A TAXONOMIC REVIEW OF THE TITI MONKEYS, GENUS *CALLICEBUS* THOMAS, 1903, WITH THE DESCRIPTION OF TWO NEW SPECIES, *CALLICEBUS BERNHARDI* AND *CALLICEBUS STEPHENNASHI,* FROM BRAZILIAN AMAZONIA

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Abstract

This paper provides a taxonomic review of the titi monkeys, genus *Callicebus,* and describes two new species from central Brazilian Amazonia, *Callicebus bernhardi* and *Callicebus stephennashi.* Previous revisions include Hershkovitz (1988, 1990), Kobayashi (1995), Kobayashi and Langguth (1999) and Groves (1993, 2001). Here we arrange the titi monkeys, genus *Callicebus* Thomas, 1903, into five Species Groups or clades, and a total of 28 species. The *Callicebus donacophilus* Group is represented by the following species: *Callicebus modestus* Lönnberg, 1939, *Callicebus donacophilus* (d'Orbigny, 1836), *Callicebus pallescens* Thomas, 1907 (treated by Hershkovitz as a subspecies of *C. donacophilus*), *Callicebus olallae* Lönnberg, 1939, and *Callicebus oenanthe* Thomas, 1924. The *Callicebus moloch* Group is represented by the following species: *Callicebus cinerascens* (Spix, 1823), *Callicebus hoffmannsi* Thomas, 1908, *Callicebus baptista* Lönnberg, 1939 (treated by Hershkovitz as a subspecies of *C. hoffmannsi*), *Callicebus brunneus* (Wagner, 1842), *Callicebus moloch* (Hoffmannsegg, 1807), and the new species here described as *Callicebus bernhardi*. The *Callicebus cupreus* Group is represented by the following species: *Callicebus cupreus* (Spix, 1823), *Callicebus discolor* (I. Geoffroy & Deville, 1848) (treated by Hershkovitz as a subspecies of *C. cupreus*), *Callicebus ornatus* (Gray, 1866) (treated by Hershkovitz as a subspecies of *Callicebus cupreus*), *Callicebus caligatus* (Wagner, 1842), *Callicebus dubius* Hershkovitz, 1988, and the new species here described as *Callicebus stephennashi.* The *Callicebus torquatus* Group is represented by the following species: *Callicebus torquatus* (Hoffmannsegg, 1807), *Callicebus lugens* (Humboldt, 1811) (treated by Hershkovitz as a subspecies of *C. torquatus*), *Callicebus purinus* Thomas, 1927 (treated by Hershkovitz as a subspecies of *C. torquatus*), *Callicebus lucifer* Thomas, 1914 (treated by Hershkovitz as a subspecies of *C. torquatus*), *Callicebus regulus* Thomas, 1927 (treated by Hershkovitz as a subspecies of *C. torquatus*), and *Callicebus medemi* Hershkovitz, 1963 (treated by Hershkovitz as a subspecies of *C. torquatus*). The *Callicebus personatus* Group is treated separately from the *Callicebus moloch* Group and is represented by the following species: *Callicebus personatus* (É. Geoffroy, 1812), *Callicebus melanochir* (Wied-Neuwied, 1820) (treated by Hershkovitz as a subspecies of *C. personatus*), *Callicebus nigrifrons* (Spix, 1823) (treated by Hershkovitz as a subspecies of *C. personatus*), *Callicebus barbarabrownae* Hershkovitz, 1990 (treated by Hershkovitz as a subspecies of *C. personatus*), and *Callicebus coimbrai* Kobayashi & Langguth, 1999. *Callicebus bernhardi* was discovered in the Rio Aripuanã basin in 1996 by M. G. M. van Roosmalen, who also discovered *Callicebus stephennashi* in 2001, while traveling on the Rio Purus. The geographic distributions of all hitherto recognized *Callicebus* species are updated, and the validity of the river barrier hypothesis for titis and other Amazonian primates is discussed, along with their conservation status.

Key Words - Primates, Pitheciidae, *Callicebus,* titi monkeys, distribution, *Callicebus bernhardi* new species, *Callicebus stephennashi* new species, Amazonia, Brazil.

Resumo

Este artigo apresenta uma revisão taxonômica dos macacos 'zogue-zogues', gênero *Callicebus,* e descreve duas espécies novas descobertas na Amazônia central, *Callicebus bernhardi* e *Callicebus stephennashi.* Revisões recentes desse gênero incluem Hershkovitz (1988, 1990), Kobayashi (1995), Kobayashi e Langguth (1999) e Groves (1993, 2001). Aqui nos classificamos zogue-zogues da Amazônia e sauás da Mata Atlântica, gênero *Callicebus* Thomas, 1903, em cinco Grupos de Espécies, ou 28 clados: Grupo *C. donacophilus* (*Callicebus modestus* Lönnberg, 1939, *Callicebus donacophilus* [d'Orbigny, 1836], *Callicebus pallescens* Thomas, 1907 [considerada uma subespécie de *C. donacophilus* por Hershkovitz], *Callicebus olallae* Lönnberg, 1939 e *Callicebus oenanthe* Thomas, 1924); Grupo *C. moloch* (*Callicebus cinerascens* [Spix, 1823], *Callicebus hoffmannsi* Thomas, 1908, *Callicebus baptista* Lönnberg, 1939 [considerada uma subepécie de *C. hoffmannsi* por Hershkovitz], *Callicebus brunneus* [Wagner, 1842], *Callicebus moloch* [Hoffmannsegg, 1807], e a espécie nova aqui descrita como *Callicebus bernhardi*); Grupo *C. cupreus* (*Callicebus cupreus* [Spix, 1823], *Callicebus discolor* [I. Geoffroy & Deville, 1848] [considerada uma subespécie de *C. cupreus* por Hershkovitz], *Callicebus ornatus* [Gray, 1866] [considerada uma subespécie de *C. cupreus* por Hershkovitz], *Callicebus caligatus* [Wagner, 1842], *Callicebus dubius* Hershkovitz, 1988, e uma espécie

nova aqui descrita como *Callicebus* stephennashi); Grupo *C. torquatus* (*Callicebus torquatus* [Hoffmannsegg, 1807], *Callicebus lugens* [Humboldt, 1811] [considerada uma subespécie de *C. torquatus* por Hershkovitz], *Callicebus purinus* Thomas, 1927 [considerada uma subespécie de *C. torquatus* por Hershkovitz], *Callicebus lucifer* Thomas, 1914 [considerada uma subespécie de *C. torquatus* por Hershkovitz], *Callicebus regulus* Thomas, 1927 [considerada uma subespécie de *C. torquatus* por Hershkovitz] e *Callicebus medemi* Hershkovitz, 1963 [considerada uma subespécie de *C. torquatus* por Hershkovitz]; e o Grupo *C. personatus* que foi incluído no Grupo *moloch* por Hershkovitz (*Callicebus personatus* [É. Geoffroy, 1812], *Callicebus melanochir* [Wied-Neuwied, 1820] [considerada uma subespécie de *C. personatus* por Hershkovitz], *Callicebus nigrifrons* [Spix, 1823] [considerada uma subespécie de *C. personatus* por Hershkovitz], *Callicebus barbarabrownae* Hershkovitz, 1990 [considerada uma subespécie de *C. personatus* por Hershkovitz] e *Callicebus coimbrai* Kobayashi & Langguth, 1999). *Callicebus bernhardi* foi descoberta na bacia do rio Aripuanã, Amazonas, por M. G. M. van Roosmalen em 1996. *Callicebus stephennashi* foi descoberta recentemente em 2000 pelo mesmo pesquisador no rio Purus, Amazonas. A probabilidade da existência de outras espécies de 'zogue-zogues' até então desconhecidas na Amazônia está discutida. A distribuição geográfica de todas as espécies está atualizada. Discute-se a validade da hipótese dos rios da bacia Amazônica como barreiras geográficas para os 'zogue-zogues' e outros primatas Amazônicos.

Palavras-Chave - Primatas, Pitheciidae, *Callicebus*, zogue-zogues, distribuição, *Callicebus bernhardi* espécie nova, *Callicebus stephennashi* espécie nova, Amazônia, Brasil.

Introduction

The titi monkeys of the genus *Callicebus* are a diverse group of Neotropical monkeys found mainly in the tropical forests of the Amazon and Orinoco basins, but also extending into the Atlantic forest region of Brazil, and the *Chaco* and dry forests of Paraguay and Bolivia as far south as the Ríos Pilcomayo and Paraguay. They are small to medium in size, roughly between the tamarins and the pitheciines, weighing 1–2 kilograms, and ranging from 270–450 mm in head-body length (Hershkovitz, 1990). Locomotion consists mainly of quadrupedal walking, climbing and leaping. All modern revisions of this genus were by Hershkovitz, the first being in 1963, followed by two other major papers in 1988 and 1990. These were followed by a study by Kobayashi (1995) and the description of a new species from the Atlantic forest by Kobayashi and Langguth (1999).

Once considered a moderately diverse Neotropical genus, *Callicebus* is now emerging as one of the most diverse of all primate genera, competing with *Saguinus* for the largest number of taxa in the New World. In Hershkovitz's (1963) revision, he recognized only two species from the Amazon and Orinoco river basins, *Callicebus moloch* with seven subspecies and *Callicebus torquatus* with three subspecies, including one, *Callicebus torquatus medemi,* described in that paper. He did not treat Atlantic forest *Callicebus personatus* in 1963, but indicated that the three subspecies there might be conspecific with *Callicebus moloch*. Consequently, the number of *Callicebus* taxa recognized as of 1963 was 13.

In 1988, Hershkovitz published a more detailed revision of the *Callicebus* in which he divided the genus into four species groups (*Callicebus modestus, Callicebus donacophilus, Callicebus moloch,* and *Callicebus torquatus*), with 13 species and 24 taxa, nearly double what was recognized in 1963. This increase resulted mainly from the resurrection of a number of taxa described earlier in the 20th century by Thomas (1907, 1908, 1917, 1924, 1927) and Lönnberg (1939) (*modestus, pallescens, olallae, oenanthe, cinerascens, baptista, lucifer, regulus, purinus*), and one by Wagner (1842; *caligatus*), but also included the description of a new form, *Callicebus dubius*. In addition, four of the taxa recognized as subspecies of *Callicebus moloch* in Hershkovitz (1963) were elevated to full species status (*donacophilus, hoffmannsi, brunneus, cupreus*), whereas three others continued to be considered subspecies (*baptista, discolor, ornatus*). All taxa of *Callicebus torquatus* were treated as subspecies, including the three recognized in 1963 (*torquatus, lugens, medemi*) and the three resurrected from Thomas' earlier papers (*lucifer, regulus, purinus*). Hershkovitz appears to have decided whether a given taxon was a full species or just a subspecies based mainly on distributional evidence indicating partial sympatry.

Finally, in 1990, Hershkovitz published his final contribution to *Callicebus* taxonomy, a full revision in which he recognized the same four species groups, 13 species and 24 taxa, but adding a new subspecies of *Callicebus personatus, C. p. barbarabrownae*, for a total of 25. Although a thorough review of the genus, this publication included only a handful of color illustrations and a number of black and white photographs of skins and live animals, the latter mostly by Mittermeier, many of them published again here in color along with many new color photographs. Given the importance of coloration in these animals, we believe it essential that color illustrations be provided for all taxa. This we have done here by providing both pencil drawings of every taxon and photographs of live animals wherever available.

Since 1990, the only addition to our knowledge of *Callicebus* taxonomy has been a review by Kobayashi

(1995) and a paper by Kobayashi and Langguth (1999), in which they described a new *Callicebus* from the state of Sergipe in northeastern Brazil, *Callicebus coimbrai.* In his 1995 paper, Kobayashi reviewed the taxonomy of the genus based mainly on cranial measurements, and made several modifications to Hershkovitz's earlier breakdown of species into clades.

Groves (2001), although largely following Hershkovitz (1990), also made some decisions on *Callicebus* taxonomy. In particular, he decided that *C. moloch* and *C. cinerascens* are distinct; that *C. brunneus, C. hoffmannsi hoffmannsi, C. hoffmannsi baptista,* and *C. moloch* are four full species; that *C. caligatus* and *C. cupreus cupreus* are essentially the same; and that *C. dubius* is not distinct at all. We are in agreement with his first two observations, but disagree with the second two, continuing to recognize *C. caligatus* and *C. dubius* as distinct species. Like Hershkovitz (1990), he placed them in four species groups (*C. modestus, C. donacophilus, C. moloch* (including *C. personatus*), and *C. torquatus*), but increased the number of species to 15, while reducing the total number of taxa to 24. He recognized all members of the *C. modestus* and *C. donacophilus* groups and all members of his *C. moloch* group except for *C. personatus* as full species. With *C. personatus*, he recognized four of the five taxa as subspecies, but agreed with Kobayashi and Langguth (1999) that *C. coimbrai* is a distinct species. With the *C. torquatus* group, he elevated *C. medemi* to full species status, but continued to list the other five taxa as subspecies.

In this paper, we provide a thorough reanalysis of the genus *Callicebus*, complete with distribution maps and color illustrations of each taxon. In addition, we describe two new species from central Brazilian Amazonia, *Callicebus bernhardi* and *Callicebus stephennashi.* Together with Kobayashi and Langguth's new taxon, *Callicebus coimbrai*, these new animals raise the total number of *Callicebus* to 28, second only to the 33 taxa of *Saguinus* (Rylands *et al.*, 2000) among New World primate genera. Furthermore, since we increasingly find the concept of subspecies to be of minimal value in describing the diversity of Neotropical primates, we have elevated all *Callicebus* to full species status.

To enable the reader to better comprehend the evolution of *Callicebus* taxonomy over the past 40 years, we also provide a comparative table listing the *Callicebus* taxa recognized by Hershkovitz in 1963, 1988 and 1990, Kobayashi in 1995 (including Kobayashi and Langguth, 1999), Groves in 2001, and in this paper (Table 1).

Geographic Distribution

The genus *Callicebus* has a broad range in western and central Amazonia, including the drainage basin of the Rio Amazonas from the foothills of the Andes in Colombia, Ecuador, Peru and Bolivia east into central Brazilian Amazonia as far as the Rio Araguaia to the south of the mainstream and the Rio Branco to the north. It also occurs in the drainage basin of the Rio Orinoco from the foothills of the Andes to the Rio Caroni to the south of the mainstream of the Orinoco, including gallery forests along Orinoco tributaries in the Colombian llanos. East of the Rio Araguaia, there is a large gap in distribution in easternmost Amazonia, the *Cerrado* and the *Caatinga*, until one reaches the Atlantic forest region of eastern Brazil. There, the *Callicebus personatus* group has a large but highly fragmented range from the state of Sergipe in tiny remnant patches of northeastern Atlantic forest south through Bahia, Minas Gerais, Espírito Santo, and Rio de Janeiro, as far as the Rio Tietê in São Paulo. South of Amazonia, the genus extends into the dry forests and *Chaco* formations of Paraguay and Bolivia as far as the Rios Pilcomayo and Paraguay, the southernmost distribution on this side of the continent being roughly parallel to the southern limits of *Callicebus personatus* in the Atlantic forests of São Paulo. Although present on the eastern slopes of the Andes, it does not cross over to the Pacific side of the continent, nor does it come close to extending into Central America. Interestingly, it is also entirely absent from the northeastern quadrant of Amazonia and is not found east of the Rio Branco-Uraricoeira in Brazil nor in the three Guianas.

A New Taxonomic Arrangement for the Genus *Callicebus*

Hershkovitz (1990) systematically arranged titi monkeys, genus *Callicebus*, in four groupings or clades. Here, we prefer to follow the more recent phylogenetic study, based on cranial measurements, by Kobayashi (1995), which includes *Callicebus modestus* in the *C. donacophilus* clade, splits the *C. moloch* clade into two clades, the *C. moloch* and the *C. cupreus* clades, and puts *Callicebus personatus* in its own clade because of its long separation from Amazonian titis both in historical and geographical terms, for a total of five in all. Each of these is referred to here as a Species Group named after the first described taxon from each group.

I. *C. donacophilus* Group
Callicebus donacophilus (d'Orbigny, 1836)
Callicebus pallescens Thomas, 1907
Callicebus oenanthe Thomas, 1924
Callicebus modestus Lönnberg, 1939
Callicebus olallae Lönnberg, 1939

This group, on average, is comprised of the smallest species of *Callicebus,* and is closely related to the *moloch* group. Brain-case volume of *C. modestus* is smallest for cebids, and the species represents probably the most primitive form among Cebidae. Diploid chromosome number for *C. donacophilus* = 50 (De Boer, 1974).

II. *C. cupreus* Group
Callicebus cupreus (Spix, 1823)
Callicebus caligatus (Wagner, 1842)
Callicebus discolor (I. Geoffroy & Deville, 1848)

Callicebus ornatus (Gray, 1866)
Callicebus dubius Hershkovitz, 1988
Callicebus stephennashi new species

Diploid chromosome number only known for *Callicebus cupreus, C. ornatus* and *C. discolor* = 46 (De Boer, 1974; Schneider *et al.* 1993). See *C. moloch* Group for comparisons.

III. *C. moloch* Group

Callicebus moloch (Hoffmannsegg, 1807)
Callicebus cinerascens (Spix, 1823)
Callicebus brunneus (Wagner, 1842)
Callicebus hoffmannsi Thomas, 1908
Callicebus baptista Lönnberg, 1939
Callicebus bernhardi new species

The *cupreus* and *moloch* clades are composed of the typical titis that were once regarded as conspecific (as subspecies of *Callicebus moloch*; Hershkovitz, 1963). They belong to the same so-called "eco-species" in the sense that they occupy the same ecological niche. Members of this group are invariably adapted to disturbed habitat and cannot occur sympatrically. Sympatry only occurs between members of the *moloch cupreus* groups and the *torquatus* group species, which are adapted to undisturbed *terra firme* or high dryland rainforest. Diploid chromosome number only known for *C. moloch* and *C. brunneus* = 48 (Pieczarka and Nagamachi, 1988; Minezawa *et al.,* 1989; Schneider *et al.,* 1993).

Table 1. A comparison of the classifications of the titi monkeys, *Callicebus,* by Hershkovitz (1963), Hershkovitz (1988, 1990), Kobayashi & Langguth (1999), Groves (2001), and this paper.

Hershkovitz (1963)	Hershkovitz (1988, 1990)	Kobayashi (1995), Kobayashi & Langguth (1999)	Groves (2001)	This paper (2002)
C. moloch moloch	***C. modestus* Group**	***C. donacophilus* Group**	***C. modestus* Group**	***C. donacophilus* Group**
C. m. cupreus	*C. modestus*	*C. modestus*	*C. modestus*	*C. donacophilus*
C. m. donacophilus	***C. donacophilus* Group**	*C. donacophilus donacophilus*	***C. donacophilus* Group**	*C. pallescens*
C. m. brunneus	*C. donacophilus donacophilus*	*C. d. pallescens*	*C. donacophilus*	*C. oenanthe*
C. m. discolor	*C. d. pallescens*	*C. olallae*	*C. pallescens*	*C. modestus*
C. m. ornatus	*C. oenanthe*	***C. cupreus* Group**	*C. oenanthe*	*C. olallae*
C. m. hoffmannsi	*C. olallae*	*C. cupreus cupreus*	*C. olallae*	***C. cupreus* Group**
C. torquatus torquatus	***C. moloch* Group**	*C. c. discolor*	***C. moloch* Group**	*C. cupreus*
C. t. lugens	*C. moloch*	*C. c. ornatus*	*C. cupreus cupreus*	*C. caligatus*
C. t. medemi	*C. cinerascens*	***C. moloch* Group**	*C. c. discolor*	*C. discolor .*
	C. cupreus cupreus	*C. moloch*	*C. c. ornatus*	*C. ornatus*
	C. c. discolor	*C. cinerascens*	*C. moloch*	*C. dubius*
	C. c. ornatus	*C. brunneus*	*C. cinerascens*	*C. stephennashi*
	C. caligatus	*C. hoffmannsi hoffmannsi*	*C. brunneus*	***C. moloch* Group**
	C. brunneus	*C. h. baptista*	*C. hoffmannsi*	*C. moloch*
	C. hoffmannsi hoffmannsi	***C. personatus* Group**	*C. baptista*	*C. cinerascens*
	C. h. baptista	*C. personatus*	*C. personatus personatus*	*C. brunneus*
	C. dubius	C. *melanochir*	*C. p. melanochir*	*C. hoffmannsi*
	C. personatus personatus	*C. nigrifrons*	*C. p. nigrifrons*	*C. baptista*
	C. p. melanochir	*C. barbarabrownae*	*C. p. barbarabrownae*	*C. bernhardi*
	C. p. nigrifrons	*C. coimbrai*	*C. coimbrai*	***C. torquatus* Group**
	C. p. barbarabrownae	***C. torquatus* Group**	***C. torquatus* Group**	*C. torquatus*
	***C. torquatus* Group**	*C. torquatus torquatus*	*C. torquatus torquatus*	*C. lugens*
	C. torquatus torquatus	*C. t. lugens*	*C. t. lugens*	*C. lucifer*
	C. t. lugens	*C. t. lucifer*	*C. t. lucifer*	*C. purinus*
	C. t. lucifer	*C. t. purinus*	*C .t. purinus*	*C. regulus*
	C. t. purinus	*C .t. regulus*	*C. t. regulus*	*C. medemi*
	C. t. regulus	*C. t. medemi*	*C. medemi*	***C. personatus* Group**
	C. t. medemi			*C. personatus*
				C. melanochir
				C. nigrifrons
				C. barbarabrownae
				C. coimbrai

IV. *C. torquatus* Group

Callicebus torquatus (Hoffmannsegg, 1807)
Callicebus lugens (Humboldt, 1811)
Callicebus lucifer Thomas, 1914
Callicebus purinus Thomas, 1927
Callicebus regulus Thomas, 1927
Callicebus medemi Hershkovitz, 1963

This group is distinguished from all other titis by an overall dark reddish to blackish color of the fur, by hair that is in general uniform in color and not banded by a white collar or throat, and by certain cranial and post-cranial skeletal characters. All members of the *torquatus* Group belong to the same so-called "eco-species," and are undisturbed high dry-land (*terra firme*) rainforest habitat specialists (Kinzey, 1977, 1981; Defler, 1994). Their diet is basically frugivorous, but includes insects as well, whereas the other Groups are partial folivores. Sympatry only occurs with members of the *cupreus* clade south of the Rios Amazonas, Solimões, Marañon, Napo, Aguarico. Average size is larger than *donacophilus, cupreus* and *moloch* Group members, but slightly less than members of the *personatus* Group. Diploid number of chromosomes = 20, the lowest for primates and among the lowest for mammals in general (Benirschke and Bogart, 1976; Egozcue *et al.*, 1969).

V. *C. personatus* Group

Callicebus personatus (É. Geoffroy, 1812)
Callicebus melanochir (Wied-Neuwied, 1820)
Callicebus nigrifrons (Spix, 1823)
Callicebus barbarabrownae Hershkovitz, 1990
Callicebus coimbrai Kobayashi & Langguth, 1999

This group is composed of on average the largest species of *Callicebus*, and inhabits coastal and inland forests of southeastern Brazil. It is geographically separated from the nearest member of the *moloch* clade (*Callicebus moloch*) to the northwest by at least 1,000 km, and from the nearest member of the *donacophilus* clade (*Callicebus pallescens*) to the west by at least 500 km.

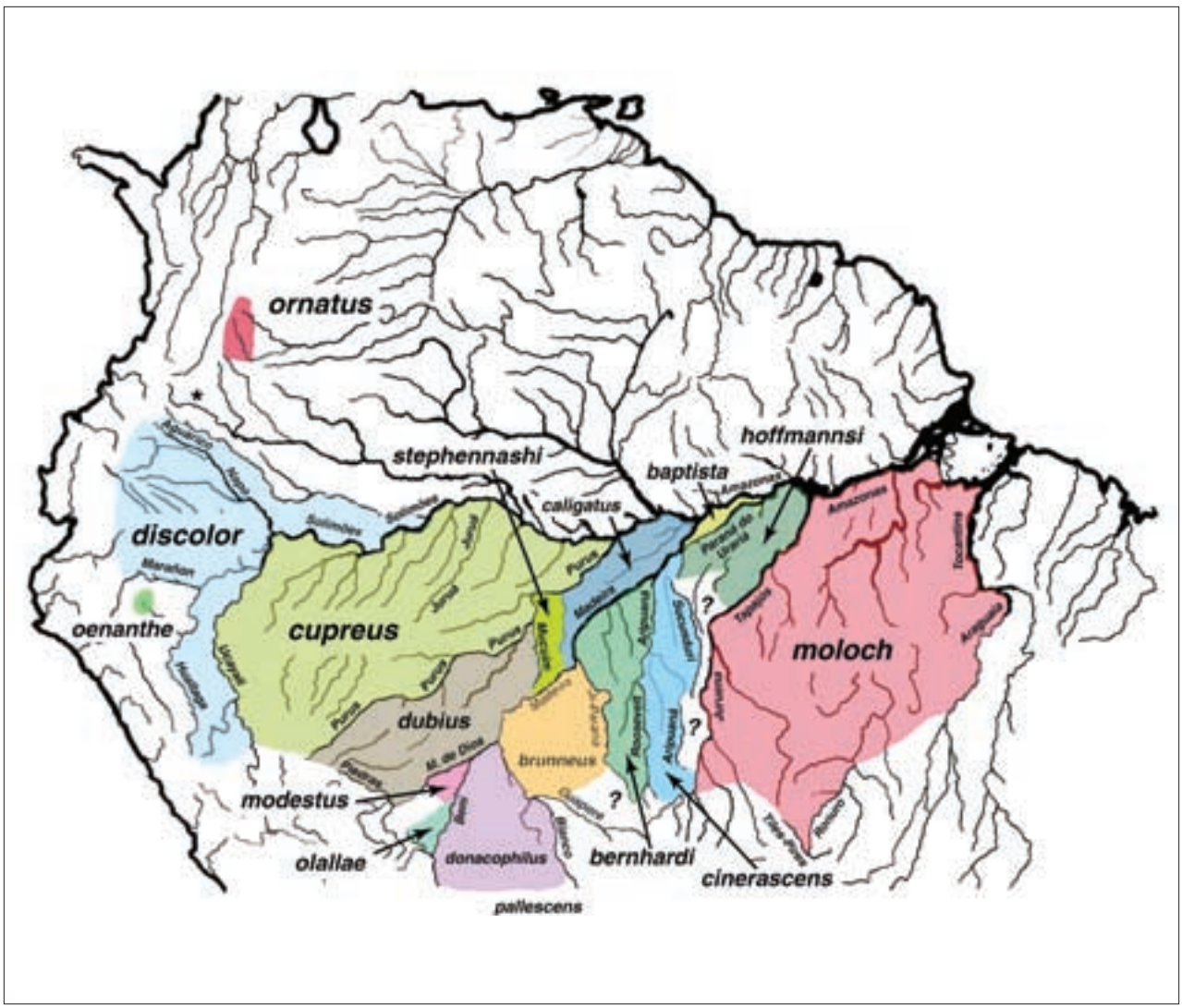


Figure 1. Distributions of the Amazonian titi monkeys, genus *Callicebus*, belonging to the *donacophilus*, *cupreus* and *moloch* Groups. The asterisk marks the location of the municipality of Valparaiso, Columbia, where Moynihan (1976) recorded the presence of titi monkeys not identifiable with *discolor* or *ornatus*. Map by Stephen D. Nash.

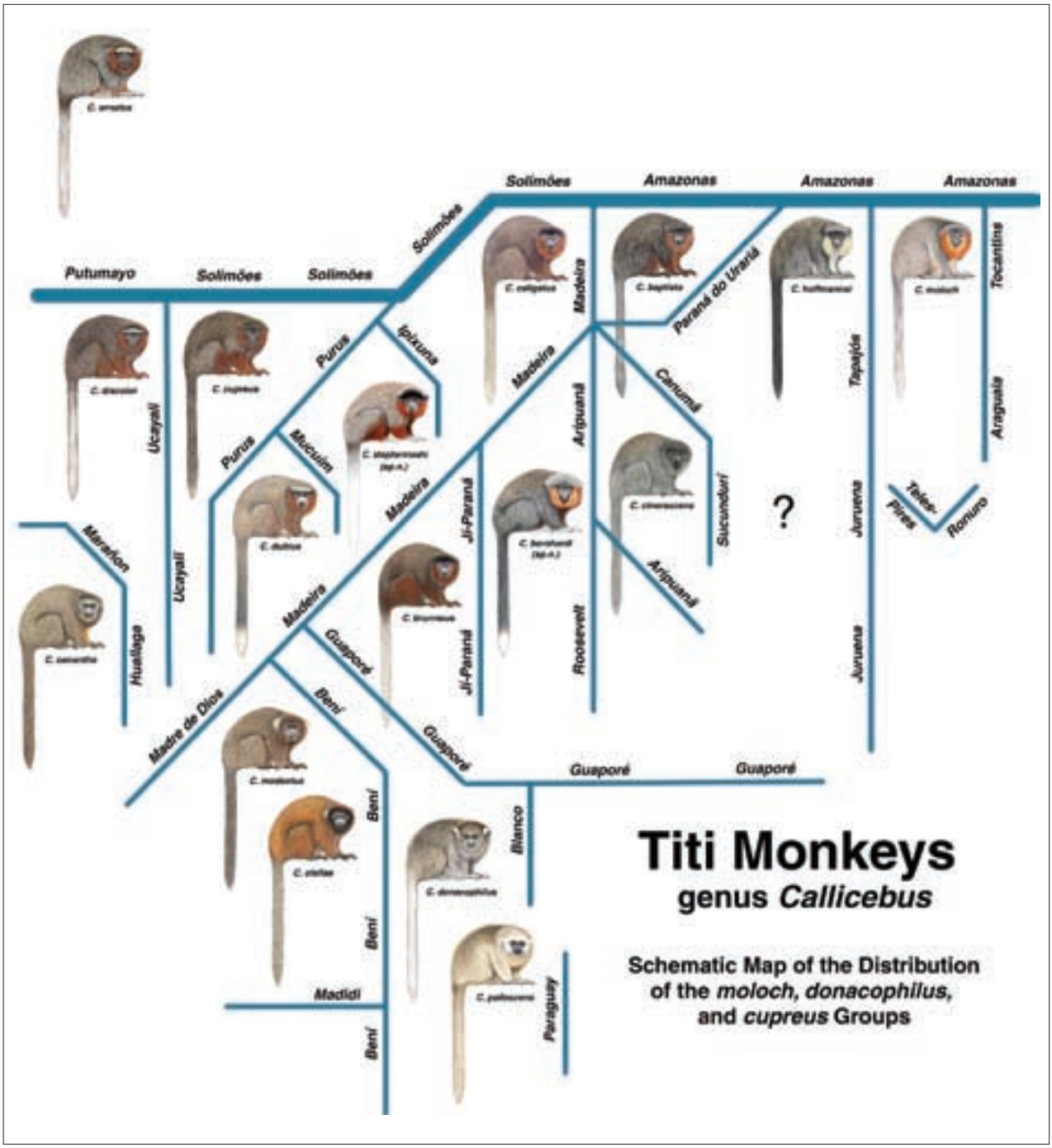


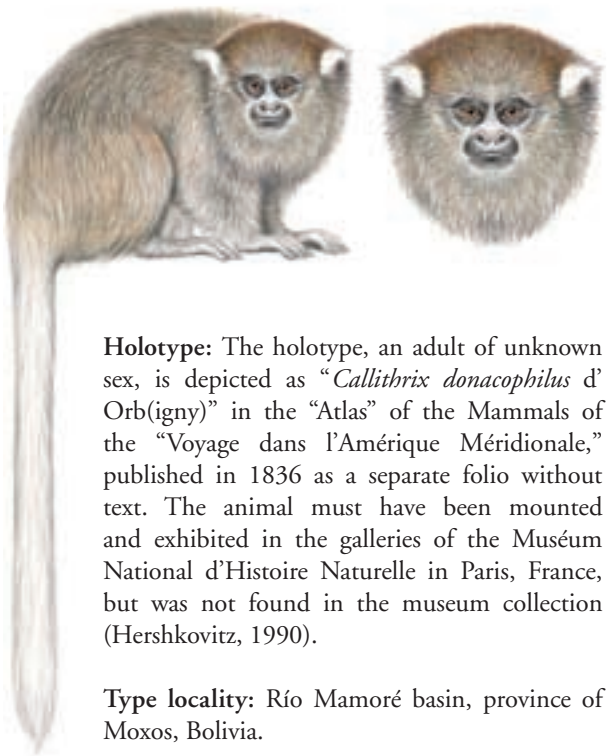
Figure 2. Schematic map of the distribution of Amazonian titi monkeys, belonging to the *donacophilus, cupreus* and *moloch* Groups. Illustration by Stephen D. Nash.

Figure 3. The Amazonian taxa of titi monkeys, genus *Callicebus,* more or less geographically arranged. Illustration by Stephen D. Nash.

SPECIES ACCOUNTS

I. *C. DONACOPHILUS* GROUP

Callicebus donacophilus (d'Orbigny, 1836)



Holotype: The holotype, an adult of unknown sex, is depicted as "*Callithrix donacophilus* d' Orb(igny)" in the "Atlas" of the Mammals of the "Voyage dans l'Amérique Méridionale," published in 1836 as a separate folio without text. The animal must have been mounted and exhibited in the galleries of the Muséum National d'Histoire Naturelle in Paris, France, but was not found in the museum collection (Hershkovitz, 1990).

Type locality: Río Mamoré basin, province of Moxos, Bolivia.

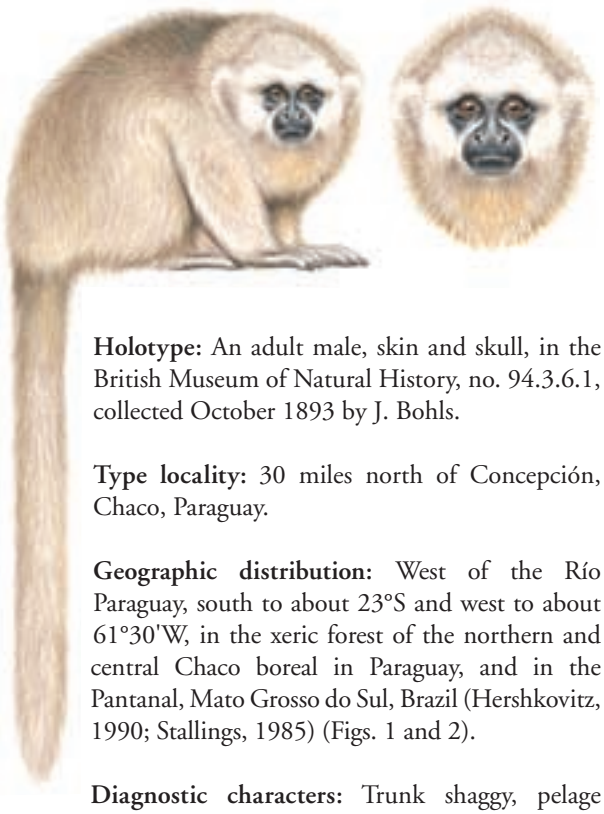
Geographic distribution: Upper Ríos Mamoré-Grande and San Miguel basins, Beni and Santa Cruz provinces, west central Bolivia (Figs. 1 and 2).

Figure 4. The white-eared titi, *Callicebus donacophilus* (d'Orbigny, 1836). An adult female in the Kilverstone Wildlife Park, Thetford, UK, in 1981. Photograph by R. A. Mittermeier.

Diagnostic characters: Lacking distinct sideburns; upper and outer parts of head and body, and outer and inner sides of limbs buff or grayish agouti to dominantly orange agouti, not contrasting; forehead like crown; blackish superciliary fringe absent; most of chest and belly uniformly orange; upper surface of cheiridia buffy or buffy agouti, paler than forearms; tail buffy mixed with blackish, contrastingly paler at base; ears very hairy, with whitish tufts.

Distinguished from *Callicebus pallescens* by more saturated coloration, whitish ear tufts, and less shaggy pelage; from *Callicebus brunneus* by well-developed malar stripe, pale agouti forehead, forearms, legs, cheiridia, paler under-parts and lacking distinct sideburns; from *Callicebus modestus* by well-developed malar stripe, overall buffy to orange agouti instead of light brownish to reddish agouti coloration and lack of distinct sideburns; from *Callicebus olallae* by well-developed malar stripe, overall buffy to orange agouti instead of reddish brown agouti coloration, lack of distinct sideburns, and lack of a blackish facial fringe (Fig. 4).

Callicebus pallescens Thomas, 1907



Holotype: An adult male, skin and skull, in the British Museum of Natural History, no. 94.3.6.1, collected October 1893 by J. Bohls.

Type locality: 30 miles north of Concepción, Chaco, Paraguay.

Geographic distribution: West of the Río Paraguay, south to about 23°S and west to about 61°30'W, in the xeric forest of the northern and central Chaco boreal in Paraguay, and in the Pantanal, Mato Grosso do Sul, Brazil (Hershkovitz, 1990; Stallings, 1985) (Figs. 1 and 2).

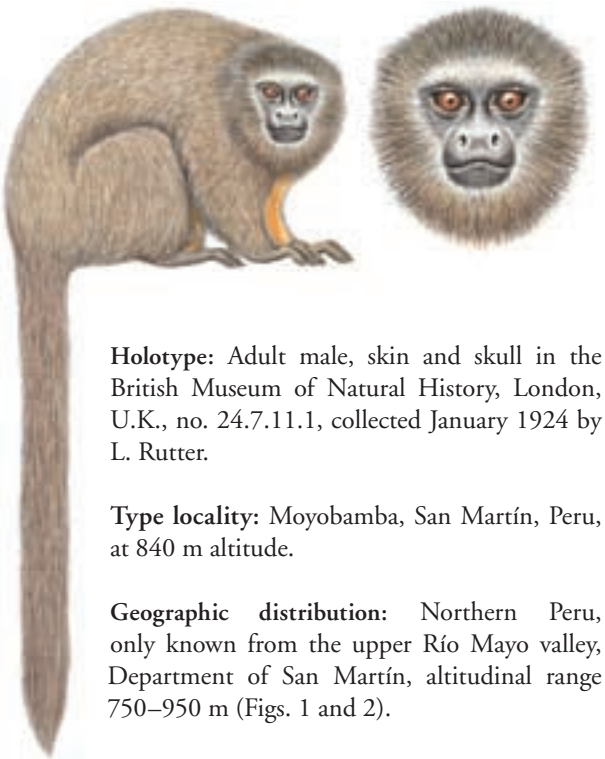
Diagnostic characters: Trunk shaggy, pelage extremely long, upper and outer sides of head and body, and outer sides of limbs pale buff agouti; facial hairs nearly concealing skin, malar stripe well-developed, blackish superciliary fringe (almost) absent; tail pale buff agouti not contrasting with rest of body.

Distinguished from *Callicebus donacophilus* and other titis by extreme pallor and shagginess of pale buff agouti coat; tail, cheiridia, forehead, and outer side of limbs uniformly

pale buff agouti, not contrastingly colored except for the conspicuous whitish ear tufts (Fig. 5).

Figure 5. *Callicebus pallescens* (Thomas, 1907). Photograph by B.A. Luscombe.

Callicebus oenanthe Thomas, 1924



Holotype: Adult male, skin and skull in the British Museum of Natural History, London, U.K., no. 24.7.11.1, collected January 1924 by L. Rutter.

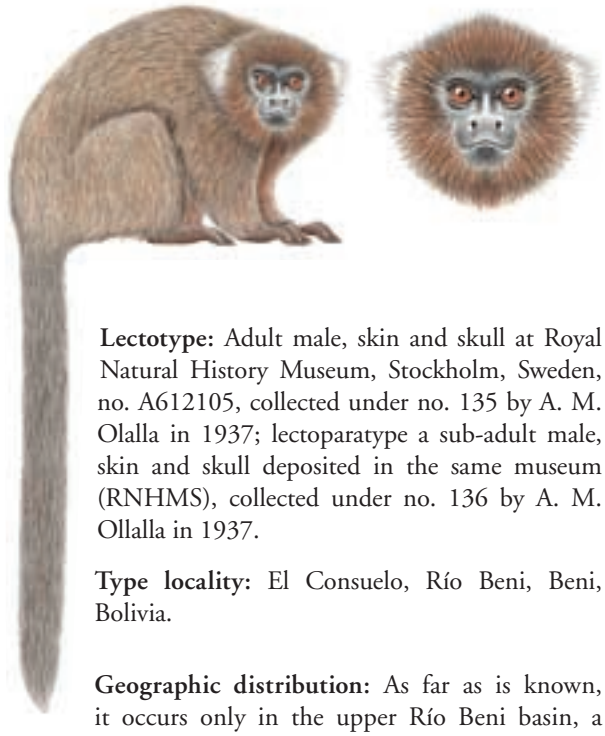
Type locality: Moyobamba, San Martín, Peru, at 840 m altitude.

Geographic distribution: Northern Peru, only known from the upper Río Mayo valley, Department of San Martín, altitudinal range 750–950 m (Figs. 1 and 2).

Diagnostic characters: Frontal blaze buffy or whitish, continuous with long cresting whitish hairs bordering the face; malar stripe present, whitish; sideburns, crown, outer surface of limbs, cheiridia and tail uniformly and dominantly to entirely dark brown agouti; inner surface of limbs, chest, and belly orange; pelage thick, that of the face longer than usual but not concealing the skin.

Distinguished from *Callicebus discolor* by whitish or buffy facial fringe or ruff of crested hairs, presence of a malar stripe, and outer surface of limbs, cheiridia and tail dark brown agouti.

Callicebus modestus Lönnberg, 1939



Lectotype: Adult male, skin and skull at Royal Natural History Museum, Stockholm, Sweden, no. A612105, collected under no. 135 by A. M. Olalla in 1937; lectoparatype a sub-adult male, skin and skull deposited in the same museum (RNHMS), collected under no. 136 by A. M. Ollalla in 1937.

Type locality: El Consuelo, Río Beni, Beni, Bolivia.

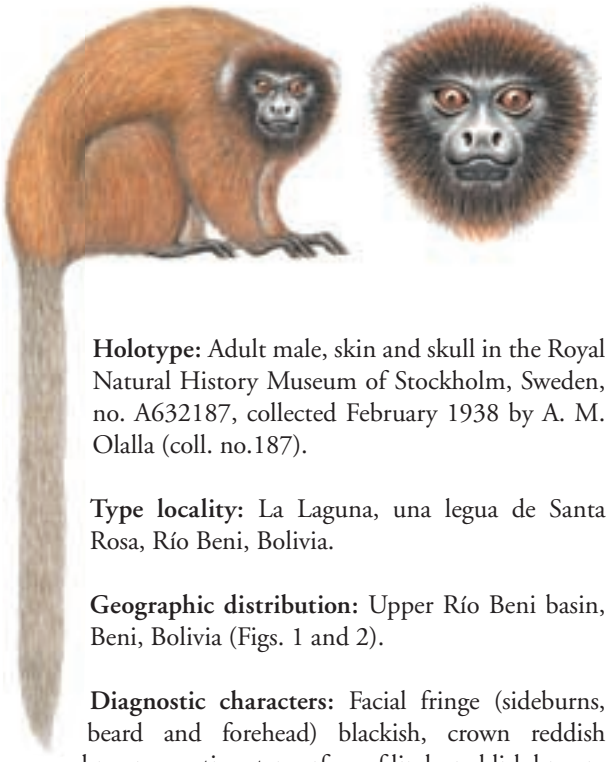
Geographic distribution: As far as is known, it occurs only in the upper Río Beni basin, a tributary of the upper Rio Madeira, Beni, Bolivia. The species is parapatric with *Callicebus dubius* along the north bank of the Río Madre de Dios, with *Callicebus donacophilus* along the east bank of the Río Beni, and with *Callicebus olallae* along the west bank of the upper Río Beni (Figs. 1 and 2).

Diagnostic characters: Upper and outer parts of body light brownish or reddish agouti except for white to whitish ear tufts, reddish brown agouti forehead and crown, and thin blackish superciliary fringe; outer surface of limbs reddish brown agouti; hands and feet blackish or blackish mixed with reddish; sideburns same color as forehead and crown; tail blackish agouti, darker than dorsum.

Distinguished from *Callicebus brunneus* by paler coloration, whitish ear tufts, and dominantly blackish tail; from *Callicebus olallae* by overall light brownish or reddish agouti instead of orange coloration, and face not framed with blackish fur; from *Callicebus donacophilus* by upper and

outer parts of body light brownish or reddish agouti instead of buffy to orange agouti, and dominantly blackish agouti tail and cheiridia instead of buffy mixed with blackish.

Callicebus olallae Lönnberg, 1939



Holotype: Adult male, skin and skull in the Royal Natural History Museum of Stockholm, Sweden, no. A632187, collected February 1938 by A. M. Olalla (coll. no.187).

Type locality: La Laguna, una legua de Santa Rosa, Río Beni, Bolivia.

Geographic distribution: Upper Río Beni basin, Beni, Bolivia (Figs. 1 and 2).

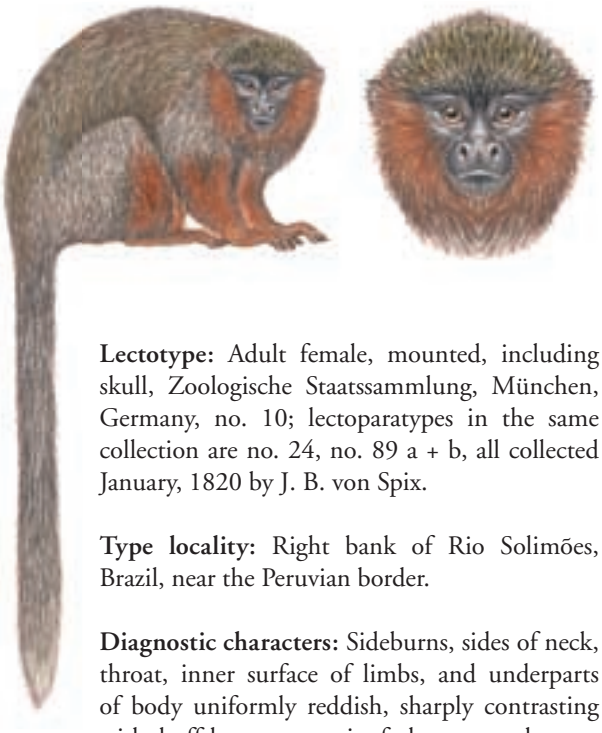
Diagnostic characters: Facial fringe (sideburns, beard and forehead) blackish, crown reddish brown agouti; outer surface of limbs reddish brown; cheiridia dominantly blackish; blackish suborbital vibrissae conspicuous; back and limbs uniformly orange (hairs with extremely broad orange median band); tail entirely dark agouti sharply contrasting with orange back; whitish ear tufts weakly developed.

Figure 6. Olalla Brothers' titi monkey, *Callicebus olallae* Lönnberg, 1939.

Distinguished from *Callicebus donacophilus* by blackish facial fringe, lack of malar stripe, weakly developed whitish ear tufts, dominantly brownish or blackish cheiridia and lack of a sharp contrast between coloration of under-parts and sides of body; from *Callicebus modestus* by blackish facial fringe, individual hairs of back showing a broad orange median band, and lack of well-developed whitish ear tufts (Fig. 6).

II. *C. CUPREUS* GROUP

Callicebus cupreus (Spix, 1823)



Lectotype: Adult female, mounted, including skull, Zoologische Staatssammlung, München, Germany, no. 10; lectoparatypes in the same collection are no. 24, no. 89 a + b, all collected January, 1820 by J. B. von Spix.

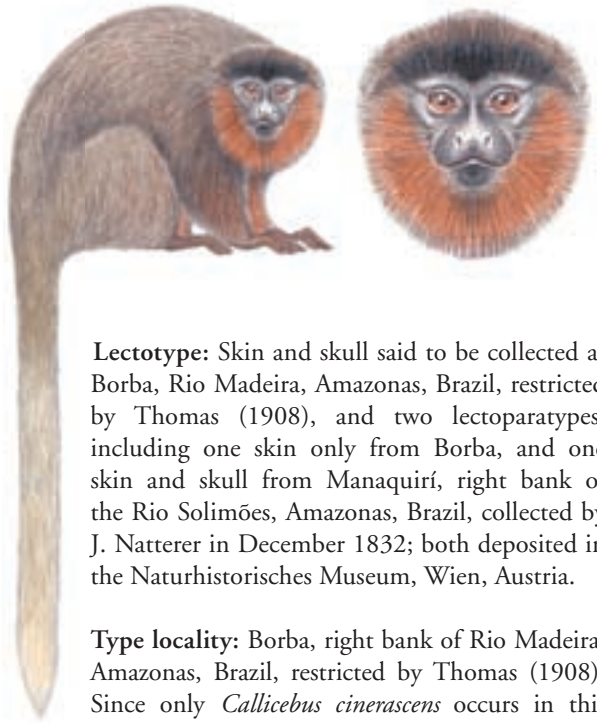
Type locality: Right bank of Rio Solimões, Brazil, near the Peruvian border.

Diagnostic characters: Sideburns, sides of neck, throat, inner surface of limbs, and underparts of body uniformly reddish, sharply contrasting with buff-brown agouti of dorsum and outer sides of trunk, basal part of tail, and crown; forehead as crown, reddish-brown agouti, often fringed with blackish superciliary vibrissae and marginal hair bases.

Distinguished from other members of the *cupreus* Group, except for *C. caligatus* and *C. stephennashi,* by absence of distinct pale transverse frontal blaze, and from all members of the *cupreus* Group by an overall dark tail with pencil only white; from *Callicebus caligatus* by lacking a broad black frontal transverse blaze; from *Callicebus stephennashi* by lacking a black frontal transverse blaze that contrasts sharply against a silvery crown, and having an overall dark tail instead of a three-quarters to entirely buffy to white tail; from *Callicebus brunneus* by its red sideburns, forearms, lower legs, cheiridia and under-parts of the body (Fig. 7).

Figure 7. The red or coppery titi, *Callicebus cupreus* (Spix, 1823). Top photograph by Chris Zagazzo. Middle and Bottom photographs by R. A. Mittermeier.

***Callicebus caligatus* (Wagner, 1842)**



Lectotype: Skin and skull said to be collected at Borba, Rio Madeira, Amazonas, Brazil, restricted by Thomas (1908), and two lectoparatypes, including one skin only from Borba, and one skin and skull from Manaquirí, right bank of the Rio Solimões, Amazonas, Brazil, collected by J. Natterer in December 1832; both deposited in the Naturhistorisches Museum, Wien, Austria.

Type locality: Borba, right bank of Rio Madeira, Amazonas, Brazil, restricted by Thomas (1908). Since only *Callicebus cinerascens* occurs in this region along the right bank of the Rio Madeira, Hershkovitz (1990) assumed that Natterer should have collected and mislabelled these specimens elsewhere. Since M.G.M. van Roosmalen found the species to occur in the lower Rios Purús/Solimões/Madeira interfluve south as far as the Rio Ipixuna, the specimens collected at Borba, right bank of the Rio Madeira, must have originated from the left bank of the Rio Madeira in the vicinity of Borba. The other type locality, Manaquirí, right bank of the Rio Solimões, falls within the supposed distribution.

Geographic distribution: Central Amazonia, Amazonas state, Brazil, south of the Rio Solimões in the interfluve delineated by the lower Rios Purús, Solimões and Madeira, south as far as the Rio Ipixuna (or Paranapixuna). Hershkovitz (1990) considered the species sympatric with *Callicebus dubius, C. brunneus,* and *C. cupreus*, based on, in his view, mislabelled specimens collected by the Olalla brothers at Boca Río Inuya, Iquitos, the Río Orosa, Río Tapiche, and Sarayacu, Rio Ucayali, in the department of Loreto, Peru. Voss and Emmons (1996) note that Hershkovitz' report on the sympatry of two members of the *moloch/cupreus* Group (*C. cupreus* and *C. caligatus*) was an error caused by "inadvertently listing both original and revised identifications of the same series from Orosa among the specimens examined." The correct identification for the monkeys is *Callicebus (cupreus) cupreus.* Specimens collected by Peres (1993) along both banks of the Rio Juruá and deposited in the Muséu Goeldi, Belém, all were identified as *Callicebus (cupreus) cupreus.*

The distribution of *C. caligatus* contradicts that given by Hershkovitz (1990), who fills in its actual distribution with *C. dubius.* Four specimens of real *C. caligatus* were caught in July 2001 by locals along the north bank of

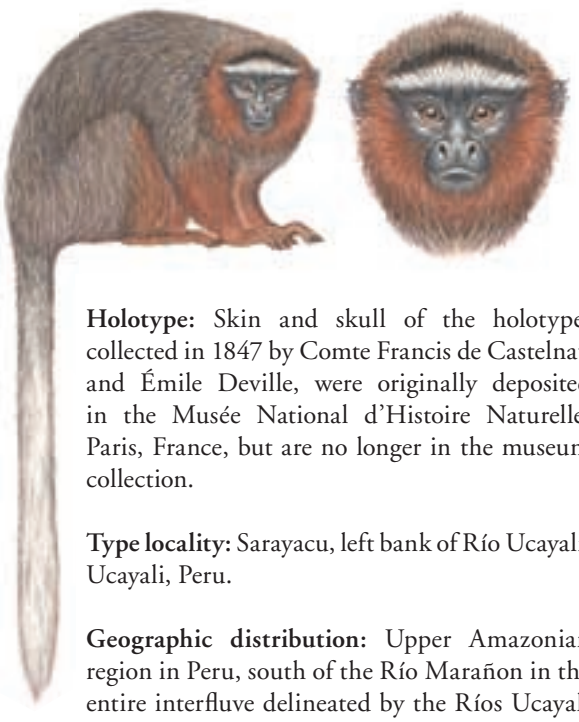
Figure 8. The chestnut-bellied titi, *Callicebus caligatus* (Wagner, 1842), an adult male and female caught from the wild by local people on the west bank of the Lago Jarí, Rio Purus, on July 27th, 2001. Upper right shows close up of the hands, and lower right, the tail. Photographs by M. G. M. van Roosmalen.

Lago Jarí at the mouth of Igarapé Bacaba and released at the same place after being measured and photographed, and a complete skeleton with some hair found on the forest floor was collected (private collection no. MGMR55) on the north bank of Rio Ipixuna near its mouth, a few kilometers south of the town of Tapauá (Van Roosmalen and Van Roosmalen, in prep.). (Figs. 1 and 2).

Diagnostic characters: Forehead and anterior part of crown black, rest of crown dark red-brown as neck, back and sides of body, each hair red-brown with a black tip; sideburns, under-parts and inner sides of limbs reddish to red-brown; back reddish-brown agouti; forearms and lower legs dark red-brown; cheiridia, including wrists and ankles black as blaze and basal part of tail; proximal 10 cm of tail dark black, next 25 cm blackish mixed with buffy (hairs blackish with 0.7 cm long white tip), distal 15 cm forming a buffy pencil.

Distinguished from *Callicebus stephennashi* by dark red-brown agouti instead of bright reddish forearms, forelegs, sideburns, and under-parts, black-brown to black instead of buffy to white cheiridia, and forehead and anterior part of crown not sharply contrasting with rest of crown, nape, and sides of body; from *C. cupreus*, with which it is parapatric along the lower Rio Purús in the west, by entirely black forehead and anterior part of crown, dark black-brown cheiridia, and the dominantly buffy tail mixed with blackish, and the white pencil; from *C. dubius*, by black forehead and anterior part of crown lacking a contrasted pale or whitish frontal tuft or transverse blaze; from *C. cinerascens*, with which it is parapatric along the lower Rio Madeira in the east, by reddish to dark red-brown sideburns, under-parts and inner sides of limbs, and the dominantly buffy tail and white pencil (Fig. 8).

Callicebus discolor (I. Geoffroy & Deville, 1848)



Holotype: Skin and skull of the holotype, collected in 1847 by Comte Francis de Castelnau and Émile Deville, were originally deposited in the Musée National d'Histoire Naturelle, Paris, France, but are no longer in the museum collection.

Type locality: Sarayacu, left bank of Río Ucayali, Ucayali, Peru.

Geographic distribution: Upper Amazonian region in Peru, south of the Río Marañon in the entire interfluve delineated by the Ríos Ucayali and Huallaga, and north of the Río Marañon between the Ríos Napo and Santiago; in Ecuador from the Andean foothills east to the Río Napo/Aguarico basin, and north to the Río Putumayo, and in Colombia to the right bank

of the Río Guamués (Hernández-Camacho and Cooper, 1976). Brooks and Pando-Vasquez (1997) recorded this species just to the north of the Río Napo on the left bank of its northern tributary, the Rio Sucusari, in Peru. Hernández-Camacho and Cooper (1976) recorded its range in the Colombian trapezium, between the Ríos Putumayo and Amazonas. In Figure 1, *C. discolor* is given as occurring throughout the interfluvium between the Ríos Putumayo-Içá and Amazonas-Solimões extending into Brazil, although this has yet to be confirmed. In the eastern part of its range the species is parapatric with *Callicebus cupreus* along the Río Ucayali (Figs. 1 and 2).

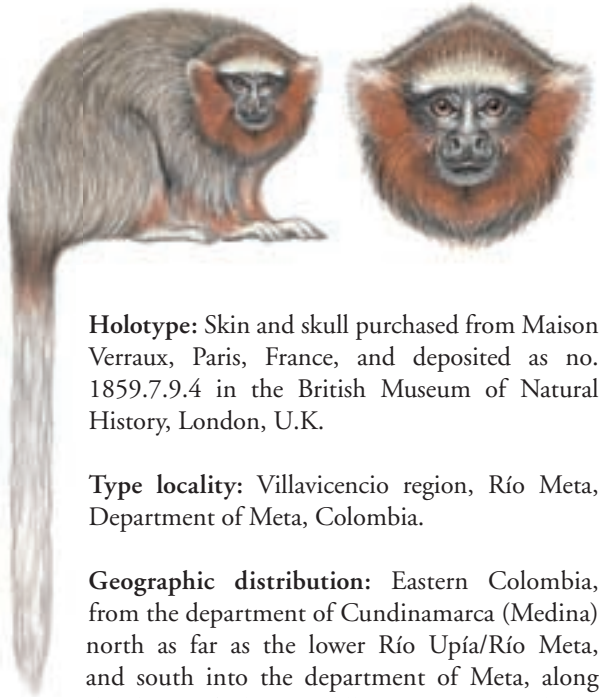
Moynihan (1976, p.75) mentions the presence of titi monkeys of the *moloch* Group in the close vicinity of the town of Valparaiso, between the Ríos Caquetá and Orteguaza in Colombia. These "lacked the white stripe above the eyes that is typical of both *ornatus* to the north and *discolor* to the south," and Moynihan indicated that they could be an unnamed subspecies (Fig. 1).

Diagnostic characters: Forehead with white or buffy tuft, contrasting with dark-brown transverse band, or blaze, this sharply contrasting with reddish crown and sideburns; often small white patches present alongside the lower jaw sharply contrasted with the reddish sideburns; sideburns, crown, side of neck, forearms, lower legs, cheiridia, chest and belly reddish, sharply contrasted with agouti back, sides of body, and tail; tail mixed brownish and buff-agouti, distal one-third to three-quarters predominantly buffy or white.

Figure 9. *Callicebus discolor* (I. Geoffroy & Deville, 1848), an adult female from unknown locality donated to M.G.M. van Roosmalen in 1988. Photographs by M. G. M. van Roosmalen.

Distinguished from *Callicebus oenanthe* and *C. ornatus* by entirely reddish forearms and cheiridia, from *C. cupreus* by one-third to three-quarters of tail buffy, white or buffy frontal tuft, and dark-brown blaze or transverse band (Fig. 9).

Callicebus ornatus (Gray, 1866)



Holotype: Skin and skull purchased from Maison Verraux, Paris, France, and deposited as no. 1859.7.9.4 in the British Museum of Natural History, London, U.K.

Type locality: Villavicencio region, Río Meta, Department of Meta, Colombia.

Geographic distribution: Eastern Colombia, from the department of Cundinamarca (Medina) north as far as the lower Río Upía/Río Meta, and south into the department of Meta, along the base of the Cordillera Oriental and the Sierra de la Macarena to the Río Guayabero/upper Río Guaviare. This species is the only member of the *cupreus* and *moloch* Group occurring north of the Rios Amazonas/Solimões/Napo axis, in the upper Río Orinoco basin and is separated from its nearest other member of the *cupreus* Group (*Callicebus discolor*) in the south by at least 350 km (Figs. 1 and 2).

Diagnostic characters: Ears and frontal tuft, transverse band or blaze whitish, sharply contrasted with reddish brown crown, the hair bases buffy; sideburns, under-parts, and inner side of limbs reddish; outer surface of thighs, upper arms, upper legs and sides of body buff-agouti; outer side of lower legs and lower part of forearms reddish, sharply contrasted with pale to whitish feet or toes only, and hands or digits only, respectively; proximal one-quarter of tail dark red-brown, distal three-quarters white.

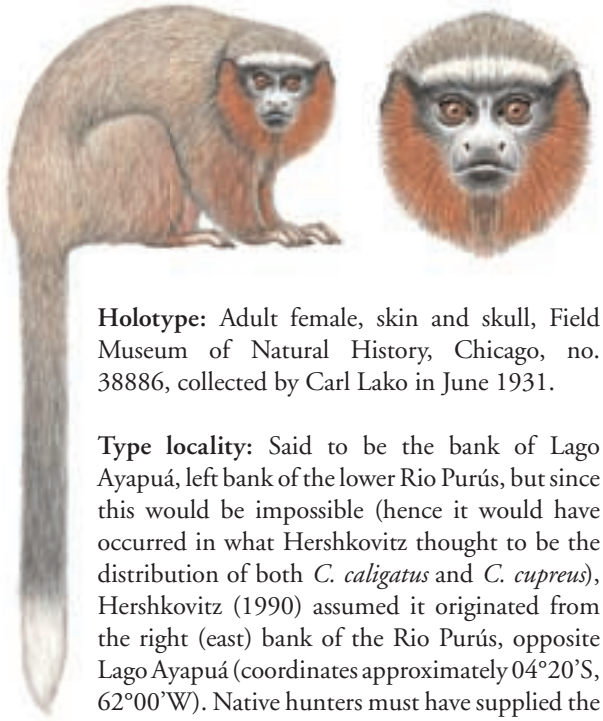
Distinguished from *Callicebus cupreus* and *C. discolor* by white ears, and pale or whitish digits and toes sharply contrasted with reddish wrists and ankles (Figs. 10, 11, and 12).

Figure 10. The ornate titi monkey, *Callicebus ornatus* (Gray, 1866). Photograph by R. A. Mittermeier in 1992.

Figure 11. The ornate titi monkey, *Callicebus ornatus* (Gray, 1866). An adult male from north of La Macarena, Colombia. Photographs by T. Defler at the Caparú Biological Station, Rio Apaporis, in 1992.

Figure 12. The ornate titi, *Callicebus ornatus* (Gray, 1866).

Callicebus dubius Hershkovitz, 1988



Holotype: Adult female, skin and skull, Field Museum of Natural History, Chicago, no. 38886, collected by Carl Lako in June 1931.

Type locality: Said to be the bank of Lago Ayapuá, left bank of the lower Rio Purús, but since this would be impossible (hence it would have occurred in what Hershkovitz thought to be the distribution of both *C. caligatus* and *C. cupreus*), Hershkovitz (1990) assumed it originated from the right (east) bank of the Rio Purús, opposite Lago Ayapuá (coordinates approximately 04°20'S, 62°00'W). Native hunters must have supplied the animal collector Carl Lako with specimens from either side of the Rio Purús and from far upstream, since M. G. M. and T. van Roosmalen recently located the species along the Rio Seruiní on the right bank of the Rio Purús, south of the Rio Ituxí. Some specimens in the British Museum originated from the vicinity (probably southwest) of the town of Humaitá on the left bank of the Rio Madeira, the source of the Rio Ituxí.

Geographic distribution: South of the Rio Ituxí, or maybe even the Rio Mucuím, both right bank tributaries of the Rio Purús, east as far as the Rio Madeira south of the town of Humaitá, and west to the Rio Purús, southern limit unknown. The species might be parapatric with *Callicebus stephennashi* along the Rio Ituxí or maybe the Rio Mucuím in the northern part of its range, with *Callicebus brunneus* along the upper Rio Madeira in the southern or

southeastern part of its range, and with *Callicebus cupreus* along the Rio Purús in the west (Figs. 1 and 2).

Diagnostic characters: Buffy or whitish frontal tuft, blaze, or transverse stripe, bordered below by blackish superciliary vibrissae forming narrow black line connecting the blackish ears, the crown brownish agouti; hairs of crown, nape, back, and rump with 4–5 narrow pheomelanin bands, each alternating with a eumelanin band; outer sides of thighs and upper arms brownish agouti like back; sideburns, sides of head, and beard deep reddish, outer surface of forearms and lower legs reddish; hairs of throat, chest, belly, and inner side of limbs not banded reddish to reddish brown; cheiridia blackish agouti, the fingers and toes contrasted pale or white; proximal one-third of tail red-brown agouti, as dorsum, rest of tail blackish, with a contrasted white pencil.

Distinguished from *C. caligatus* by its white or buffy frontal tuft or blaze, and lack of the black forehead and anterior part of crown; from *C. cupreus*, with which it is parapatric along the Rio Purús in the west by its white frontal tuft or blaze, and its white digits; from *C. brunneus* by its white or buffy frontal tuft or blaze and the contrasted white or buffy tail pencil; from *C. stephennashi* by its white or buffy frontal tuft or blaze and white digits only instead of entirely white cheiridia (as far as the wrists and ankles) (Fig. 13).

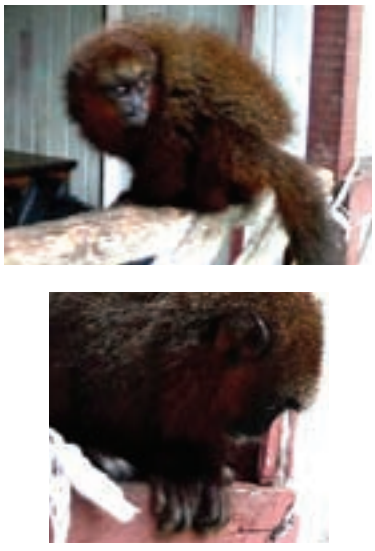
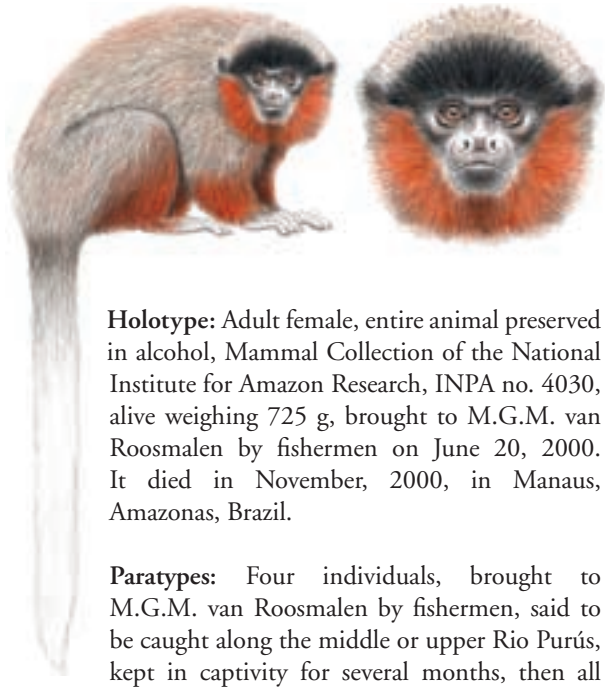


Figure 13. *Callicebus dubius* Hershkovitz, 1988, pet monkey from the Rio Seruiní, right bank of the Rio Purús, photographed in Pauiní, July 2001. Photographs by T. van Roosmalen.

Callicebus stephennashi new species



Holotype: Adult female, entire animal preserved in alcohol, Mammal Collection of the National Institute for Amazon Research, INPA no. 4030, alive weighing 725 g, brought to M.G.M. van Roosmalen by fishermen on June 20, 2000. It died in November, 2000, in Manaus, Amazonas, Brazil.

Paratypes: Four individuals, brought to M.G.M. van Roosmalen by fishermen, said to be caught along the middle or upper Rio Purús, kept in captivity for several months, then all died from dengue fever in November 2000. Adult male weighing 780 g, INPA no. 4031, three females weighing 740, 480, and 725 g, private collection numbers MGMR 51, 52 and 53, respectively, Manaus-Amazonas, Brazil (Table 2).

Type locality: Unknown. Holotype said to be caught somewhere along the middle to upper Rio Purús together with the paratypes.

Table 2. Measurements of specimens of *Callicebus* spp. collected by M.G.M. van Roosmalen.

Callicebus	Head & body (mm)	Tail	Hind foot	Ear	Weight (g)	Reference
caligatus	290	510	90	31	1000	MGMR 58
stephennashi	270	420	85	35	780	INPA 4031
stephennashi	280	420	90	30	725	INPA 4030
stephennashi	?	?	?	?	740	MGMR 51
stephennashi	?	?	?	?	480	MGMR 52
stephennashi	?	?	?	?	725	MGMR 53
bernhardi	360	550	100	35	1200	INPA 4033
bernhardi	370	?	90	30	700	INPA 4029
cinerascens	415	?	95	30	740	INPA 4085

Figure 14. Stephen Nash's titi monkey, *Callicebus stephennashi* new species. The adult female holotype, INPA 4030, and adult females MGMR 51 and MGMR 53. Photographs by M. G. M. van Roosmalen.

Geographic distribution: Since the new species seems to be phenotypically most closely related to both *C. caligatus* and *C. dubius*, we assume *Callicebus stephennashi* should occur along the right bank of the Rio Purús in between the distributions of *C. caligatus* and *C. dubius*. As a possible distribution, we suggest the interfluve delineated by the Rios Purús/Ipixuna/Madeira/Mucuím (Figs. 1 and 2).

Diagnostic characters: Forehead, superciliary vibrissae, and anterior portion of crown black, sharply contrasting with posterior portion of crown, nape, dorsum and rump which are silvery or buffy mixed with brownish agouti or brownish-black; ears blackish; lower arms and legs bright red, sometimes dark red as in *C. caligatus* and *C. baptista*, like sideburns, under parts, and inner sides of limbs, contrasting with silvery or buffy mixed with brownish agouti upper and outer parts; upper surface of cheiridia silvery buffy to white, the proximal third of foot red like lower legs, the hands entirely silvery or white; proximal portion of tail silvery mixed with brownish agouti to blackish brown, then black mixed with white or buffy, and distal half to two-third entirely white or buffy.

Distinguished from *C. caligatus* by black superciliary vibrissae, forehead and anterior portion of crown sharply contrasting with silvery agouti remainder of crown, nape and upper parts of body, by bright red instead of dark red-brown lower arms and legs, by white or buffy instead of blackish cheiridia, and almost entirely white or buffy tail; from *C. dubius* by black forehead and anterior portion of crown, lacking a white blaze, by white or buffy cheiridia instead of white digits only, and almost entirely white or buffy tail; from *C. cupreus* by black frontal blaze contrasting sharply against a silvery crown and nape, almost entirely white or buffy tail instead of an overall dark tail with white pencil, and by white or buffy instead of brown agouti cheiridia; from *C. brunneus* by its bright red sideburns, lower arms and legs, and under parts, white or

Figure 15. Stephen Nash's titi monkey, *Callicebus stephennashi* new species. Some details of the adult female holotype, INPA 4030. a. left hand, b. legs, feet and basal part of tail, c. feet aside of tail, d. middle part of tail against background of sides of body, e. detail of pelage on side of body, f. detail of pelage of underparts and lower legs. Photographs by M. G. M. van Roosmalen.

buffy cheiridia, and silvery agouti to silvery brown upper parts and sides of body (Figs. 14, 15, and 16).

Measurements: See Table 2.

External characters of holotype: Black of forehead and superciliary vibrissae continuing over anterior portion of crown as in *C. caligatus*, but sharply contrasting with posterior portion of crown, nape, back and rump which are buffy to silvery mixed with brownish agouti, the lax hairs cresting against shorter black hairs in front and longer raised nuchal hairs behind; ears blackish; hairs of dorsum and sides of body silvery mixed with brownish agouti, the individual hairs 4 cm long, six-banded as follows: proximal 1.5 cm brownish agouti to black-brown, then 3 white or silvery bands each alternating with a brown or blackish band, the tip of each hair silvery; lower arms and legs uniformly bright red like sideburns, sides of head, beard, under parts, and inner sides of limbs, contrasting with upper arms and thighs which are buffy to silvery mixed with brownish agouti; upper surface of cheiridia silvery white to buffy, the proximal (ankle) part of foot (3 cm) red like lower legs, the remaining 6 cm silvery white to buffy, upper surface of entire hands including wrists silvery or white; basal (proximal) one-sixth (ca. 8 cm) of tail same color as lower back and rump, next one-sixth (ca. 8 cm) black mixed with white or buffy (black hairs with 1 cm long white tip), remainder two-third entirely white or buffy; hairs of sideburns, throat, chest, belly, and inner side of limbs not banded red; blackish face naked except for fine buffy hairs surrounding lips and between nostrils.

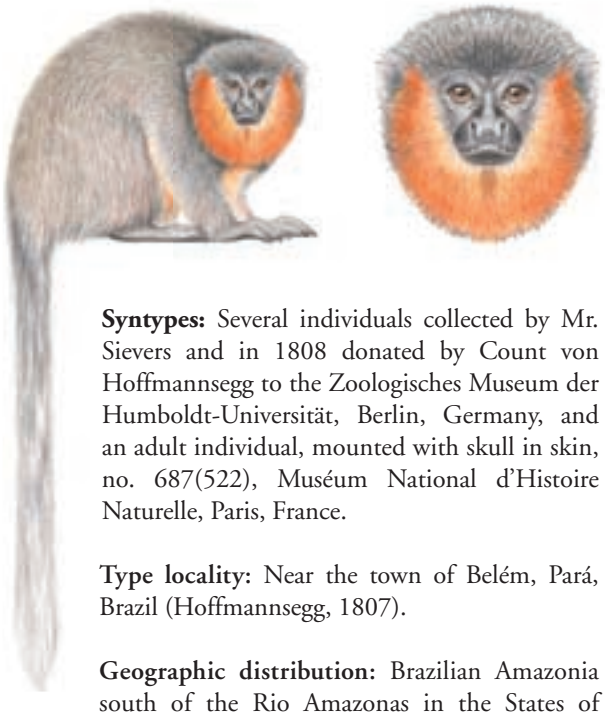
Origin of the name: This titi monkey is named in honor of our close friend and colleague, artist Stephen D. Nash, Technical Illustrator for Conservation International's President's office and its Center for Applied Biodiversity Science (CABS). He is based at the State University of New York at Stony Brook. For the past 20 years, Stephen has made major contributions to primate conservation and the science of primatology through his wonderful scientific illustrations and his educational materials, which have been widely distributed around the world.

Figure 16. Stephen Nash's titi monkey, *Callicebus stephennashi* new species. The adult female holotype, INPA 4030, and adult females MGMR 51 and MGMR 53. Photographs by M. G. M. van Roosmalen.

Vernacular name: Titi monkeys are referred to as *zog-zogs* or *zogue-zogues* by the local people in Amazonia. For an English name, we suggest Stephen Nash's titi monkey.

III. *C. MOLOCH* GROUP

Callicebus moloch (Hoffmannsegg, 1807)



Syntypes: Several individuals collected by Mr. Sievers and in 1808 donated by Count von Hoffmannsegg to the Zoologisches Museum der Humboldt-Universität, Berlin, Germany, and an adult individual, mounted with skull in skin, no. 687(522), Muséum National d'Histoire Naturelle, Paris, France.

Type locality: Near the town of Belém, Pará, Brazil (Hoffmannsegg, 1807).

Geographic distribution: Brazilian Amazonia south of the Rio Amazonas in the States of Pará and Mato Grosso. In Pará, from the west bank of Rio Tocantins/Araguaia west as far as the east bank of Rio Tapajós, south as far as Ilha do Bananal, north of the confluence of Rio das Mortes with the Rio Araguaia; in Mato Grosso, as far west as the Rio Juruena, including the headwaters of the Rio Xingú (M. G. M. van Roosmalen collected a specimen shot by a Waurá Indian hunter along Rio Von den Steinen) (Fig. 18). In the northwestern part of its range, the species

Figure 17. Captive adult red-bellied titi, *Callicebus moloch* (Hoffmannsegg, 1807). Photograph by R. A. Mittermeier.

is parapatric with *C. hoffmannsi* along the lower Rio Tapajós, and in the southwestern corner of its range it is parapatric with *C. cinerascens* along the upper Rio Juruena (Figs. 1 and 2).

Diagnostic characters: Upper and outer surface of head, trunk, and limbs buffy or grayish to pale brown agouti; forehead not sharply defined from grayish crown or distinctly paler, lacking whitish ear tufts; sideburns, under parts of body, and inner side of limbs sharply contrasting light orange to buff-orangish; cheiridia not sharply contrasting buffy; hairs of tail blackish agouti terminally, orange or buffy basally, distal half of tail including pencil buffy.

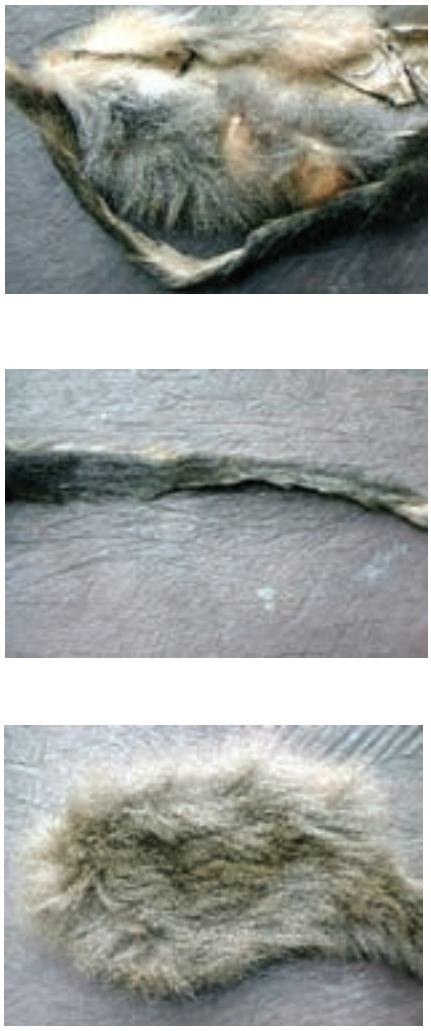
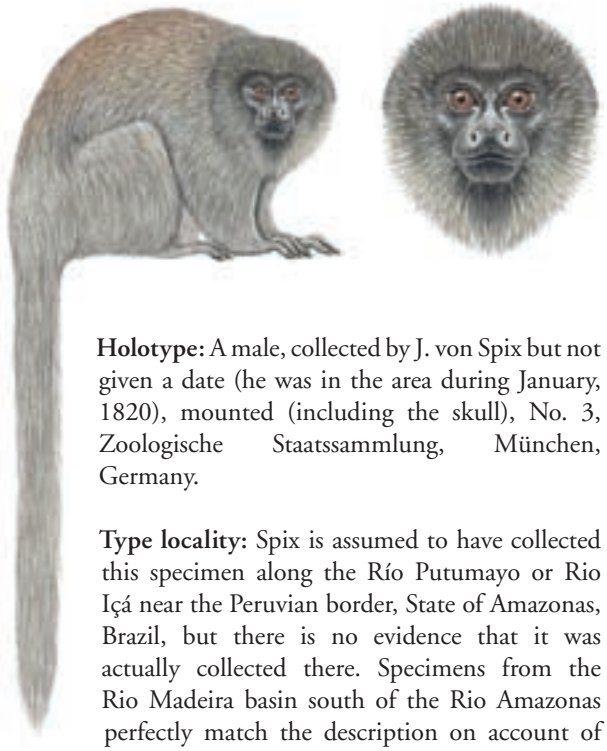


Figure 18. Specimen of the red-bellied titi monkey, *Callicebus moloch* (Hoffmannsegg, 1807) from the left bank of Rio Von den Steinen, upper Rio Xingú Indigenous Park, Mato Grosso, Brazil, representing the most southerly limit to its range. The skin was being used by a Waurá Indian hunter to make a headband. In the private collection of M. G. M. van Roosmalen (MGMR 56). Photographs by M. G. M. van Roosmalen.

Distinguished from *C. cinerascens* by uniformly light orange instead of grayish sideburns and inner sides of limbs, chest, and belly; from *C. brunneus* by grayish agouti instead of dark-brown to black forehead and crown; from *C. hoffmannsi* by rather contrasting buffy instead of undefined blackish agouti upper surface of hands and feet, and distal half of tail buffy instead of entirely blackish agouti to black; from *C. bernhardi* by lack of silvery to whitish ear tufts, light orange to buff-orangish instead of dark orange sideburns, under parts of body, and inner side of limbs, upper and outer surface of head, trunk, and limbs buffy or grayish to pale brown agouti instead of blackish agouti mixed with brown on the back, the distal half of the tail buffy instead of an entirely blackish agouti to black tail with sharply contrasted white pencil, and buffy upper surface of hands and feet slightly paler than outer side of arms and legs much less strikingly contrasted than in *C. bernhardi* with its white upper surface of hands and feet (Fig. 17 and 18).

Callicebus cinerascens (Spix, 1823)



Holotype: A male, collected by J. von Spix but not given a date (he was in the area during January, 1820), mounted (including the skull), No. 3, Zoologische Staatssammlung, München, Germany.

Type locality: Spix is assumed to have collected this specimen along the Río Putumayo or Rio Içá near the Peruvian border, State of Amazonas, Brazil, but there is no evidence that it was actually collected there. Specimens from the Rio Madeira basin south of the Rio Amazonas perfectly match the description on account of the holotype. Therefore, the type locality given by Spix must be wrong.

Geographic distribution: Hershkovitz (1990) includes three localities in his gazetteer: Prainha, right bank of Rio Aripuanã, Amazonas, Brazil (162[a]); São João, right bank of Rio Roosevelt (Hershkovitz gives here Rio Aripuanã, but his map indicates the Rio Roosevelt, a left bank tributary of Rio Aripuanã), Mato Grosso (205); and Otoho, right bank of upper Rio Roosevelt (Hershkovitz gives here Rio Ji-Paraná, but his map indicates Rio Roosevelt, Rondônia). This species has been observed in the wild by M.G.M.

van Roosmalen at the following localities along the right bank of Rio Aripuanã: Cipotuba, situated on the east bank of Lago Cipotuba (05°48'23"S, 60°12'76"W), Prainha, Igarapé da Prainha (05°45'S, 60°12'W), São João, Igarapé Terra Preta (05°28'S, 60°22'W), and along the right bank of the Rio Madeira in the vicinity of the town of Novo Aripuanã (05°07'08"S, 60°22'45"W), left bank of lower Rio Arara (40 km E of Novo Aripuanã, 05°12'S, 60°04'W), and in the vicinity of the town of Borba (04°22'S, 59°35'W). Rylands (1982) observed *C. cinerascens* on the east bank of the Rio Aripuanã at the Núcleo Pioneiro de Humboldt, Aripuanã, (then of INPA) (10°10'S, 59°27'W). M. G. M. van Roosmalen kept a live specimen from the left bank of the Rio Canumã, which was deposited in the Mammal Collection of the National Institute for Amazon Research (INPA) in Manaus, Amazonas, Brazil, under INPA 4085 (Table 2).

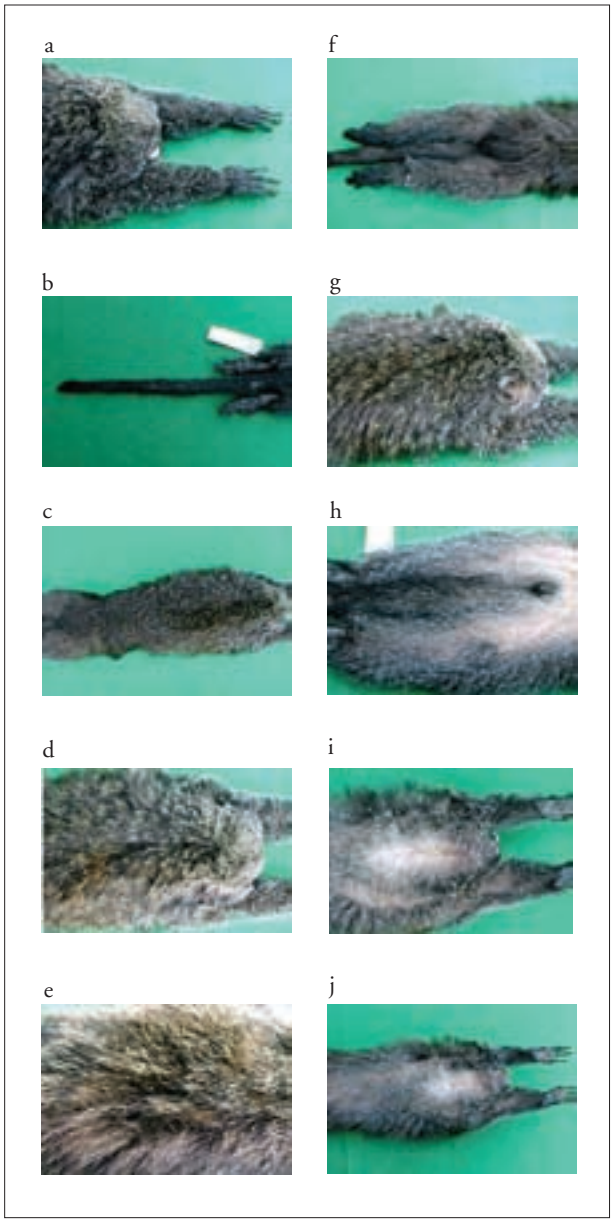


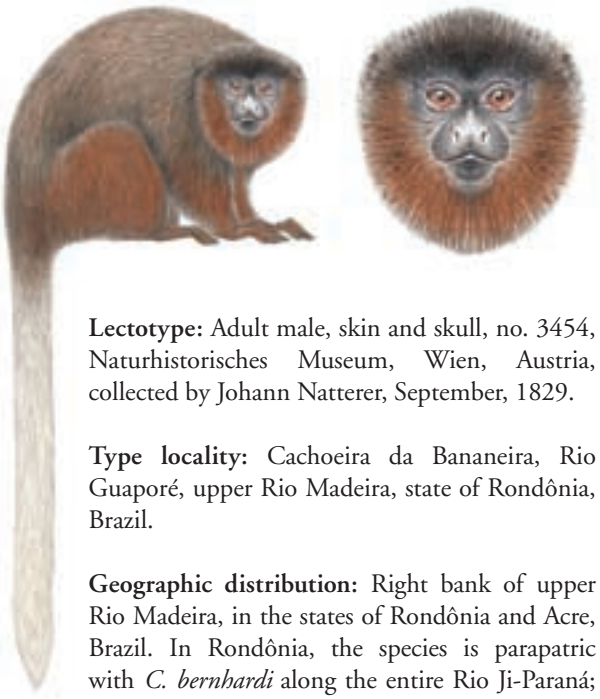
Figure 19. The ashy black titi, *Callicebus cinerascens* (Spix, 1823). Details of the dorsal (a–g) and ventral (h–j) pelage of an adult male from the left bank of the Rio Canumã, a right bank affluent of the Rio Madeira, not far south of the town of Nova Olinda do Norte (INPA 4085). Photographs by M. G. M. van Roosmalen.

The species is parapatric with *C. hoffmannsi* along the east bank of the Rio Canumã in the interfluve delineated by the lower Rio Madeira and Rio Canumã, with *C. baptista* along the north bank of the Paraná do Urariá, at the northern tip of its range, with *C. bernhardi* (a new species to be described below) along the west bank of the lower Rio Aripuanã in the interfluve delineated by the Rios Aripuanã and Roosevelt (its left bank tributary) and Rio Sucundurí, most likely including the interfluve between the Rios Acarí and Sucundurí, with *C. hoffmannsi* or a new, still to be described species of titi along the east bank of the Rio Sucundurí (east as far as the Rio Juruena) (Figs. 1 and 2).

Diagnostic characters: Forehead, crown, sides of body, chest, belly, limbs, and tail grayish to blackish agouti, all contrasting with tawny or reddish brown agouti mid-dorsum; upper surface of cheiridia blackish mixed with gray (hair tips grayish); tail predominantly blackish, mixed with gray, proximal one third mixed with tawny agouti like the outer surface of legs; arms blackish, the hairs grayish-tipped as in crown; hairs of dorsum and sides of body with 4 bands, a 2 cm wide blackish tawny proximal one, a 1 cm wide tawny band, a 1 cm wide black band, and a 0.3 cm wide, tawny agouti distal tip.

Distinguished from all other titi species by grayish agouti forehead, crown, sides of body, chest, belly, and limbs; sideburns and throat usually grayish to grayish agouti. (Fig. 19).

Callicebus brunneus (Wagner, 1842)



Lectotype: Adult male, skin and skull, no. 3454, Naturhistorisches Museum, Wien, Austria, collected by Johann Natterer, September, 1829.

Type locality: Cachoeira da Bananeira, Rio Guaporé, upper Rio Madeira, state of Rondônia, Brazil.

Geographic distribution: Right bank of upper Rio Madeira, in the states of Rondônia and Acre, Brazil. In Rondônia, the species is parapatric with *C. bernhardi* along the entire Rio Ji-Paraná;

in the north of its distribution, it is parapatric with *C. dubius* along the west bank of the Rio Madeira; in the west of its distribution, it is parapatric with *C. cupreus* along the upper Rio Purús; in the south of its distribution, it is parapatric with *C. modestus* in the interfluve of the Ríos Beni and Madre de Dios, and with *C. donacophilus* in the upper Río Mamoré and San Miguel basins, Bolivia (Figs. 1 and 2).

Diagnostic characters: Darkest species of the *moloch* group, the forehead, forearms, legs, cheiridia, and base of the tail blackish to dark reddish-brown, but rest of tail contrasted pale or dominantly buffy mixed with blackish; sideburns blackish to dark reddish-brown; upper parts and sides of body brownish or red-brown agouti, underparts brownish or reddish, not sharply defined from sides of body.

Distinguished from *C. bernhardi* by generally blackish or dark brown forehead, lack of white ear tufts, blackish- or reddish-brown instead of contrasted bright orange sideburns and under parts, and brownish or blackish not whitish cheiridia; from *C. cinerascens* by its generally blackish or dark brown instead of grayish appearance, blackish or reddish-brown instead of grayish sideburns, and tail dominantly buffy intermixed with black (Figs. 20 and 21).

Figure 20. The brown titi monkey, *Callicebus brunneus* (Wagner, 1842). Juvenile (left) and adult photographed in the National Zoo, Washington, DC, August 1988, by M. G. M. van Roosmalen.

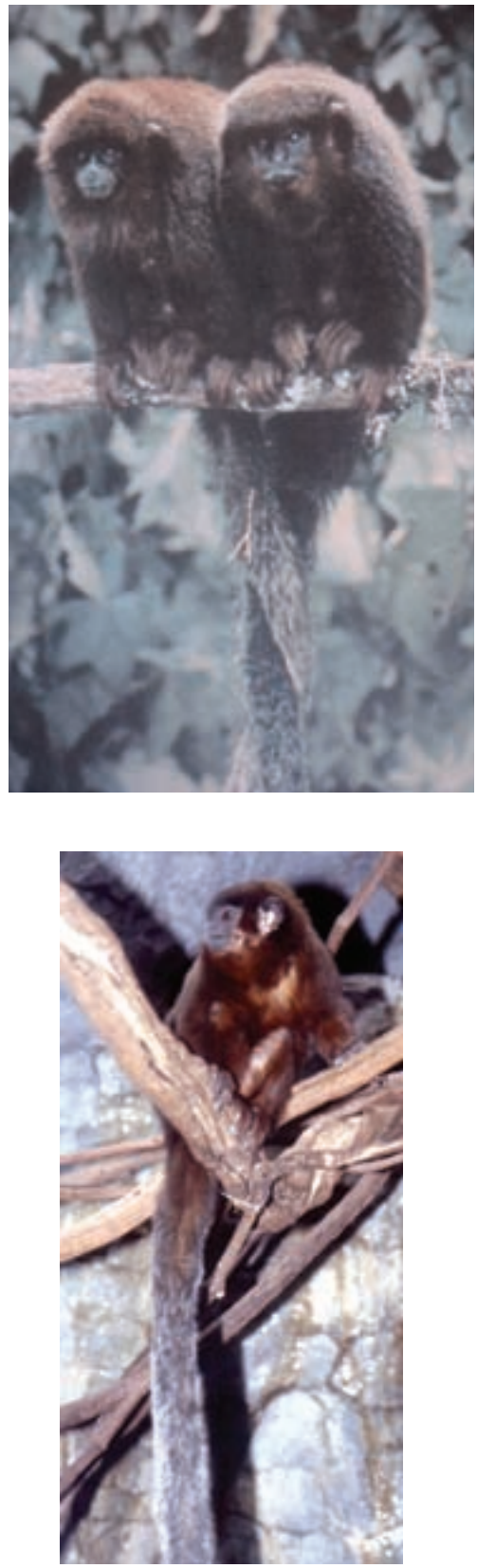
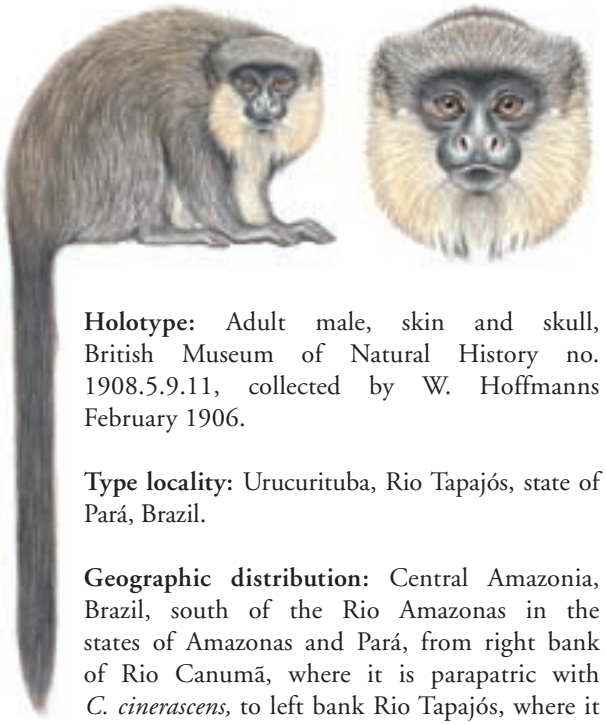


Figure 21. The brown titi monkey, *Callicebus brunneus* (Wagner, 1842). Top. Adult pair with the tails entwined typical for titis. Bottom. Adult photographed in the National Zoo, Washington, DC, August 1988, by M. G. M. van Roosmalen.

Callicebus hoffmannsi Thomas, 1908



Holotype: Adult male, skin and skull, British Museum of Natural History no. 1908.5.9.11, collected by W. Hoffmanns February 1906.

Type locality: Urucurituba, Rio Tapajós, state of Pará, Brazil.

Geographic distribution: Central Amazonia, Brazil, south of the Rio Amazonas in the states of Amazonas and Pará, from right bank of Rio Canumã, where it is parapatric with *C. cinerascens,* to left bank Rio Tapajós, where it is parapatric with *C. moloch*, south to the north (right) bank of Rio Sucundurí, where it is parapatric with an as yet undescribed species of titi, and north along the south bank of the Paraná do Urariá and Paraná do Ramos, east along the left bank of the Rio Andirá and the right bank of the Rio Uíra-Curupá south of the town of Parintins where it is parapatric with *C. baptista* (in the lower Rios Andirá/Uirá-Curupá interfluve and north of the Paraná do Urariá and Paraná do Ramos) (Figs. 1 and 2).

Diagnostic characters: Basically a two-colored (grayish and yellowish-white) titi. Upper and outer surface of head, trunk, and limbs grayish agouti, sometimes light gray to almost white; forehead grayish as crown, with or without a black or blackish coronal band not as far as the grayish ears; lacking white ear tufts; sideburns, under parts of body, inner side of limbs sharply contrasted yellowish to white; mid-dorsum olivaceous-grayish; tail blackish agouti to black; no whitish cheiridia nor tail-tip.

Distinguished from *C. moloch* by upper surface of hands and feet blackish agouti and black tail; from *C. baptista* by pale yellowish, not bright reddish or mahogany, sideburns and under parts, and black tail; from *C. cinerascens* by chest, belly, and inner side of limbs uniformly buffy (yellowish-white); from *C. bernhardi* by lacking white ear tufts, white cheiridia and white tip of the tail and having yellowish-white instead of bright orange sideburns, beard, under parts of body, and inner side of limbs (Figs. 22 and 23).

Figure 22. Hoffmann's titi monkey, *Callicebus hoffmannsi* Thomas, 1908. Top. Photographs by R. A. Mittermeier in the Belém Primate Center, Belém, Pará.

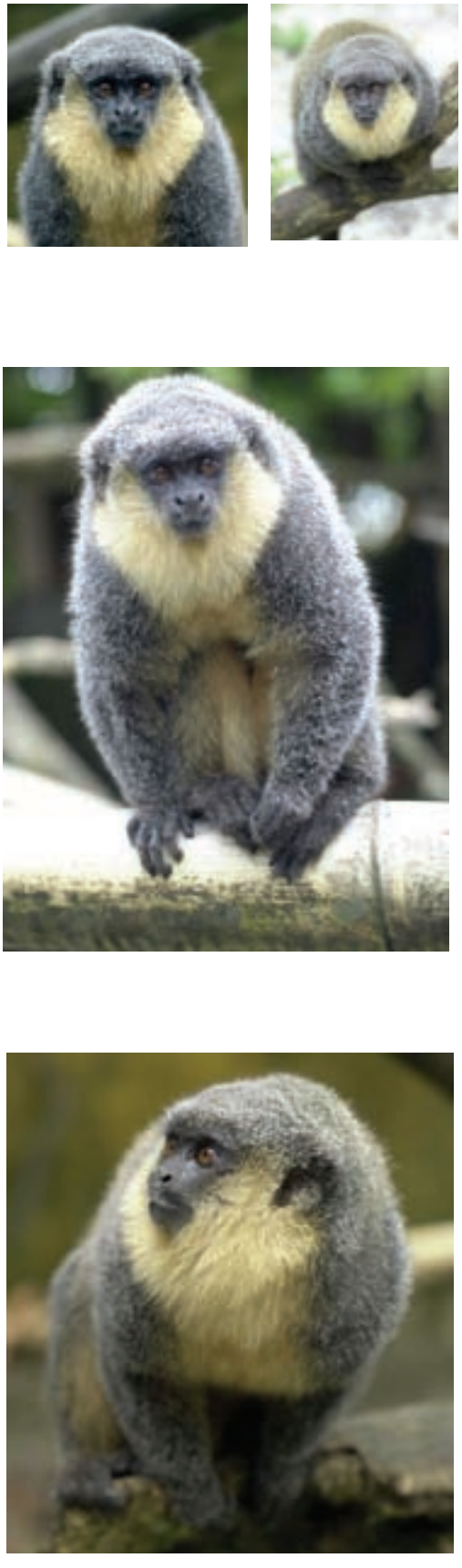
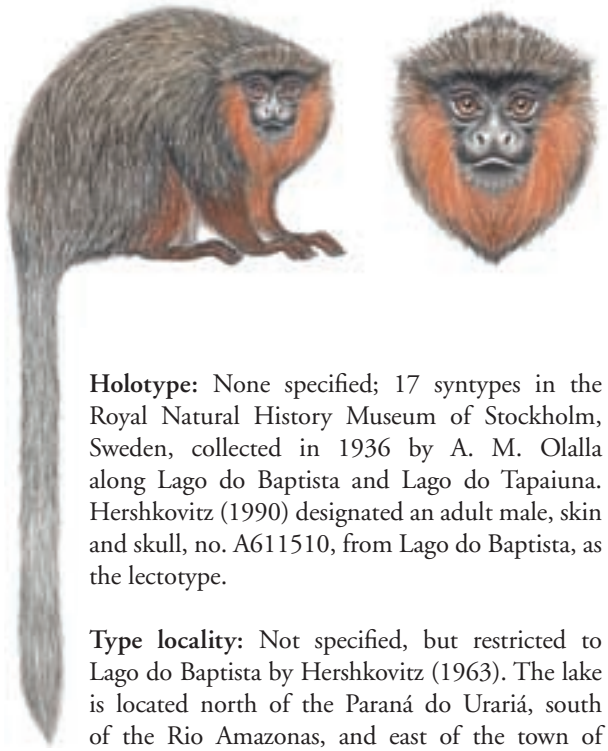


Figure 23. Hoffmann's titi monkey, *Callicebus hoffmannsi* Thomas, 1908. Photographs by Gary Comer.

Callicebus baptista Lönnberg, 1939



Holotype: None specified; 17 syntypes in the Royal Natural History Museum of Stockholm, Sweden, collected in 1936 by A. M. Olalla along Lago do Baptista and Lago do Tapaiuna. Hershkovitz (1990) designated an adult male, skin and skull, no. A611510, from Lago do Baptista, as the lectotype.

Type locality: Not specified, but restricted to Lago do Baptista by Hershkovitz (1963). The lake is located north of the Paraná do Urariá, south of the Rio Amazonas, and east of the town of Novo Olinda do Norte on the right bank of the Rio Madeira.

Geographic distribution: Central Amazonian Brazil, south of the Rio Amazonas and east of the Rio Madeira in the state of Amazonas east almost as far as the western limit of the state of Pará, and north of the Paraná do Canumã, Paraná do Urariá, and Paraná do Ramos. It was observed in the wild by the first author on the west (left) bank of the Rio Uíra-Curupá, and is believed to have crossed over the Paraná do Ramos west of the

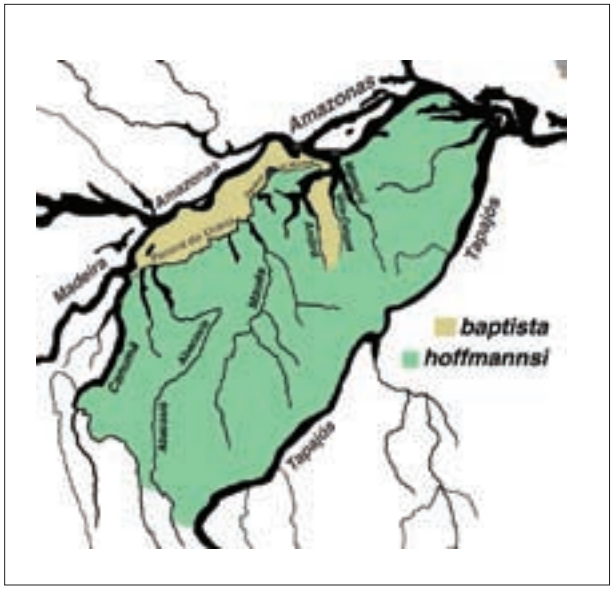


Figure 24. The distributions of *Callicebus baptista* and *Callicebus hoffmannsi* between the lower Rios Madeira and Tapajós in the central Brazilian Amazon. Map by Stephen D. Nash.

town of Parintins, forming an enclave population in the interfluve delineated by the lower Rio Uíra-Curupá and lower Rio Andirá. M. G. M. van Roosmalen also observed populations of entirely pale yellowish to almost white color morphs of *Callicebus hoffmannsi* along the Rio Mamurú, one river further to the east, and classic yellowish-white and gray *Callicebus hoffmannsi* on both banks of the middle and upper Rio Andirá (Fig. 24)**.** These observations confirm the parapatry of *Callicebus hoffmannsi* and *C. baptista*, and therefore they are elevated to full species here, whereas Hershkovitz (1990) considers them subspecies of *Callicebus hoffmannsi* (Figs. 1, 2, and 24).

Diagnostic characters: Sideburns, under parts, and inner side of limbs bright to dark reddish, or reddish brown (saturate pheomelanin); upper and outer surface of head, trunk, and limbs grayish to blackish agouti; forehead like crown, whitish ear tufts lacking; tail dominantly blackish agouti to entirely blackish, often intermixed with buff and gray hairs.

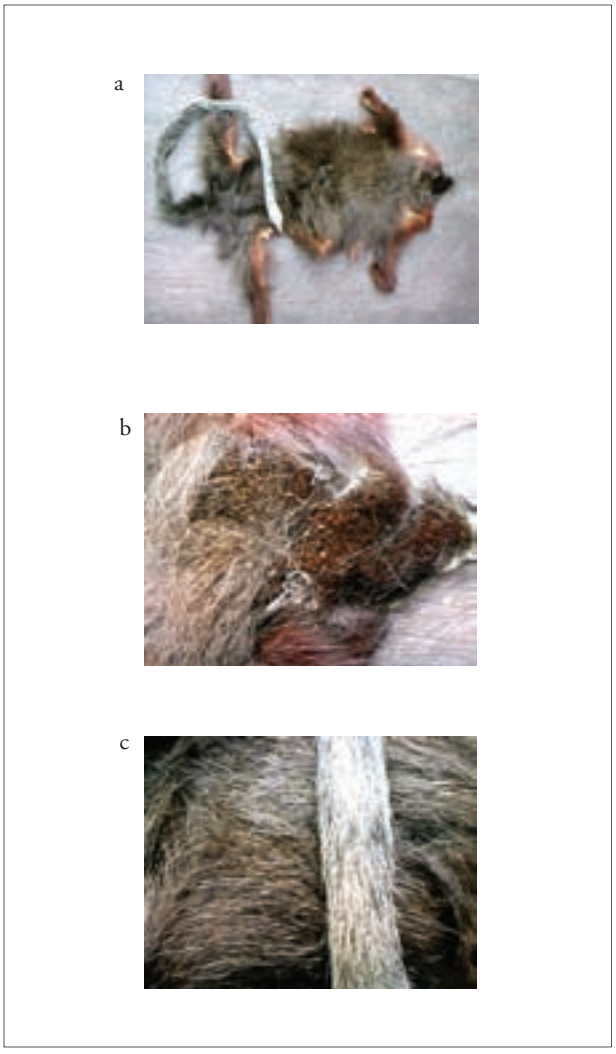
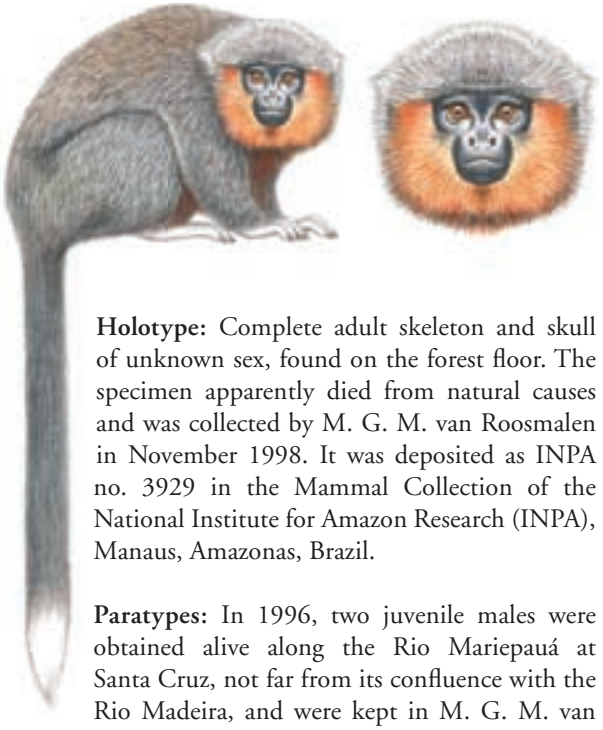


Figure 25. The Baptista Lake titi monkey, *Callicebus baptista* Lönnberg, 1939. A skin obtained from the left bank of the Rio Uíra-Curapá, a right bank affluent of the Rio Amazonas: a. whole skin, b. crown and nape, c. tail on the background of the dorsum. In the private collection of M. G. M. van Roosmalen (MGMR 50). Photographs by M. G. M. van Roosmalen.

Distinguished from *C. cinerascens* and *C. hoffmannsi* by uniformly reddish or reddish brown sideburns, and underparts and inner surface of limbs; from *C. bernhardi* by lack of white ear tufts, white cheiridia and white tail tip; from *C. moloch* by dark brownish or grayish agouti upper and outer parts of trunk, limbs, crown and forehead, reddish or reddish brown instead of bright orange sideburns, and lacking the buffy upper surface of the cheiridia and buffy pencilled tip of tail (Fig. 25).

Callicebus bernhardi new species



Holotype: Complete adult skeleton and skull of unknown sex, found on the forest floor. The specimen apparently died from natural causes and was collected by M. G. M. van Roosmalen in November 1998. It was deposited as INPA no. 3929 in the Mammal Collection of the National Institute for Amazon Research (INPA), Manaus, Amazonas, Brazil.

Paratypes: In 1996, two juvenile males were obtained alive along the Rio Mariepauá at Santa Cruz, not far from its confluence with the Rio Madeira, and were kept in M. G. M. van Roosmalen's Breeding Center for Endangered Amazonian Monkeys in Manaus, Brazil. They died in April and August 2001 and are deposited as INPA no. 4029 and INPA no. 4033, respectively, in the Mammal Collection of the National Institute for Amazon Research (INPA), Manaus, Amazonas, Brazil.

Type locality: West bank of the lower Rio Aripuanã, at the edge of the settlement of Nova Olinda, 41 km southwest of the town of Novo Aripuanã, Amazonas state, Brazil. This region is located in south-central Amazonia, south of Rio Amazonas and east of Rio Madeira. Coordinates for the type locality are: 05°30'63"S, 60°24'61"W. Altitude 45 m. (Fig. 26).

Geographic distribution: Interfluve delineated by the Rios Madeira-Jí-Paraná and Rios Aripuanã-Roosevelt, in the states of Amazonas and Rondônia, Brazil. In Rondônia, the species is parapatric in the west with *C. brunneus* along the entire Rio Jí-Paraná, and in the east

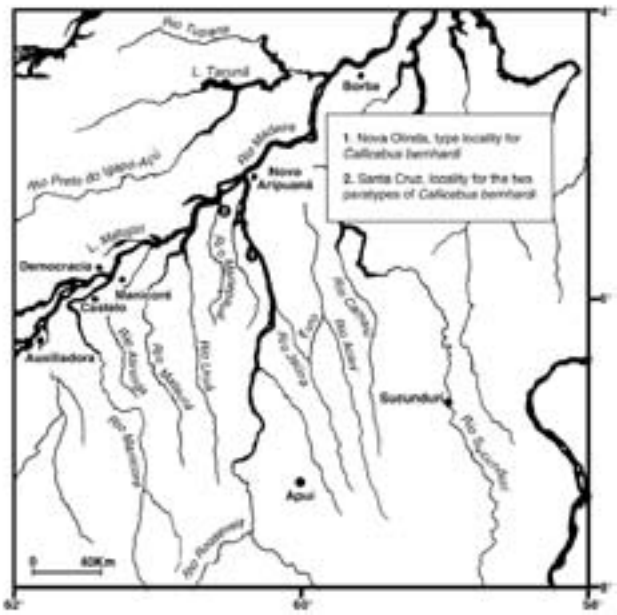


Figure 26. Collecting localities for *Callicebus bernhardi* new species.

Figure 27. Prince Bernhard's titi monkey, *Callicebus bernhardi* new species. The adult male paratype INPA 4033 from the Rio Mariepauá, affluent of the Rio Madeira, in 1998. Photographs by M. G. M. van Roosmalen.

with *C. cinerascens* along the Rio Roosevelt; in Amazonas, the species is parapatric with *C. dubius* in the west along the middle Rio Madeira, and with *C. cinerascens* in the east along the Rio Aripuanã (Figs. 1 and 2). Ferrari *et al.* (1996) observed a grey titi monkey at Pimenta Bueno in Rondônia, on the west bank of the Rio Ji-Paraná. They noted that it was not the distinctively brown-colored *C. brunneus* and were unable to identify it. It may have been *C. bernhardi*, which would extend its range a little to the west across the upper the Rio Ji-Paraná, but this requires confirmation.

This species has been observed in the wild by M.G.M. van Roosmalen at the following localities: west bank of lower Rio Aripuanã, Nova Olinda, Amazonas state, 05°30'01"S, 60°24'27.4"W; west bank of lower Rio Aripuanã, Monte Alegre, Reserva Florestal Getal, 05°34'68"S, 60°23'40"W; west bank of lower Rio Aripuanã, Novo Oriente (Capimtuba), 05°43'41"S, 60°17'09"W; east bank of middle Rio Madeira, seringal São Luis, ca. 5 km south of the town of Manicoré, 05°50'28"S, 61°18'19"W, altitude 45 m.

Diagnostic characters: Upper and outer surface of head, trunk, and limbs grayish black, on the back mixed with brownish agouti or red-brown; forehead not defined from crown, grayish black to gray; ears black with conspicuous whitish tufts; sideburns, under parts of body, and inner side of limbs sharply contrasted dark orange; cheiridia sharply contrasted white against grayish black lower limbs; tail black except for a sharply contrasted white pencil.

Distinguished from *C. cinerascens* by uniformly dark orange instead of grayish sideburns and inner sides of limbs, chest, and belly, and tail with white pencil; from *C. brunneus* by grayish instead of dark brown to black forehead and crown, and dark orange sideburns, inner sides of limbs, chest, and belly; from *C. hoffmannsi* and *C. baptista* by strikingly contrasting white ear tufts, cheiridia and tip of the tail (pencil); from *C. moloch* by grayish forehead and crown, white ear tufts, and blackish tail with a distinct white pencil; from *C. dubius* by lack of black vibrissae and white blaze (Figs. 27, 30–34).

External characters of holotype: Forehead, crown, sides of body, and outer sides of limbs grayish; rump, mid-dorsum,

back, and nape grayish mixed with brownish agouti to reddish brown, the hairs 5 cm long, with 5 blackish bands alternating with 4 narrow brownish agouti to red-brown ones, the most proximal (2 cm long) and the distal one (tip) black; face black with some white hairs around mouth and nostrils; ears black with white tufts contrasted with light grayish forehead and crown; tail ca. 55 cm long, the distal 7 cm forming a white pencil (Table 2).

Figure 28. Skull and mandible of the adult (unknown sex) holotype of *Callicebus bernhardi* (INPA 3929). Photographs by M. G. M. van Roosmalen.

Cranial measurements: See Table 3 and Figures 28 and 29.

Habitat: Titi monkeys of the *cupreus* and *moloch* Group essentially are secondary and disturbed forest specialists. The various groups of *C. bernhardi* observed in the wild by M. G. M. van Roosmalen were invariably in naturally or anthropogenically disturbed forest, such as *blow-downs* (large patches of secondary forest after massive deforestation caused by dramatic rainstorm events), liana forest on abandoned *terras pretas*, secondary forest surrounding plantations and fields, and so-called *seringais,* an early form of agroforestry, in which areas of high riverbank forests along Amazonian white-water rivers were turned into productive multi-species forests. These forests are rich in a number of commercially valuable and edible fruit-producing native trees, including rubber (*Hevea brasiliensis*), Brazil nut (*Bertholletia excelsa*), wild cocoa (*Theobroma* spp.), 'bacurí' (*Rheedia* spp., *Platonia insignis*), 'ingá' (*Inga* spp.), 'taperebá' (*Spondias mombin*), 'biribá' (*Rollinia squamosa*), 'soursop' (*Annona* spp.), and a number of tree species belonging to the sapotilla family (Sapotaceae) and palms (Palmae or Arecaceae). These *seringais* seem to

Table 3. Cranial and dental measurements of the holotype *Callicebus bernhardi* (INPA 3929) (mm) (measurements taken by R. Voss).

Cranial measurements	**(mm)**
Greatest skull length	64
Condylobasal length	53
Zygomatic breadth	40
Biorbital breadth	36
Postorbital constriction	31
Brain-case length	52
Brain-case width:	34
Greatest skull length	64
Condylobasal length	53

Dental measurements **Outside crown-to-crown dimensions**	**(mm)**
$I – M^3$	23.19
$C – M^3$	18.06
$PM^2 – M^3$	15.62
$M^1 – M^3$	9.76
$I^2 – I^2$	10.08
$C^1 – C^1$	14.47
$M^1 – M^1$	21.31
$M^3 — M^3$	20.49

Mandible measurements	**(mm)**
Mandible length	42.76
Mandible height	34.44

offer optimal habitat and a year-round food supply for titi monkeys, marmosets, tamarins, and night monkeys. The highest densities of titi monkeys of the *cupreus* and *moloch* Group can be found in these *seringais,* if the local people do not hunt them. Often before dawn in the early morning, all pairs living in the area can be heard performing duet calls and, therefore, local densities of titis can be easily estimated.

Origin of the name: This titi monkey is named in honor of His Royal Highness Prince Bernhard of the Netherlands, who for half a century has been a global leader in nature conservation. In particular, the authors are grateful to him for having created the Order of the Golden Ark, a highly prestigious award, equivalent to knighthood, which is presented every year to a select group of conservationists from around the world. Two of the authors (RAM in 1995; MGMR in 1997) have been thus honored and are naming this new titi as a small token of their appreciation.

Vernacular name: This titi monkey is referred to as *zog-zog* or *zogue-zogue* by the local people. For an English name, we suggest Prince Bernhard's titi monkey.

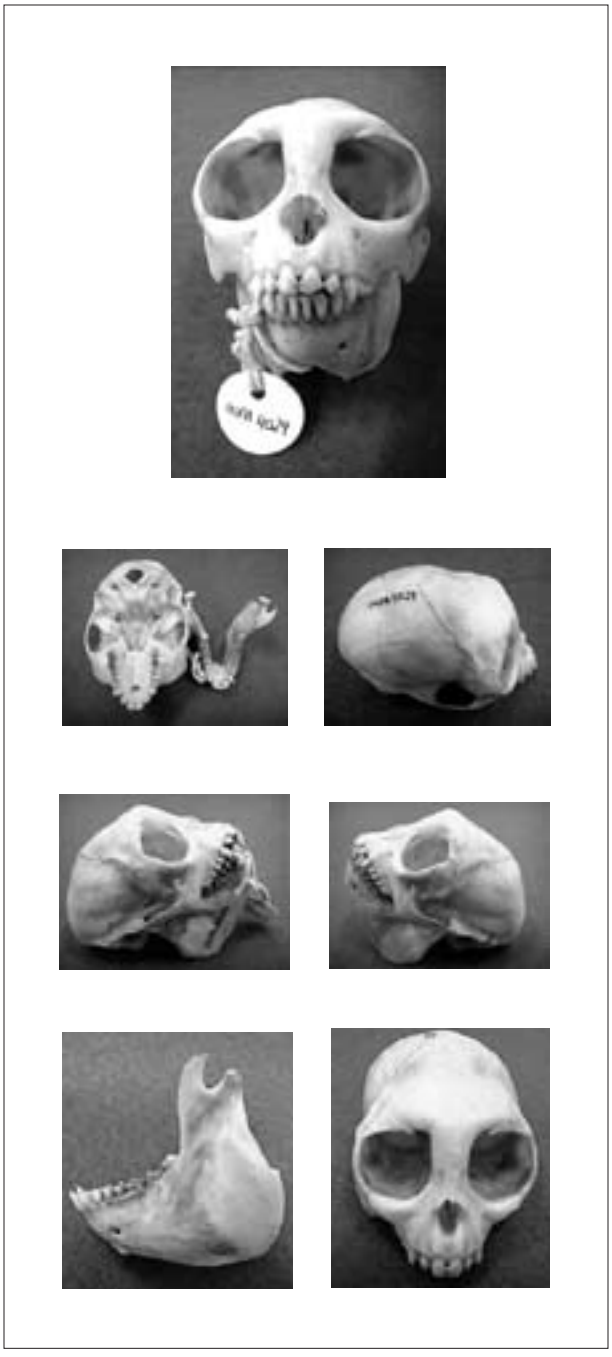


Figure 29. Skull and mandible of the adult male paratype of *Callicebus bernhardi* (INPA 4029). Photographs by M. G. M. van Roosmalen.

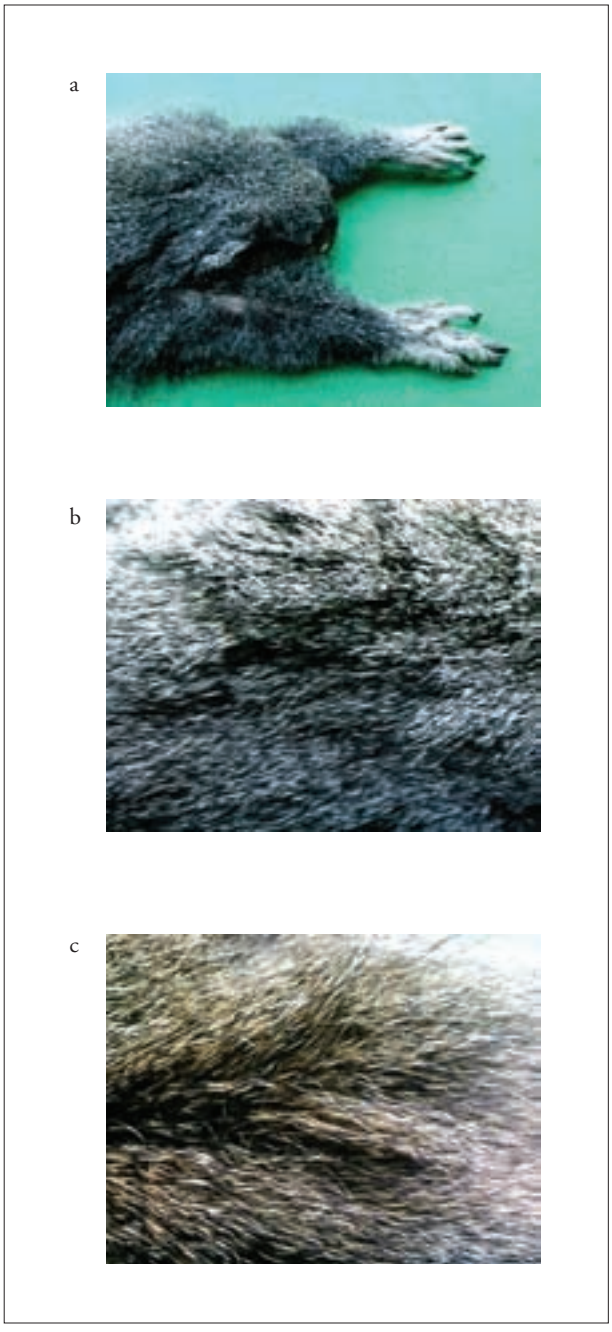


Figure 30. Dorsal views of the adult male paratype of *Callicebus bernhardi* (INPA 4029): a. crown, forearms and hands, b. close up of hairs of the nape, and c. close up of the hairs of the mid-dorsum. Photographs by M. G. M. van Roosmalen.

a

b

c

d

e

Figure 31. Details of the adult male paratype of *Callicebus bernhardi* (INPA 4033): a. dorsal surface of feet, b. inner side of right arm and tail tip, c. dorsal surface of left hand, d. close-up of dorsal pelage, e. crown, ear, and part of sideburn. Photographs by M. G. M. van Roosmalen.

Figure 32. Prince Bernhard's titi monkey, *Callicebus bernhardi* new species. Views of the adult male paratype (INPA 4029). Photographs by Gary Comer.







Figure 33. Prince Bernhard's titi monkey, *Callicebus bernhardi* new species. Views of the adult male paratype (INPA 4029). In the top left photograph it is with a Sateré marmoset, *Mico saterei* (Sousa e Silva & Noronha, 1998). Photographs by M. G. M. van Roosmalen.

Figure 34. Prince Bernhard's titi monkey, *Callicebus bernhardi* new species. Views of the adult male paratype (INPA 4029). Photographs by M. G. M. van Roosmalen.

IV. *C. TORQUATUS* GROUP

Callicebus torquatus (Hoffmannsegg, 1807)

Syntypes: One, perhaps the holotype, mounted in the Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; another syntype, no. 687(522), in the Muséum National d'Histoire Naturelle, Paris, collected before 1806 by F.W. Sieber, donated in 1808 to the Lisbon Museum, Portugal, by Count von Hoffmannsegg, and later removed to Paris, France.

Type locality: Interior of state of Pará (before 1850 including the state of Amazonas), Brazil, re-determined by Hershkovitz (1963) as Codajás, a town on the north bank of the Rio Solimões, state of Amazonas.

Geographic distribution: State of Amazonas, Brazil; left (north) bank of Rio Solimões/Rio Japurá, west as far as Río Apaporis/upper Río Vaupés. The range in the north is delineated by the Rio Negro/Rio Uaupés, east at least as far as the town of Codajás, maybe even as far as the town of Manacapurú, both on the north bank of the Rio Solimões, west of Manaus (Figs. 35 and 37).

Diagnostic characters: Forehead, crown, sideburns, back, trunk and outer surface of limbs uniformly dark reddish to blackish brown; underparts, chest and belly reddish or reddish brown; throat collar weakly defined, buffy, not extending to ear base; hands and feet whitish or buffy; tail blackish mixed with reddish.

Distinguished from *C. purinus* by blackish forehead and dark reddish crown not sharply demarcated from mahogany nape, hairs of back uniformly colored or faintly banded, and white cheiridia; from *C. regulus* by reddish brown instead of brown to blackish underparts, back of crown not markedly differentiated from forehead and nape, and white cheiridia; from *C. lucifer* and *C. lugens* by overall reddish brown or mahogany coloration and white hands and feet; from *C. medemi* by buffy or white instead of black cheiridia (Fig. 36).

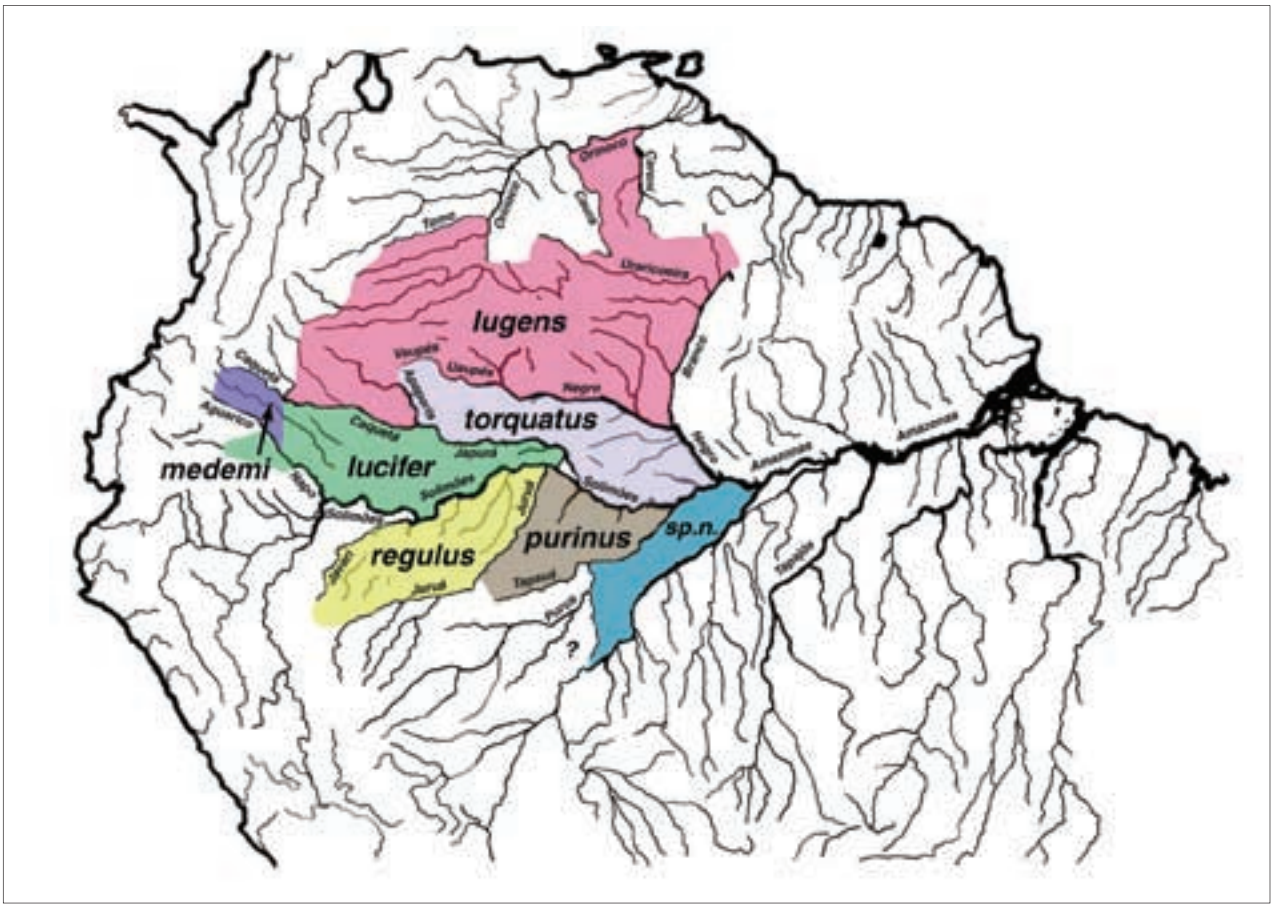
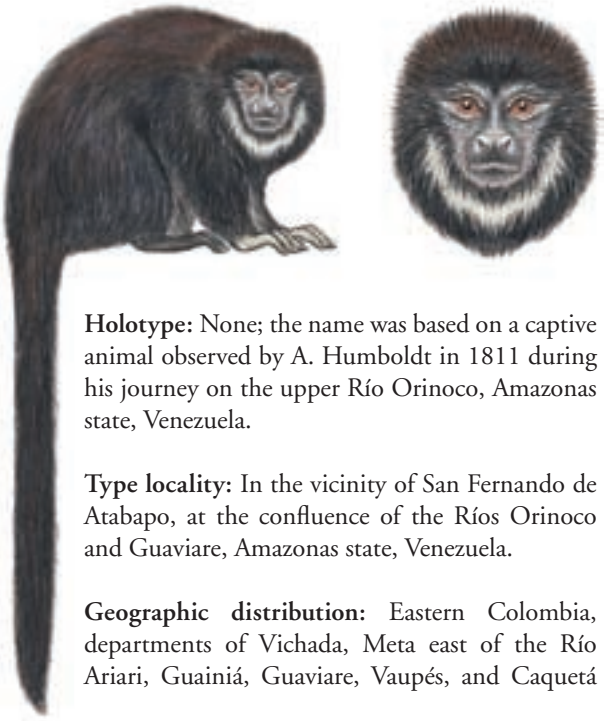


Figure 35. Distributions of the Amazonian titi monkeys, genus *Callicebus,* belonging to the *torquatus* Group. Map by Stephen D. Nash.

Figure 36. The collared titi monkey, *Callicebus torquatus* (Hoffmannsegg, 1807). A pet seen in 1973 in Tefé, Amazonas, Brazil. Photographs by R. A. Mittermeier.

***Callicebus lugens* (Humboldt, 1811)**



Holotype: None; the name was based on a captive animal observed by A. Humboldt in 1811 during his journey on the upper Río Orinoco, Amazonas state, Venezuela.

Type locality: In the vicinity of San Fernando de Atabapo, at the confluence of the Ríos Orinoco and Guaviare, Amazonas state, Venezuela.

Geographic distribution: Eastern Colombia, departments of Vichada, Meta east of the Río Ariari, Guainiá, Guaviare, Vaupés, and Caquetá

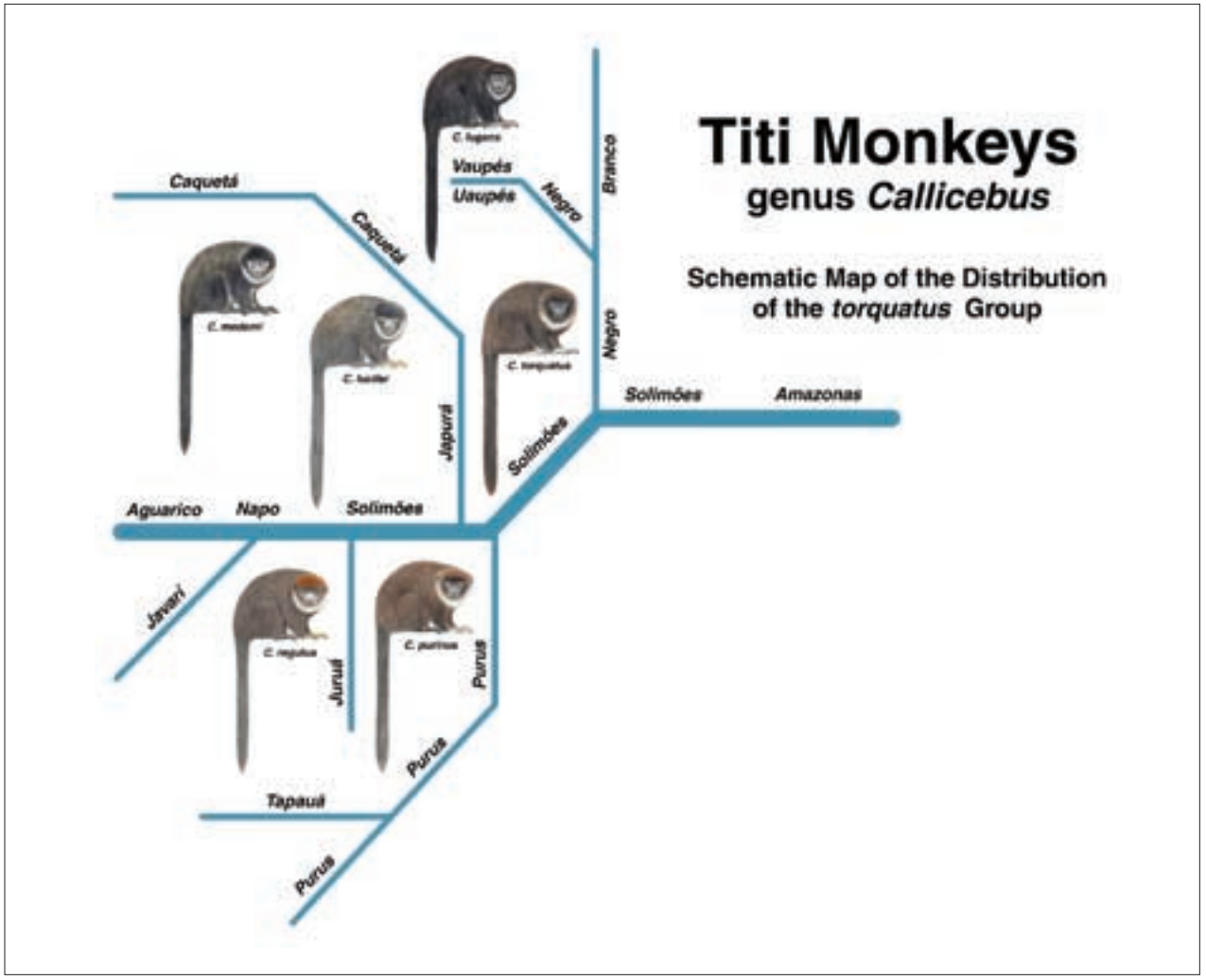


Figure 37. Schematic map of the distribution of the Amazonian titi monkeys belonging to the *torquatus* Group. Illustrations by by Stephen D. Nash.

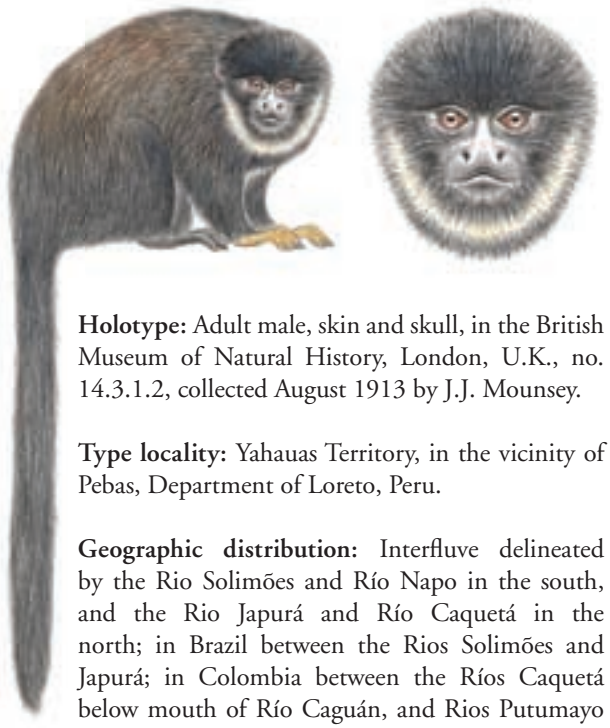
east of the Río Caguán, between the Río Tomo in the north and Río Caguán-Caquetá in the south; southern Venezuela, state of Amazonas south of the Río Ventuari, and state of Bolívar between the Ríos Caura, Caroni, and Orinoco; and bordering parts of northwestern Brazil, Amazonas state north of the Rios Uaupés-Negro, and the state of Roraima west of the Rio Branco, north as far as the foothills of Mount Roraima (personal observations by M.G.M. van Roosmalen) (Figs. 35 and 37).

Diagnostic characters: Feet, tail, head, sideburns, and under parts except throat entirely blackish, hairs of back and sides of body blackish intermixed with dark chestnut, the hairs uniformly colored or faintly banded, hands and throat contrasted white.

Figure 38. *Callicebus lugens* (Humboldt, 1811). An adult female from the interfluve of the Río Caquetá (left bank) and the Río Apaporis (right bank), west of the main portage between the two rivers and downriver from La Pedrera, near the border between Colombia and Brazil. Photographed at the Caparú Biological Station, Río Apaporis, by R. A. Mittermeier in August, 1995.

Most blackish of the *C. torquatus* Group, distinguished from *C. torquatus, C. purinus,* and *C. regulus* by blackish chest and belly, and white hands combined with black feet; from *C. lucifer* by lack of contrast between blackish crown and reddish brown or blackish nape, hairs of back uniformly colored or faintly banded, and white instead of orange hands; from *C. medemi* by white instead of blackish hands (Fig. 38).

Callicebus lucifer Thomas, 1914



Holotype: Adult male, skin and skull, in the British Museum of Natural History, London, U.K., no. 14.3.1.2, collected August 1913 by J.J. Mounsey.

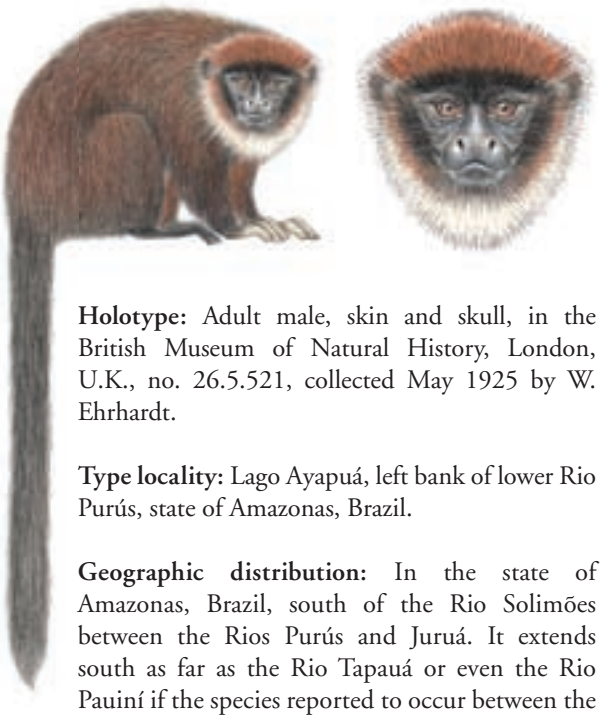
Type locality: Yahauas Territory, in the vicinity of Pebas, Department of Loreto, Peru.

Geographic distribution: Interfluve delineated by the Rio Solimões and Río Napo in the south, and the Rio Japurá and Río Caquetá in the north; in Brazil between the Rios Solimões and Japurá; in Colombia between the Ríos Caquetá below mouth of Río Caguán, and Rios Putumayo and Amazonas in the departments of Caquetá, Putumayo and Amazonas; in Ecuador between the upper Ríos Aguarico and Putumayo, Napo province; and in Peru in northern Loreto, between the Ríos Putumayo, Nanay, and Amazonas. Campos *et al.* (1992) and De la Torre *et al.* (1995) report on the presence of *C. torquatus*, which we presume to be *C. lucifer* (but may, alternatively, be *C. medemi*) in the Cuyabeno Reserve, Río Aguarico, province of Sucumbios, in northeastern Ecuador (Figs. 35 and 37).

Diagnostic characters: Feet, tail, head, sideburns, and under parts except throat entirely blackish, hairs of back and sides of body brownish or reddish brown, the hairs distinctly to weakly banded, throat white, hands orange.

Distinguished from *C. lugens* by brownish agouti upper parts and orange instead of white hands; from *C. torquatus* and *C. purinus* by orange instead of white hands and blackish under parts; from *C. regulus* by blackish (except white throat) head and hairs surrounding ears uniformly blackish, and orange hands; from *C. medemi* by dominantly or entirely orange instead of black hands.

Callicebus purinus Thomas, 1927



Holotype: Adult male, skin and skull, in the British Museum of Natural History, London, U.K., no. 26.5.521, collected May 1925 by W. Ehrhardt.

Type locality: Lago Ayapuá, left bank of lower Rio Purús, state of Amazonas, Brazil.

Geographic distribution: In the state of Amazonas, Brazil, south of the Rio Solimões between the Rios Purús and Juruá. It extends south as far as the Rio Tapauá or even the Rio Pauiní if the species reported to occur between the Rios Tapauá and Pauiní, left bank of tributaries of the Rio Purús, does not represent a new form (Figs. 35 and 37).

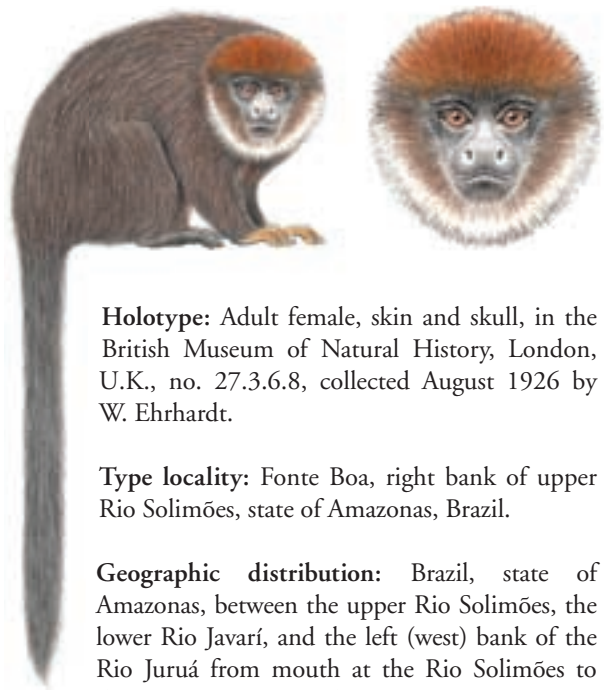
Figure 39. *Callicebus purinus* Thomas, 1927. An adult female, a pet monkey photographed at the seringal/castanhal Camaruã, at the north bank near the mouth of the Rio Tapauá with the Rio Purús, August 2, 2001. Photographs by M. G. M. van Roosmalen.

Figure 40. *Callicebus purinus* Thomas, 1927. An adolescent male from seringal/castanhal Camaruã, near the mouth of the Rio Tapauá with the Rio Purús, August, 2001. Photographs by M. G. M. van Roosmalen.

Diagnostic characters: Hands whitish, lower arms and feet black, hairs of back and sides dark red-brown, strongly to faintly banded, tail blackish with mixture of reddish, under parts except throat dark reddish brown or reddish, throat collar contrastingly colored buffy, yellowish, or whitish, the collar well developed and extending to ear base, sideburns, forehead (blaze) and ears black, sharply contrasting with white whiskers and bright red crown.

Distinguished from *C. torquatus* by bright reddish crown sharply contrasting with black forehead and sideburns, marked strongly to faintly banded agouti pattern of back, throat collar more developed and sharply defined from surrounding parts, and black instead of white or buffy feet; from *C. regulus, C. lugens* and *C. lucifer* by reddish brown instead of blackish under-parts (chest and belly) and by more reddish coloration throughout, the crown always sharply defined from nape; and from *C. medemi* by more reddish coloration throughout, and white or yellowish instead of black hands (Figs. 39 and 40).

Callicebus regulus Thomas, 1927



Holotype: Adult female, skin and skull, in the British Museum of Natural History, London, U.K., no. 27.3.6.8, collected August 1926 by W. Ehrhardt.

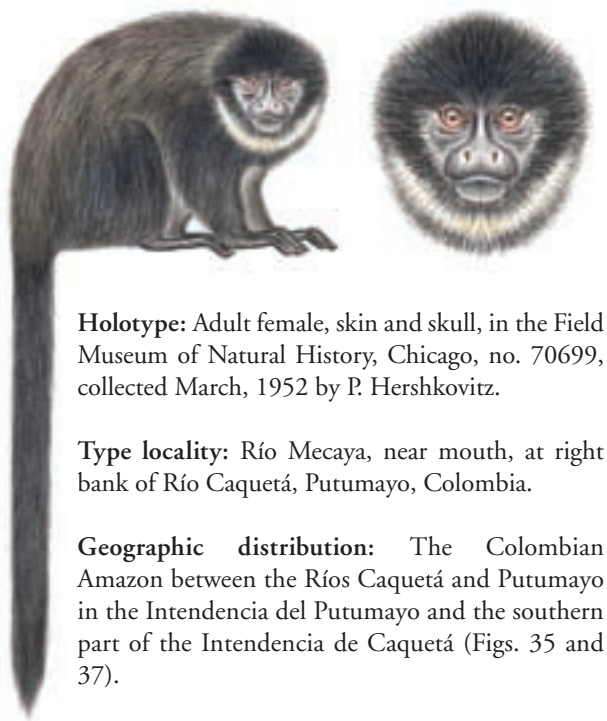
Type locality: Fonte Boa, right bank of upper Rio Solimões, state of Amazonas, Brazil.

Geographic distribution: Brazil, state of Amazonas, between the upper Rio Solimões, the lower Rio Javarí, and the left (west) bank of the Rio Juruá from mouth at the Rio Solimões to about 7º S (Figs. 35 and 37).

Diagnostic characters: Hands orange, tail blackish, inner side of arms entirely blackish, under parts (chest and belly) except throat brown or blackish, hairs above and behind ears more or less banded, sideburns brownish, crown strongly contrasted reddish, and throat collar well developed, white.

Distinguished from *C. purinus* by dark brown chest and belly, brownish sideburns, hairs above and behind ears more or less banded, and orange instead of white hands; from *C. torquatus* by inner side of arms entirely blackish, more developed white throat collar, a strongly contrasting reddish crown, and blackish instead of white feet; from *C. lucifer* by indistinctly banded hairs of back and sides of body, and a contrasting reddish instead of blackish crown; from *C. lugens* by paler back, sides of body, and under-parts, and a strongly contrasting reddish crown; and from *C. medemi* by orange instead of blackish hands, and contrasting reddish instead of blackish crown.

Callicebus medemi Hershkovitz, 1963



Holotype: Adult female, skin and skull, in the Field Museum of Natural History, Chicago, no. 70699, collected March, 1952 by P. Hershkovitz.

Type locality: Río Mecaya, near mouth, at right bank of Río Caquetá, Putumayo, Colombia.

Geographic distribution: The Colombian Amazon between the Ríos Caquetá and Putumayo in the Intendencia del Putumayo and the southern part of the Intendencia de Caquetá (Figs. 35 and 37).

Diagnostic characters: Head, sideburns, hands, feet, tail, and under parts except throat entirely or predominantly blackish, throat white.

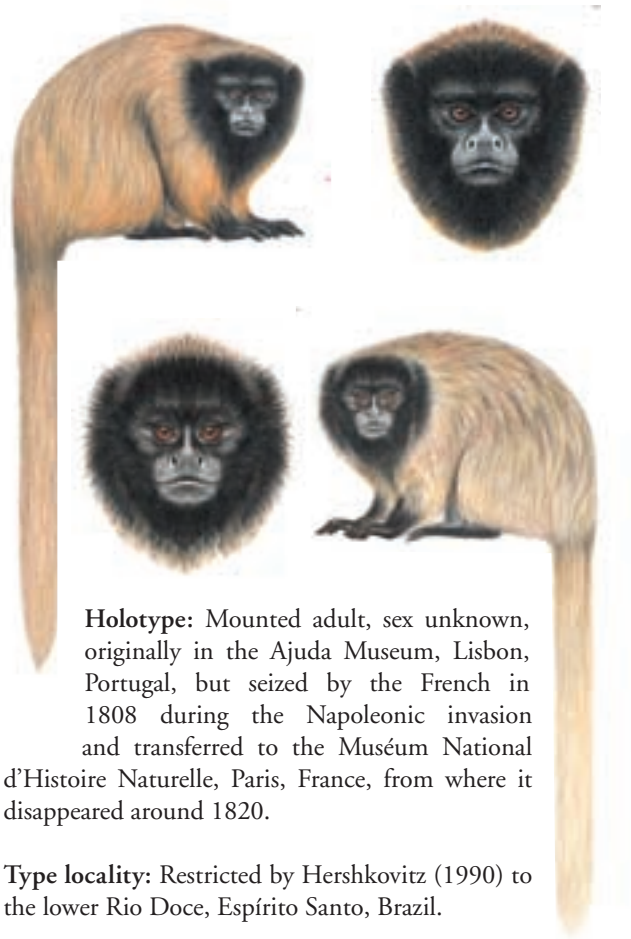
Distinguished from *C. torquatus, C. regulus,* and *C. purinus* by much darker (blackish) coloration throughout, including the blackish hands, legs, and under parts; from *C. lucifer* and *C. lugens* by upper surface of hands uniformly or dominantly blackish instead of orange and white, respectively.

V. *C. PERSONATUS* GROUP

Undescribed form of the *Callicebus torquatus* group

Figure 41. This individual was being kept in captivity at Boca Manu, Rio Manu, Peru, in 1983 and probably represents an undescribed form of the *Callicebus torquatus* group. Photographs by A. Young and R. A. Mittermeier.

Callicebus personatus (É. Geoffroy, 1812)



Holotype: Mounted adult, sex unknown, originally in the Ajuda Museum, Lisbon, Portugal, but seized by the French in 1808 during the Napoleonic invasion and transferred to the Muséum National d'Histoire Naturelle, Paris, France, from where it disappeared around 1820.

Type locality: Restricted by Hershkovitz (1990) to the lower Rio Doce, Espírito Santo, Brazil.

Geographic distribution: In the Atlantic forest of southeastern Brazil, in the state of Espírito Santo, south from the region of the lower Rio Itaúnas (Kinzey, 1982; Oliver and Santos, 1991). The Rio Mucurí, to the north of the Rio Itaúnas was marked as the limit by Hershkovitz (1990), but Oliver and Santos (1991) reported that *C. melanochir* may occur south of the lower Itaúnas as far as Barra Nova (18º54'S, 39º47'W). Oliver and Santos (1991) indicated that the region of the Rios Itaúnas and Mucurí may be a zone of intergradation between the *personatus* (to the south) and *melanochir* (to the north). *C. personatus* occurs further inland into northwestern Minas Gerais, east at least as far as Teófilo Otoni (Kinzey, 1982; Hershkovitz, 1990) and the east (right) bank of the Rio Jequitinhonha (Rylands *et al.* 1988). South of the Rios Mucurí/Itaúnas, they occur throughout the state of Espírito Santo and in the north of Rio de Janeiro (M. C. M. Kierulff in Rylands, 1988), although now extremely scarce (Oliver and Santos, 1991). *C. personatus* extends west along the Rio Doce valley into Minas Gerais as far as the Serra da Mantiqueira (Serra do Brigadeiro) (Cosenza, 1993), and at least as far south as Juiz de Fora, Minas Gerais. It remains unclear if *C. personatus*, or another species, occurs northwest of the Rio Jequitinhonha. Hershkovitz (in litt. to A. B. Rylands, January 1988) listed Buenópolis, near the

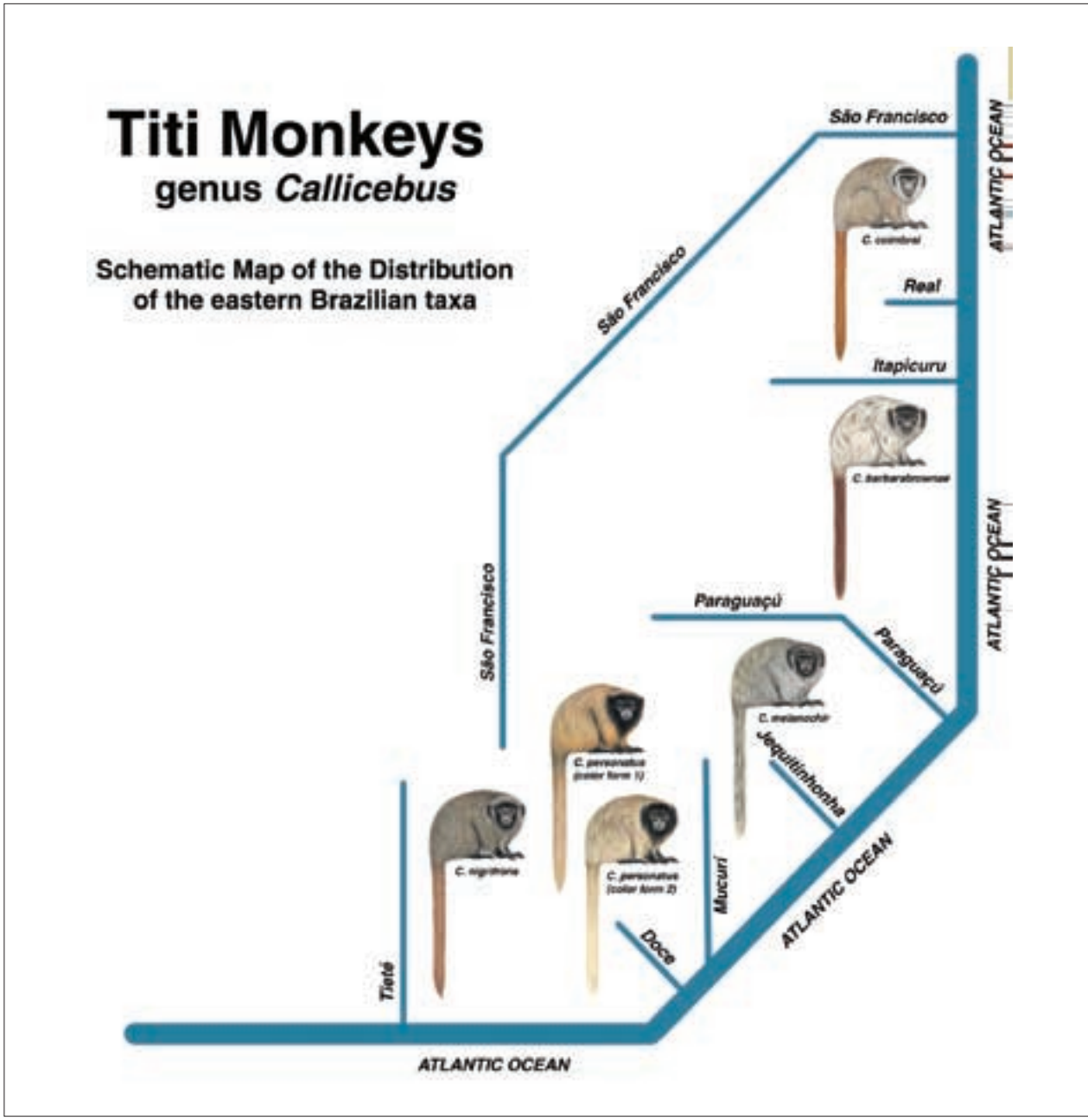


Figure 42. Schematic map of the distribution of the southern Brazilian titi monkeys of the *personatus* Group, genus *Callicebus*.

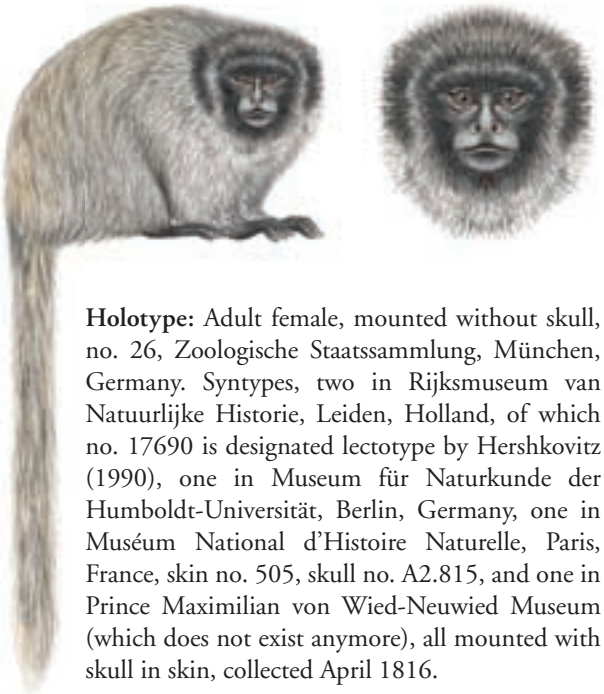
Figure 43. *Callicebus personatus* É. Geoffroyi, 1812, from Minas Gerais, Brazil. Photographs by R. A. Mittermeier.

Serra do Cabral (17º54'S, 44º11'W), northwestern Minas Gerais, as a locality for *C. personatus*, but it was not included as a locality in his publication in 1990 (Figs. 42 and 44).

Diagnostic characters: Throat, sideburns, forehead and crown blackish to plane of ears, rest of body sharply defined uniformly buffy to orange like nape except blackish hands, lower arms and feet. Two color variations, body and tail uniformly buffy or orange (Figs. 3 and 37).

Distinguished from *C. nigrifrons, C. melanochir,* and *C. barbarabrownae* by blackish forehead, crown to line of ears, cheeks, ear tufts, and throat, the hairs not banded; and back of crown sharply contrasting orange; from *C. coimbrai* by black instead of buffy cheeks, sideburns, chest, back of head, and nape (Fig. 43).

Callicebus melanochir Wied-Neuwied, 1820



Holotype: Adult female, mounted without skull, no. 26, Zoologische Staatssammlung, München, Germany. Syntypes, two in Rijksmuseum van Natuurlijke Historie, Leiden, Holland, of which no. 17690 is designated lectotype by Hershkovitz (1990), one in Museum für Naturkunde der Humboldt-Universität, Berlin, Germany, one in Muséum National d'Histoire Naturelle, Paris, France, skin no. 505, skull no. A2.815, and one in Prince Maximilian von Wied-Neuwied Museum (which does not exist anymore), all mounted with skull in skin, collected April 1816.

Type locality: Morro d'Arara or Fazenda Arara, state of Bahia, Brazil.

Geographic distribution: Hershkovitz (1990) gives the range as the Atlantic coastal forest of eastern Brazil, north from the Rio Mucurí in the state of Espírito Santo to the Rio Paraguaçú in Bahia. As discussed for *C. personatus*, it would seem that the southern limit is not clearcut, and is possibly marked by a zone of intergradation in the valleys of the Rios Itaúnas and Mucurí in northern Espírito Santo. To the north, *C. melanochir* extends as far as the Rio Paraguaçú, where it meets the range of *C. barbarabrownae* (Hershkovitz, 1990; Oliver and Santos, 1991; Flesher, 1999). Inland it would appear that its range is limited by inhospitable liana forests and dry forests of the interior of the state of Bahia. South of the Rio Jequitinhonha, it is restricted to coastal forest, being replaced by *C. personatus* further inland (Figs. 42 and 44).

Diagnostic characters: Forehead, crown, and throat dominantly grayish agouti, buffy or pale brownish agouti, the hairs finely banded, cheiridia and facial fringe blackish, overall the least colorful member of the *personatus* Group.

Distinguished from *C. nigrifrons* and *C. personatus* by the forehead not being sharply defined blackish, entire crown blackish agouti or grayish agouti like nape, and sides of neck and throat grayish or blackish agouti; from *C. barbarabrownae* by overall much darker coloration; from *C. coimbrai* by grayish agouti, buffy or pale brownish agouti forehead, crown, and throat.

Callicebus nigrifrons Spix, 1823

Lectotype: Adult, sex unknown, mounted skin only, no. 88, Zoologische Staatssammlung, München, Germany, collected 1817 by the Spix and Martius expedition.

Type locality: Interpreted by Hershkovitz (1990) to be the Rio Onças, municipality of Campos, state of Rio de Janeiro, Brazil.

Geographic distribution: Southeastern Brazil, in the states of Rio de Janeiro, São Paulo north from the Rio Tietê, east of the Rio Paraná but restricted to the right bank of the Rio Paranaíba in western Minas Gerais. It occurs on both sides of the uppermost reaches of the Rio São Francisco, extending to the east as far as the Serra da Mantiqueira and Serra do Espinhaço in Minas Gerais, where it meets the range of *C. personatus* (Figs. 42 and 44). As in all of the Atlantic forest titi monkeys, although widespread, the extreme fragmentation and urbanization of the forests within its range means that today populations are isolated and generally very small, and in many places they are locally or regionally extirpated even where forests patches remain.

Figure 44. Distributions of the Atlantic forest titi monkeys, genus *Callicebus*, belonging to the *personatus* Group. Map by Stephen D. Nash.

Figure 45. Top. The southern masked titi, *Callicebus nigrifrons* (Spix, 1823). An individual from the south-east of the state of Minas Gerais, Brazil, 1979. Bottom. A titi monkey from Guapí-Mirim, São Paulo, Brazil. This is within the recognized distribution of *Callicebus nigrifrons*, but this individual had a darker mask and mantle and a more orange, rather than rusty-brown, tail. Photographs by R. A. Mittermeier.

Diagnostic characters: Forehead and crown blackish to about halfway plane of ears, rest of crown grading into coarsely banded brownish agouti or orange-brown of nape; throat pale brownish agouti like chest; cheiridia and ears black; tail orange.

Distinguished from *C. melanochir* and *C. barbarabrownae* by blackish forehead, and anterior portion of crown blackish thinly mixed with buff-banded hairs; from *C. personatus* by blackish front of crown grading into agouti of nape without line of demarcation, and throat pale brownish agouti like chest; from *C. coimbrai* by pale brownish agouti sideburns, throat, and chest (Fig. 45).

Callicebus barbarabrownae Hershkovitz, 1990

Holotype: Skin and skull, no. 3.9.5.7, British Museum of Natural History, London, U.K., collected June 1903 by Alphonse Robert.

Type locality: Lamarão, Bahia, Brazil, altitude about 300 m above sea level.

Geographic distribution: According to Hershkovitz (1990), the coastal highlands of the north-central part of the state of Bahia, Brazil, between the Rios Paraguaçú, just north of the city of Salvador, and Itapicurú. The western limits to its range are unknown but probably, at least historically, the middle reaches of the Rio São Francisco. Ricardo B. Machado and the late A. Brandt (pers. comm. 1988) recorded a population of *Callicebus* at the Serra da Quixaba in the municipalities of Canudos and Monte Santo, north of the Rio Vaza-Barris, northern Bahia (39°20'W, 10°15'S). Ilmar B. Santos also recorded *Callicebus* at Jeremoabo, a little to the east, on the northern margin of the Rio Vaza-Barris in 1990 (pers. comm.). Marinho-Filho and Veríssimo (1997) confirmed the westernmost locality. They observed it in gallery forest at Mirorós, municipality of Ibipeba, western Bahia (11°24'S, 42°17'W). *C. barbarabrownae* was evidently once widespread in forests east and south of the Rio São Francisco

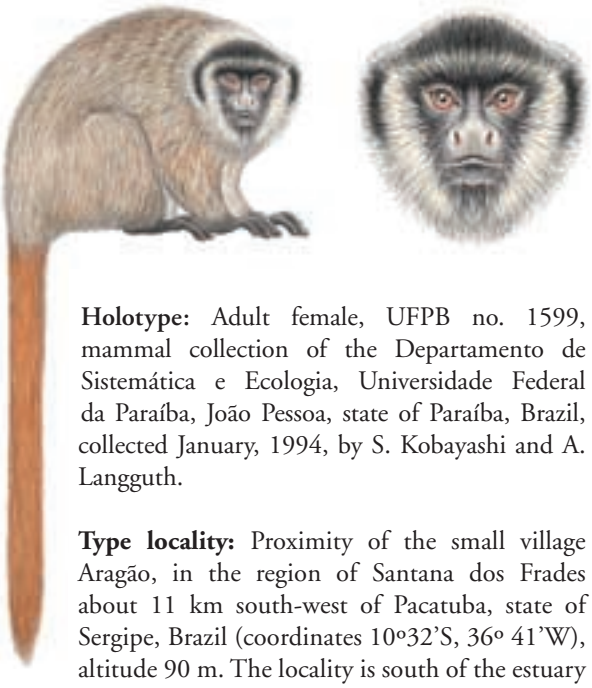
Figure 46. The blond titi, *Callicebus barbarabrownae* Hershkovitz, 1990. In captivity at the Federal University of Minas Gerais, Belo Horizonte, in the mid-1980s before the species was described. Photograph by R. A. Mittermeier.

(see Coimbra-Filho and Câmara, 1996), but today survives only in small forest enclaves in what is now predominantly *caatinga* (dry thorn scrub) (Figs. 42 and 44).

Diagnostic characters: Superciliary vibrissal line black, forehead and crown to anterior plane of ears dominantly buffy; raised hairs of rest of crown buffy, the fine tips blackish; sideburns, nape, and shoulders pale buff; hairs of back and sides of body banded pheomelanin and eumelanin; thighs and upper arms paler, forearms and legs like back; cheiridia blackish; throat, chest, and belly nearly entirely buffy; tail dominantly orange, base of tail yellowish; ears and skin blackish.

Distinguished from *C. melanochir* by dominantly buffy crown, sideburns, throat, trunk, and limbs with the subterminal pheomelanic (buffy) bands of hairs paler; from *C. nigrifrons* and *C. personatus* by forehead buffy instead of blackish; from *C. coimbrai* by buffy forehead and crown. (Fig. 46).

Callicebus coimbrai
Kobayashi & Langguth, 1999



Holotype: Adult female, UFPB no. 1599, mammal collection of the Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, state of Paraíba, Brazil, collected January, 1994, by S. Kobayashi and A. Langguth.

Type locality: Proximity of the small village Aragão, in the region of Santana dos Frades about 11 km south-west of Pacatuba, state of Sergipe, Brazil (coordinates 10º32'S, 36º 41'W), altitude 90 m. The locality is south of the estuary of the Rio São Francisco.

Geographic distribution: First described from three localities in eastern Brazil, along the coast of the state of Sergipe, between the Rio São Francisco in the north and the Rio Real in the south (the southern border of Sergipe). Oliver and Santos (1991) obtained reports of the occurrence of titi monkeys in the vicinities of Umbauba, Estância, and Aruá in coastal southern Sergipe, and also at Cachoeira da Abadia and Jandaira in north-east Bahia, which are probably referable to *C. coimbrai*. They indicated that the Rio São Francisco was the northern limit to the range of the genus in the Atlantic forest. Sousa (2000) reported two further localities in Sergipe: Mata do Crasto in the municipality Santa Luzia do Itanhy, and the Mata do Dira in the municipalities of Itaporanga and Laranjeiras. Sousa (2000) also reported hearing vocalizations of titi monkeys in the Matas do Conde, municipalities of Conde and Jandaira in extreme northern Bahia in 1996. The western limits of its range are unknown, but Ricardo B. Machado (pers. comm. 1989), Marinho-Filho and Veríssimo (1997) recorded *Callicebus* in forest patches in the Caatinga, inland between Monte Santo and Uauá in the upper valley of the Rio Vaza-Barris, and Jeremoabo and Canudos in northern Bahia. Marinho-Filho and Veríssimo (1997) identified them as the form *barbarabrownae*, although they are at about the same latitude as *coimbrai*. The evidence obtained by Kobayashi and Langguth (1999) indicated that *C. coimbrai* is today restricted to the humid coastal Atlantic forest of Sergipe, and that its southern limit is the Rio Itapicurú in Bahia, the northern limit to the range of *C. barbarabrownae* (Hershkovitz, 1990). Considering the widespread and rapid destruction of the forests in northern Bahia and Sergipe even in the early 16th Century (Coimbra-Filho and Câmara, 1996), *C. coimbrai* undoubtedly had a much broader range in the past (Figs. 39 and 40).

Diagnostic characters: Forehead, crown, and ears black; trunk buffy; cheiridia blackish; tail orange; sideburns, cheeks, back of head, and nape pale buffy; anterior half of dorsum saddle-backed (with striped pattern).

Distinguished from all other titis of the *C. personatus* Group by black forehead, crown, and ears sharply contrasting with buffy sideburns, cheeks, back of head, nape, and trunk.

Discussion

In this review, we elevate all currently known taxa of titi monkeys, genus *Callicebus*, to full species status using the same arguments as De Vivo (1991), Van Roosmalen *et al.* (1998), and Van Roosmalen *et al.* (2000) in their respective reviews of Amazonian marmosets, genus *Callithrix*. As in Amazonian *Callithrix* (or *Mico*, following Rylands *et al.,* 2000), titi monkeys in lowland Amazonia invariably have their distributions confined by river barriers. These rivers may fall in the 'black-water', 'clear-water' or 'white-water' category. Both Amazonian *Callicebus* and *Callithrix* (*Mico*) are restricted to dry-land (*terra firme*) rain forests, and only titis of the *C. moloch* and *C. cupreus* Groups tend to seasonally venture into flooded forest habitat along black-water and clear-water streams, to feed on certain fruits only available there during high water. Individuals belonging to both of these genera are unable to swim, meaning that an accidental fall into the water will quickly result in drowning. Passive transfer to the other side of a river barrier through river bend cut-offs has probably not occurred either because populations of Amazonian titis and marmosets are not found in white-water flooded forest (*várzea*), the only kind of habitat that is usually subjected to cross-river transfers. Also, they probably cannot survive on temporary *igapó* (black-water flooded forest) islands long enough to be transferred to the other side of the river.

Most of the lowland tributaries of the Amazon River are fringed with *várzeas* and *igapós* several kilometers wide and sometimes as many as 10 kilometers, which usually stretch from the mouth to the headwaters, effectively isolating populations of *terra firme*-dwelling primates such as *Callithrix, Callicebus, Saguinus, Chiropotes, Lagothrix* and *Ateles*. For these monkeys, the only way to colonize adjacent interfluves is to circumvent river barriers near their headwaters, where the floodplain ends and the river becomes narrow enough to cross. In the vicinity of these headwaters, there should be or have been contact zones between populations of the taxa inhabiting the adjacent interfluves. If interbreeding takes place between the two taxa and broad natural hybrid zones of intergradation occur, we should treat them as races or subspecies. However, in most taxa of Amazonian *Callicebus, Callithrix,* and *Saguinus,*

these regions seem to be narrow contact zones (and not regions with broad clinal variation), where the colonizing taxon successfully excludes the resident one. In such cases of narrow zones of hybridization, the animals should continue to be considered distinct species, following Mayr (1970), the very same criteria used nearly 30 years ago to recognize most Atlantic forest *Callithrix* as good species (Coimbra-Filho and Mittermeier *et al.,* 1973).

Presently, we know of three examples of this ongoing natural process in which one monkey species, after crossing a geographic barrier, outcompetes another belonging to the same 'ecospecies' (meaning they occupy the same ecological niche). These include the following:

The central-Amazonian titi monkey, *Callicebus baptista*, classified as a subspecies of *Callicebus hoffmannsi* by Hershkovitz (1990), ranges south of the Rio Amazonas, east of the lower Rio Madeira, north of the Paranás do Canumã, Urariá, and Ramos, and east as far as the western limit of the state of Pará. However, it also occurs south of the Paraná do Ramos and west of the town of Parintins, forming a propagule population in the small interfluve delineated by the lower Rio Uíra-Curupá and the lower Rio Andirá amidst the much larger interfluve that is occupied by *Callicebus hoffmannsi*, which stretches south of the Paranás do Urariá and Ramos from the lower Rio Canumã in the state of Amazonas as far as the lower Rio Tapajós in the state of Pará. Field surveys conducted by M. G. M. and T. van Roosmalen revealed that no hybrid zones of intergradation occur. It seems that *Callicebus baptista* managed to cross the Paraná do Ramos and successfully replace *Callicebus hoffmannsi* in the interfluve delineated by the Rios Andirá and Uíra-Curupá, and the Paraná do Ramos. Their parapatry being confirmed in the field, we, therefore, elevated the two taxa to full species status.

The second example concerns the golden-handed tamarin, *Saguinus midas,* which originated in the Guianas and largely replaced the pied bare-face tamarin, *Saguinus bicolor* after possibly having colonized the entire northern lower Amazon basin delineated by the Rio Branco in the west, the Atlantic Ocean in the east, the Guayana Shield in the north, and the Rio Amazonas in the south. This area was probably formerly occupied by *Saguinus bicolor* before *S. midas* managed to cross one of the geographic barriers (either the Guayana Shield highlands and savannas at the border between Brazil and the Guianas, or some river barriers in the Brazilian state of Amapá). This natural process of species replacement reaches its dramatic final stage in the vicinity of Manaus, the capital of Amazonas state, where *Saguinus bicolor* is headed toward extinction. *Saguinus midas* is now penetrating the remaining territory of *bicolor*, a small enclave on the northern shore of the Rio Amazonas/Rio Negro and west of the Rio Trombetas. The contact zone in this case is very narrow, and interbreeding between the two species, which belong to the same 'ecospecies', has not been observed. Instead, since tamarins are extremely territorial, violent encounters between groups of both species are not uncommon (M. G. M. van Roosmalen, pers. obs.).

The third example concerns *Saguinus mystax pluto* and *Saguinus mystax pileatus,* classified as subspecies by Hershkovitz (1977), with *pileatus* occupying the entire Rios Juruá/Purús interfluve south of Rio Tapauá and north of Rio Pauiní, which are both left-bank tributaries of the Rio Purús fringed with extensive *igapós* along their entire course. These rivers have their source very close to the *várzeas* of the Rio Juruá. It is assumed that *S. m. pluto* originally inhabited the entire interfluve delineated by the Rios Juruá, Solimões, Purús, and Tapauá, where it evolved away from *S. m. pileatus* due to its separation by the strong barrier represented by the Rio Tapauá. *S. m. pileatus* must have crossed the headwaters of the Rio Tapauá somewhere near the Rio Juruá in relatively recent geological times, and colonized the territory of *S. m. pluto* from the north and the east. Today, *S. m. pileatus* has replaced *S. m. pluto* throughout the entire lower Rios Juruá/Solimões/Coarí interfluve and has already passed the headwaters of the Rio Coarí into *S. m. pluto*'s last stronghold, the Rios Solimões/Coarí/Purús interfluve as far as the Igarapé Pauapixuna. As in the case of *Saguinus midas* and *S. bicolor*, no interbreeding is taking place and there seems to be a sudden transition between populations of *S. m. pileatus* and *S. m. pluto.* These field observations by M. G. M. and T. van Roosmalen during a recent survey of the entire Rio Purús, therefore, would justify elevating these two tamarins to full species status, *Saguinus pileatus* and *Saguinus pluto*, distinct from *Saguinus mystax,* west of the Rio Juruá.

These arguments apply as well to *Callicebus*, which exhibit extreme territorial behavior centered on family groups (a pair with its offspring of subsequent years), as they do to *Saguinus* (Peres, 1989). In both genera, one can distinguish two 'ecospecies'. In the central-Amazonian *Callicebus* taxa belonging to the *C. moloch* and *C. cupreus* Groups and taxa belonging to the *C. torquatus* Group, sympatry between members of each of these two Groups is common, because they exhibit different habitat preferences, dietary requirements, and foraging behavior. In contrast, C*allicebus cupreus, C. caligatus* and *C. brunneus*, for example, can never occur sympatrically, as Hershkovitz (1990) suggested, because they ecologically exclude one another.

The research on which a large part of this paper is based indicated that the biogeography of Amazonian primates continues to be poorly known. For example, the recent survey of the Rio Purús, conducted by M. G. M. and T. van Roosmalen, revealed two species of *Callicebus* new to science (including *C. stephennashi* described here), one of *Saguinus,* and one of *Ateles*, and significant modifications in a number of distributions given by Hershkovitz in his various reviews. Zoological collections from the Rio Purús are few and far between, and many of them are quite old. Collections used to be acquired by purchasing live and dead animals from animal dealers who sent natives into the bush, often far up- or downstream from where they camped.

Consequently, errors were made in labeling and recording exact localities. Moreover, museum skins with the skull and skeleton removed often do not clearly show characteristics of head, hands, and feet, which are so important in identification, especially for *Callicebus, Mico, Saguinus* and *Ateles.* Another complication is the under-representation of monkey species occurring on dry-land or *terra firme* rainforests, among them *Saguinus, Mico, Callicebus, Chiropotes, Ateles,* and *Lagothrix*. In part this is because it is hard to reach the *terra firme* hinterland along most of the major Amazonian rivers. Rivers such as the Solimões, Juruá, Purús, and Madeira are fringed with almost impenetrable stretches, often as wide as 10 kilometers or more, of white-water flooded forests (*várzeas*), the kind of habitat where many primate species do not venture. *Alouatta, Cacajao, Cebus, Saimiri,* and *Aotus* do occur in these habitats, but many of the others do not even go there seasonally.

Given the relative lack of study of *terra firme* areas, it is understandable that the river barrier hypothesis of Wallace (1852) is not always believed to apply to primates. Wallace, while conducting fieldwork and collecting specimens in the mid-nineteenth century in the upper Rio Negro and Rio Uaupés, noticed the isolating effect of rivers such as the Rio Amazonas and its major tributaries (Tapajós, Madeira, Branco, Negro, Purús, Juruá) on the distribution of monkeys and described it in his paper "On the Monkeys of the Amazon", published seven years before Charles Darwin's "The Origin of Species" (1859). Monkeys from the Amazon provided the data, along with many later collected in the Malay Archipelago, that led Wallace to his theory of evolution by natural selection. Only systematic field studies will test the hypothesis that rivers in lowland Amazonia can act as effective barriers to the dispersal of organisms and, as such, induce speciation and generate allopatric species. Few such studies to date include those of Capparella (1987, 1988) on the distribution of understory birds, Peres *et al.* (1996) on the primate fauna along the Rio Juruá, and M. G. M. and T. van Roosmalen's systematic surveys of the Rios Madeira/Tapajós, Madeira/Purús, and Purús/Juruá interfluves (1998, 2000, this paper). In the coming years, the latter researchers intend to systematically survey all major rivers of lowland Amazonia and their main tributaries by boat, collecting dung, tissue and/or hair samples from both wild and captive specimens of monkeys, and some other megafaunal elements such as manatees, giant otters, tapir, deer, and large cats. This project also includes several *terra firme* tree species that have their seed dispersal adapted to *terra firme* dwelling gut-dispersers, such as *Ateles* and *Lagothrix.*

In our review of Amazonian marmosets (formerly genus *Callithrix*, now *Mico*), we note that all distributional boundaries for marmosets coincide with rivers that flow from the Central Brazilian Plateau to the Rios Madeira and Amazonas (Van Roosmalen *et al.*, 2000). These rivers mostly fall within the black-water or clear-water category, which do not meander much and have not changed their courses over considerable geological times. In the current paper, the same pattern is shown for distributions of titi monkeys, genus *Callicebus,* at least in the recently inventoried basins of the Rios Madeira and Purús, conforming to Wallace's hypothesis of river barrier-assisted speciation.

Conservation Status of the Two New Species

As with all members of the *C. moloch* and *C. cupreus* Groups, *Callicebus bernhardi* and *Callicebus stephennashi* prefer lightly to heavily disturbed *terra firme* forest, liana forest, and black-water and clear-water flooded gallery forest. Densities in undisturbed matrix high dry-land rainforest are generally low and, when present, the titis seem to frequent natural edge habitats, such as tree-fall clearings, fringes of streams and lakes, and liana forest. However, wherever the rain forest has been disturbed, both naturally as well as anthropogenically, these 'ecospecies' of titi monkey seem to thrive. The highest densities of these monkeys are usually found close to human habitations, along roads, and along banks of rivers and larger creeks, where human settlements are mostly situated in this part of Amazonia. Therefore, there is no reason to suspect that *Callicebus bernhardi* and *Callicebus stephennashi* are threatened. The forests in the northern part of *Callicebus bernhardi*'s range, between the lower and middle Rio Aripuanã and Rio Madeira are still in almost pristine condition, although selective logging has taken place along the navigable rivers. There are no major towns or cities in the area, except Manicoré and Auxiliadora, both located on the right bank of the Rio Madeira. Indian tribes, which usually hunt relatively small mammals, including titis, only live in the southern part of its range. Elsewhere, the local people (*caboclos*) do not normally hunt small game and are widely scattered in small settlements of one to a few families along the major rivers, the Rios Madeira, Aripuanã, Roosevelt, and Ji-Paraná, and along the lower courses of minor rivers, such as the Rios Mataurá, Uruá, Maripauá, Arauá, Atininga, Manicoré, and Rio dos Marmelos. The interfluvial basins of these black- and clear-water rivers are practically uninhabited.

The main threat to the habitat of *Callicebus bernhardi* comes from the Transamazonian Highway that crosses its range in the south connecting the city of Humaitá on the left bank of Rio Madeira with Apuí on the Rio Sucunduri, Itaituba on the Rio Tapajós, and the states of Pará and Mato Grosso. Given that we still do not know the precise distribution of *Callicebus stephennashi*, we cannot say anything more about its current conservation status than the general comments given above, which apply to any member of the *C. moloch* and *C. cupreus* Groups.

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Figure 47. Array of faces of titi monkeys, genus *Callicebus,* arranged by group. Illustration by Stephen D. Nash.

***I. donacophilus* Group**

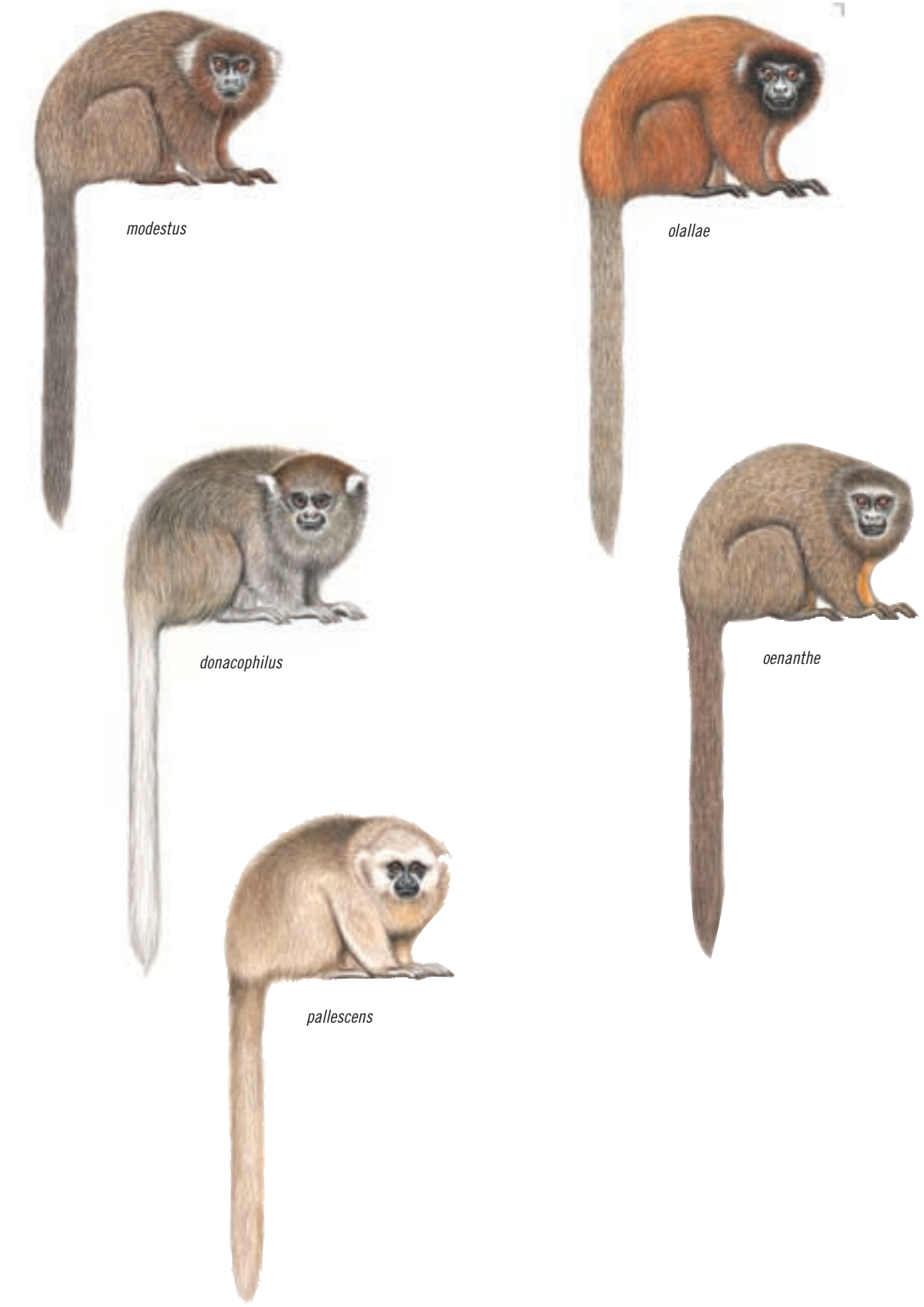

Figure 48. Titi monkeys, genus *Callicebus, donacophilus* group. Illustration by Stephen D. Nash.

Figure 49. Titi monkeys, genus *Callicebus, cupreus* group. Illustration by Stephen D. Nash.

Figure 50. Titi monkeys, genus *Callicebus, moloch* group. Illustration by Stephen D. Nash.

Figure 51. Titi monkeys, genus *Callicebus, torquatus* group. Illustration by Stephen D. Nash.

Figure 52. Titi monkeys, genus *Callicebus, personatus* group. Illustration by Stephen D. Nash.