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.

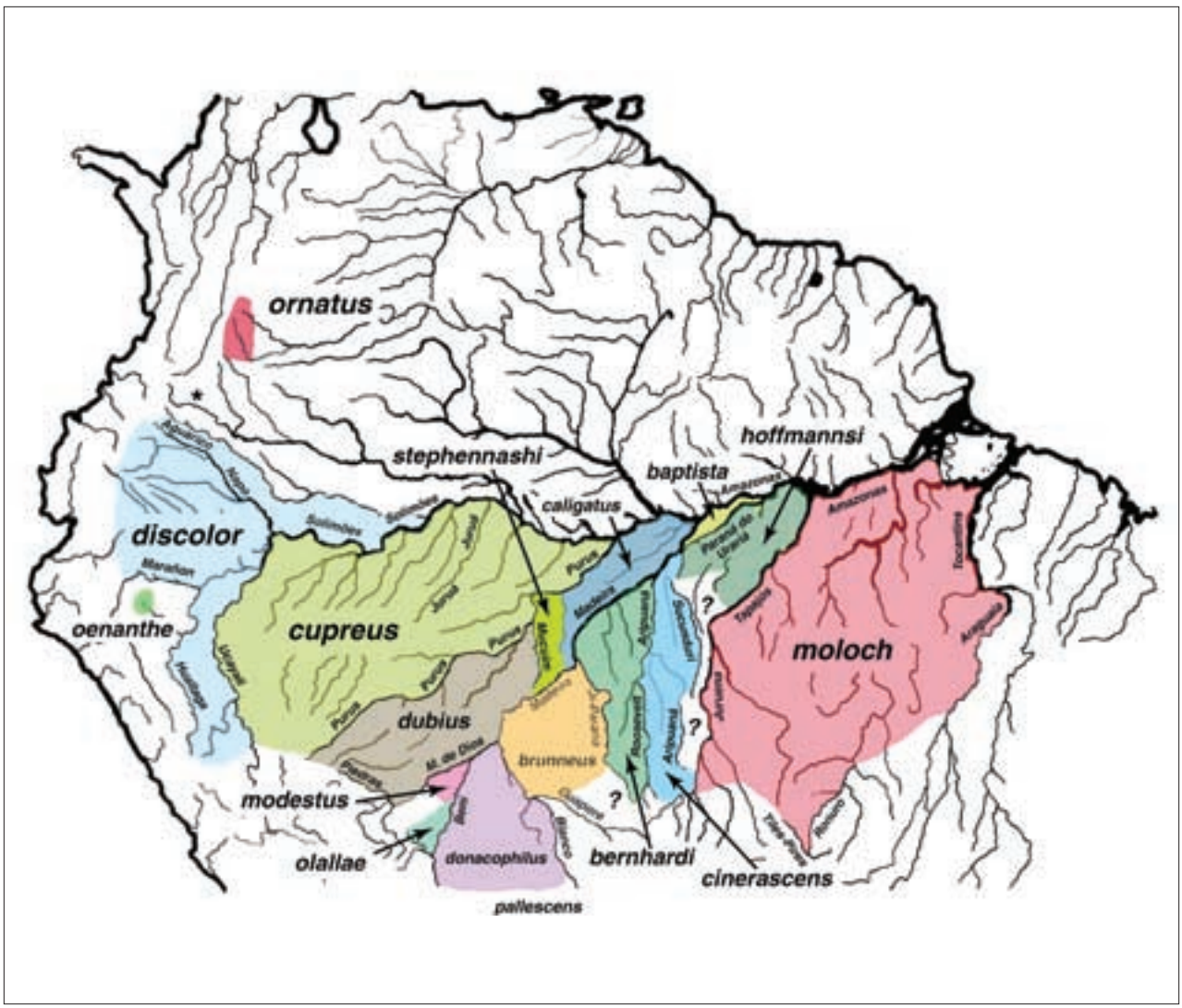

Figure 1. Distributions of the Amazonian titi monkeys, genus *Callicebus*, belonging to the *donacophilus*, *cupreus* and *moloch* Groups. The asterisk marks the location of the municipality of Valparaiso, Columbia, where Moynihan (1976) recorded the presence of titi monkeys not identifiable with *discolor*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

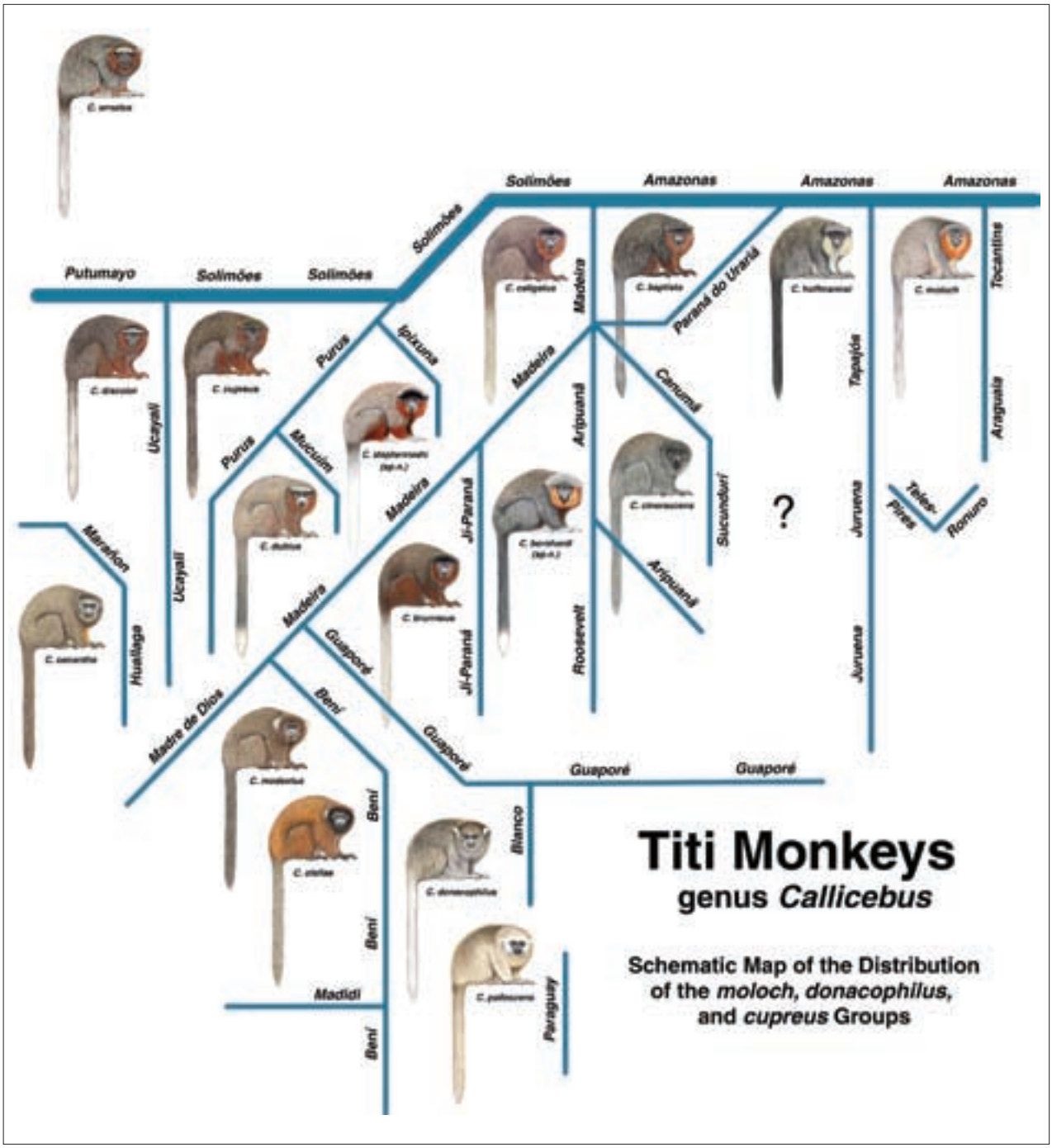

Figure 2. Schematic map of the distribution of Amazonian titi monkeys, belonging to the *donacophilus, cupreus* and *moloch* Groups. Illustration by Stephen D. Nash.

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