specimen of a red howler *Simia ursina* Humboldt (= *Alouatta seniculus arctoides* Cabrera) survived the journey, whereas the first-known douroucouli or night monkey (*Aotus trivirgatus* Humboldt [*Simia trivirgata* von Humboldt, 1812] succumbed in Guadeloupe". No mention is made by Hershkovitz of *Cebus albifrons*, but in any case the type of this species did not arrive in Paris, nor was it preserved.

[3] The "upper Orinoco" of von Humboldt is in effect the Orinoco above the rapids of Rabipelado, San Borja and Atures, which impede navigation and separate the upper from the lower Orinoco.

[4] "Matchi" is a name derived from *machín* of Quechua origin. "Machín" is a common name for *Cebus capucinus* in the Departments of Bolívar and Sucre in northern Colombia, and is also used in Colombia's middle Magdalena valley for *Cebus albifrons*, suggesting the early influence of Jesuit missionaries in disseminating Quechua names in various parts of Colombia.

[5] "Sajou" or "sapajou" (written with French phonetics) is of Tupi-Guaraní origin, attesting to the influence of early Portuguese explorers, who brought the pidgin Geral into the Amazonian region, undoubtedly disseminated by early Jesuit missionaries.

[6] "Saï" is a vernacular name of Tupi-Guarani origin that was used by von Humboldt (1812a; 1812b; 1824a) for

the weeper capuchin monkey, identified by him as *Simia capucina* [non *Simia capucina* Linnaeus (1758)].

[7] The *Warekena* Indians ("Guarekens" of Humboldt) belong to the *Maipure* linguistic group of the *Amazonian Arawak* family. They currently inhabit the banks of the Cassiquiare Canal (Estado Amazonas, Venezuela), as well as the upper rio Negro, adjacent to the Colombian and Venezuelan borders (Estado Amazonas, Brazil) (Lizarralde, 1993). Ferreira (1974: 69–73) found what he called the "Uerequena" in 1785 on the rios Içana and Xiê, northwest Amazonas, Brazil.

[8] Humboldt alluded to both the Atures and Maypures rapids.

[9] Santa Bárbara is an extinct mission that was located at the mouth of the rio Ventuari on the right bank of the río Orinoco, Amazonas, Venezuela (Hershkovitz, 1949: 370).

[10] Maipures (5º20'N, 67º45'W) (from "maypuri" meaning tapir [*Tapirus terrestris*] in the Maipures language) was a site originally established on the left bank (i.e. the Colombian side) of the Orinoco alongside the Maipures rapids, as a Jesuit cattle ranch, which was converted into a Jesuit Mission in the early 1700s. The town was founded by Don José Solano at the time of the expedition of the boundaries in 1754. Dugand and Phelps (1945) describe some of its history. "Maipures" was the name given by the Jesuits to the rapids as well as to a tribe of extinct Indians who spoke an Arawakan language which has left some toponyms in the region: i.e., "Matavén" = "black river" (Matavén River or Creek); "Amanavén" = "crocodile river" (Brazo Amanavén associated with the lower río Guaviare, Colombia). According to Humboldt (1852: 235) the "Maipures" Indians called the Maipures rapids "Quittuna" and the Atures rapids "Mapara".

Von Humboldt and Bonpland arrived for the first time with Father Zea on the night of 18 April, 1800, and left on the afternoon of 31 April. On their return downstream they arrived at Maypures on 29 May and stayed until 31 May (Dugand, 1956: 315). At that time the village consisted of fewer than 60 people living in only 7–8 huts surrounding a small church built of palm logs, but the village had a population of about 600 inhabitants during the time of the Jesuits, including several white families (von Humboldt, 1852: 297, 306). The location has become well-known as a collecting site, since von Humboldt and Bonpland collected several new species of plants there as well as closely observing and describing (although erroneously, so therefore requiring us to establish a neotype) *Cebus albifrons* for the first time. The two scientists ascended the Cerro de Manimi (near the El Tuparro National Natural Park cabaña, near the mouth of the río Tuparro) various times during their stay, where they enjoyed the magnificent landscape of the Maypures rapids, and additionally collected plants on the Cerro, particularly the type collection of *Cyperus mainimi*.

Many new taxa of birds have also been collected at Maypures by Dugand, Cherrie, and others. Fortunately Maypures rapids, and the savanna where the village stood, along with the many granitic hills and huge boulders, are now protected in El Tuparro National Park (Colombia), which is gazetted as an International Biosphere Preserve.

[11] The Mission de San Juan Nepomuceno de los Atures was founded in 1748 by the Jesuit missionary Padre Francisco González.

[12] "Parmi les singes que nous vîmes à la mission d'Aturès, nous en trouvâmes une nouvelle espèce de la tribu des *Saïs* et de *Sajous,* que les Espagnols-Américaines appellent vulgairment *Machis*. C'est l'Ouavapaví à pelage gris et a face bleuâtre. Il a les orbites et la front blancs de neige; ce quí le distingue, au premier abord, du *Simia capucina*, du *Simia apella*, du *Simia trepida*, et des autres singes pleureurs si confusément decris jusquíá. Ce petit animal est aussi doux quíl est laid. Il saisissoit tous les jours, dans la cour du missionaire, un cochon sur lequel il restoit monté, du matin au soir, en parcourant les savanes. Nous l'avons vu aussi sur le dos d'un gros chat qui avoit été élevé avec lui dans la maison de père [Bernardo] Zea."

The text of the mentioned footnote 1 is as follows: "Voyez ma monographie des singes de l'Orenoque, dans le Red[ueil] d'obs[ervations de] Zool[ogie et d'Anatomi comparée], Tom[e] I, p. 324 et 563 (éd[ition] in -4º). L'Ouavapavi (mot de la Langue guareken) est mon *Simia albifrons*, ex albo cinerascens, vertice nigro, facie caerulea, fronte et orbitis niveis, cruribus et brachiis fuscescentibus."

[13] There is no record of the occurrence of *Cebus albifrons* on the Venezuelan bank of the Orinoco below San Fernando de Atabapo or the neighborhood of Atures. *Cebus nigrivitattus* is known on the east bank by only one specimen, collected 32 km south of Puerto Ayacucho at 135 m (Handley, 1976: 42; see also Bodini and Perez-Hernández, 1987; Bodini, 1989). Further research is needed to clarify the Venezuelan distribution of the species.

[14] A karyotype of an *Aotus* captured on the banks of the río Orinoco showed a diploid number of 50, but the chromosomes were organized in a manner that suggests that it was not *A. brumbacki.* Hershkovitz (pers. comm.) felt that the specimen might be *A. trivirgatus* (Defler and Bueno, in prep.).

[15] In the original description of *Cebus flavus* É. Geoffroy Saint-Hilaire (1812: 111) *Simia flavia* Schreber (1774. p.xxxi.-b) is mentioned as a validly proposed name based on a color plate which illustrates a pale brown specimen with an almost white coronal cap. The origin of that specimen is unknown and it is not certainly identifiable as a *Cebus.* The citation of *Simia flavia* Schreber in the account of *Cebus flavus* by É. Geoffroy Saint-Hilaire implies that the latter author identified *C. flavus* with *S. flavia*; thus the epithet *flavia* was retained and emended to *flavus* when transferred

to the genus *Cebus* to fit the required grammatical concordance. For this purpose the *–i* before the termination *–us* was deleted, so that *flavia* became *flavus*. Both epithets are homonyms under article 58.15 of the 4th edition of the International Code of Zoological Nomenclature.

*Simia flavia* Schreber (1776: pl.) was regarded as unidentifiable by Cabrera (1917a: 233; 1958: 170) and Hershkovitz (1949: 336, 345), and *Cercopithecus flavus* Goldfuss 1809 (non *Cercopithecus flavus* Boddaert 1784) is based on the Schreber color plate as indicated by Hershkovitz (1949: 336) and thus is an absolute synonym of *Simia flavia*. The fact that É. Geoffroy Saint-Hilaire (1812: 111) mentioned *Simia flavia* Schreber (1776) in his description of *Cebus flavus* implies that the latter could be regarded as a nomenclatural amendment. However, according to Article 58 of the International Code of Zoological Nomenclature (ICZN, 1999: 60–61) the amended form *flavus* would not fall into homonymy of *flavia* (or *flavius*).

*Cebus flavus* is, therefore, a valid name based on a mounted specimen (with skull inside) said to be from Brazil and designated by Rode (1938: 231) as a "type" preserved in the MHNP (no. 362 of the types catalogue, and 458 of the general collection), which according to Hershkovitz (1949: 342) "is extremely faded with considerable portions of hair of the underparts, head and face missing". The specimen is part of the collection made by the Brazilian naturalist Alexandre Rodrigues Ferreira (1974) during his "Viagem Filosófica", through the states of Amazonas, Mato Grosso, Pará and Rondônia, Brazil. The collection was in the Museu Real d'Ajuda in Lisbon, until it was taken to Paris as war booty by Napoleon's troops under the care of É. Geoffroy Saint-Hilaire. Wagner (1855: 90) suggested that *Cebus flavus* was identical to *Cebus gracilis* Spix (1823), a possibility that Hershkovitz [1949: 341] accepted, writing: "In any case, the question remains whether the specimen determined as *flavus* by [É.] Geoffroy [Saint-Hilaire] is to be regarded as a specimen referring to the amended form of the name [*Simia*] *flavia* Schreber". In summary, therefore, *Cebus flavus* É. Geoffroy Saint-Hilaire 1812 would be the earliest available name for the Amazonian populations of *Cebus albifrons* if our interpretation of the nomenclatorial rules is correct. In order to preserve *Cebus flavus* it would be necessary to reinstate the validity of the former epithet. However, *unicolor* gained wide acceptance after Hershkovitz' publication in 1949. Groves (2001: 148) concurs that the type *Cercopithecus flavus* Goldfuss is indeed probably *albifrons*.

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