

The Distribution and Taxonomy of Titi Monkeys (*Callicebus*) in Central and Southern Peru, with the Description of a New Species

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Abstract: Here we report on the results of a study on the distribution and taxonomy of titi monkeys, genus *Callicebus*, in the central part of Peru. We reinstate *Callicebus toppini* Thomas, a species described in 1914, but since then neglected by science. It evidently has a wide distribution in southern Peru, western Brazil and northern Bolivia. Based on field observations, analysis of museum specimens, and photographs, we also describe a new species of *Callicebus* from the Río Urubamba basin, endemic to Peru. Reliable identification of titi monkeys observed in the wild is crucial to avoid confusion and to determine conservation strategies.

Key Words: *Callicebus*, distribution Peru, Platyrrhini, Primates, taxonomy

Introduction

More than 50 titi monkeys have been described since Hoffmannsegg's descriptions of *Cebus moloch* and *Callitrix torquatus* in 1807. Through the years, many have been synonymized, and the latest revision of the genus by Van Roosmalen *et al.* (2002) listed just 26 species. They described two more species, *C. bernhardi* and *C. stephennashi*, from the Brazilian Amazon, and a further four species have been newly described since then—*Callicebus aureipalatii* Wallace *et al.*, 2006, from Bolivia; *Callicebus caquetensis* Deffler *et al.*, 2010, from the Colombian Amazon; and *Callicebus vieirai* Gualda-Barros *et al.*, 2012, and *Callicebus miltoni* Dalponte *et al.*, 2014, from the Brazilian Amazon. This brought the total to 32 species, and more are awaiting scientific description (Araújo 2013; Van Roosmalen and Van Roosmalen 2014).

The taxonomy and distributions of the Peruvian titi monkeys are still poorly understood. Hershkovitz (1990) listed six species in Peru (*oenanthe*, *brunneus*, *cupreus*, *discolor*, *caligatus* and *lucifer*). The presence of *C. caligatus* is questionable (Aquino and Encarnación 1994; Van Roosmalen *et al.* 2002), and may be based on a misidentification of museum specimens (Voss and Emmons 1996). Titis belonging to a possibly undescribed species have been reported from northern Peru (Aquino *et al.* 2008). Three other Peruvian *Callicebus* have been described, but these Hershkovitz (1990) considered to

be junior synonyms of *C. cupreus* (*C. toppini* Thomas, 1914) or *C. discolor* (*C. subrufus* Elliot, 1907; *C. rutteri* Thomas, 1923); a viewpoint followed in subsequent revisions (Aquino and Encarnación 1994; Van Roosmalen *et al.* 2002). The species' distributions proposed by Hershkovitz (1990), Aquino and Encarnación (1994) and Van Roosmalen *et al.* (2002) are based on few museum specimens and sometimes even fewer field studies. Recent field surveys by Bóveda-Penalba *et al.* (2009) and Vermeer *et al.* (2011) have resulted in extensions of the known distributions of *C. oenanthe* and *C. discolor*, respectively.

The area around Atalaya, Ucayali Department, central Peru, is of the utmost interest for primate taxonomy. The Río Urubamba (flowing from the south), the Río Tambo (flowing from the west) and the Río Inuya (flowing from the east) come together near Atalaya and continue their course northwards as the Río Ucayali (Fig. 7). The ríos Urubamba, Ucayali and Tambo are believed to serve as geographical barriers for delimiting the ranges of primate species (Hershkovitz 1990; Aquino and Encarnación 1994; Aquino *et al.* 2013). The upper Río Inuya is known locally for its abundance of primates, which, however, are threatened by hunting and logging.

Our understanding of the distributions and taxonomy of titi monkeys around Atalaya is based mainly on a collection of specimens made by the Olalla brothers in 1927 (Wiley 2010),

now preserved in the collection of the American Museum of Natural History (AMNH); 22 specimens of three different species of titi. The dark brown specimens, labeled “Mouth Río Inuya, Río Urubamba” or “Boca Río Urubamba,” were identified by Hershkovitz (1990) as belonging to *Callicebus brunneus*. Hershkovitz (1990) identified the reddish specimens with a dark forehead, labeled “Mouth Río Urubamba” or “Mouth Río Inuya,” as *Callicebus cupreus cupreus*, and the reddish animals with a white blaze, from “Boca Río Inuya” and “Lagarto,” as *Callicebus cupreus discolor*.

In his map, Hershkovitz (1990, p.53) placed the range of *discolor* on the left bank of the Río Ucayali and that of *cupreus* on the right bank as well as on both sides of the Río Inuya. He mentioned that *C. brunneus* might occur in the Peruvian departments of Madre de Dios, Puno and Cusco, but questioned the provenance of AMNH specimens labeled as coming from the Río Inuya and Río Urubamba (in the Ucayali Department). Aquino and Encarnación (1994) followed Hershkovitz regarding the distributions of *C. discolor* and *C. cupreus*, and added that the range of *C. brunneus* extends from the upper Río Purús in Ucayali Department south to the Bolivian border. Van Roosmalen *et al.* (2002) also agreed regarding the distributions of *C. discolor* and *C. cupreus*, but restricted the range of *C. brunneus* on their map (p.5) to the east of the Río Madeira. Confusingly, their accompanying text mentions that “in the west of its distribution, it is parapatric with *C. cupreus* along the upper Río Purús,” which is not possible if the species is indeed restricted to east of the Río Madeira, while the Río Purús is west of the Río Madeira. Since then, several authors have reported the presence of *C. brunneus* in southern Peru (Philips *et al.* 2004; Solari *et al.* 2006; Palminteri *et al.* 2009).

Hershkovitz (1990) described *C. brunneus* as a species with the upper parts and sides of the body brownish agouti, underparts brownish or reddish brown, and forehead, forearms, legs, hand and feet blackish. This matches very well the original description of the species (Wagner, 1842), except that Wagner described it as being chestnut-brown. Van Roosmalen *et al.* (2002) caused confusion by picturing *C. brunneus* with reddish underparts and a buffy tail; their photographs show in fact *C. cupreus*. This was corrected by Vermeer (2009), but as Hershkovitz (1990) had mentioned that the southern departments of Peru are inhabited by *C. brunneus*, it is possible that researchers without thorough knowledge of taxonomy simply assumed that all titi monkeys encountered in southern Peru were *C. brunneus* (Philips *et al.* 2004; Solari *et al.* 2006; Palminteri *et al.* 2009), even if the animals were reddish (probably following Van Roosmalen *et al.* 2002).

A species that warrants extra attention is the earlier mentioned *Callicebus toppini*. The type locality is the Río Tahuamanu, in south-eastern Peru (not north-eastern; a *lapsus calami* by Thomas 1914). Hershkovitz (1963) first considered *C. toppini* to be a junior synonym of *C. brunneus*, but after examining more specimens, including the holotype, in his 1990 revision he synonymized it with *C. cupreus*. Partly based on the examination of the AMNH specimens from the Atalaya area, he included the Río Inuya within the range of

C. cupreus. However, the AMNH specimens from the Atalaya region all have dark tails with a whitish tip, and match well the original description and the holotype of *C. toppini* (J. Vermeer, pers. obs.). There is no apparent geographical boundary between the type locality and the Río Urubamba.

In this paper we report the results of an expedition to the Atalaya region, Ucayali Department, Peru. The goal was to identify the species of *Callicebus* living in the region and to determine their distributions. We reinstate *Callicebus toppini* as a valid taxon, phenotypically distinguishable from *C. cupreus*, with which it was synonymized for many years. The species has an extensive distribution throughout southern Peru, western Brazil and north-western Bolivia. We also describe a new species from the Río Urubamba, recognizable by its brown color and black face, and known with certainty from only a few localities. We provide images of the different species living in southern Peru and their hypothetical distributions to facilitate the identification of titi monkeys by other investigators.

Methods

Study sites

We carried out surveys for six weeks in November and December 2013 along the ríos Urubamba, Inuya and Ucayali in the area around Atalaya. The study was conducted in three sectors, thereby obtaining a good knowledge of the overall distribution of the different species and the role of the rivers as barriers for titi monkey distributions. We walked 144 km of trails and surveyed 169 km by canoe.

Sector 1: both margins of the Río Inuya. The Río Inuya is on the right bank of the Río Urubamba. We conducted surveys for nine days on both sides of the river. Some of the observations were done on forest trails, while other titi monkeys were observed during river surveys. The forest can be described as open primary forest, with “pacaes” (areas of spiny bamboo, *Guadua*).

Sector 2: both margins of the Río Urubamba. During the 11 days we spent along the Río Urubamba, most were devoted to the left bank, as the right bank was already included in the Sector 1 surveys. Most of our observations were along existing trails, but we also made a number of observations along the Río Sepa, a narrow and shallow river flowing eastwards into the Río Urubamba. The forest close to the river is comparable to that along the Río Inuya, but there is more human disturbance and most observations were made in regenerating secondary forest.

Sector 3: both margins of the Río Ucayali. The forest along the Río Ucayali is denser, with taller trees than in the southern study areas. However, there are more settlements and disturbance is very high. During the ten days in this sector, we walked many existing trails on both banks of this wide river, but also used our boat to enter some of its smaller tributaries, Quebrada Chicosillo and Quebrada Shebonillo. Pacaes are practically absent and much of the area is flooded during the wet season.

Field surveys

During our study, we applied three different methods that have proven to be successful during surveys in other parts of Peru; interviews with local people, listening to vocalizations, and direct observations. However, owing to resemblances in coloration and vocalizations between the different species, we have concentrated on direct observations for our results and conclusions.

Titi monkeys are discreet animals that are difficult to find in the forest. They advertise their presence in the morning by loud vocalizations that probably serve to define the boundaries of their territories (Robinson 1979; Aldrich *et al.* 2008). In order to stimulate titi monkeys to call, we played recordings of different *Callicebus* species in the hope that they would answer and approach us. This method has been used successfully by other researchers (Rowe and Martinez 2003; J. Lawrence, pers. comm.). If titi monkeys were heard calling, we tried to find them. When possible, we filmed and photographed the titis and recorded their vocalizations. We conducted interviews at each locality where people were present. No transects were opened up for this study, and we used solely existing trails and rivers.

No animals were killed for our study. We encountered hunters with dead titi monkeys, however, and took the opportunity each time to obtain skins and skulls. All specimens obtained are listed below and were deposited in the Natural History Museum of Lima (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos).

Results

Sector 1: Río Inuya

We saw titi monkeys at 14 localities along the Río Inuya, and heard them at three other sites. On only one occasion were we unable to identify the species observed; they disappeared into the vegetation as soon as we arrived. The 29 individuals that we observed on both sides of the river showed little color variation. They had reddish undersides and cheeks, a greyish back, a yellowish crown and a dark tail with a whitish tip. We identified these animals as being *Callicebus toppini* (see discussion). We walked 62 km of trails and surveyed 81 km of river banks.

Sector 2: Río Urubamba and Río Sepa

We encountered titi monkeys at 14 localities along the Río Urubamba and its tributary, the Río Sepa. Titis were also reported at another locality. The titi monkeys observed at all localities on the left (western) side of the Río Urubamba were very dark, brownish with black forearms, hands, feet and face. They were easily distinguishable from the titis along the Río Inuya. No variation was detected among the 35 individuals that we encountered. These titis are a new, previously undescribed species (see discussion). We obtained the skin and skull of a dead specimen shot for food by a hunter.

Animals of the reddish species, *C. toppini*, were observed at the locality that we surveyed on the right bank of the Río Urubamba. Having heard the sound of gunfire, we met a hunter

who had just killed two titis (an adult male with infant). He allowed us to remove their skins and skulls (Figs. 1–6). Titis clearly resembling *C. toppini* were also reported at another locality on the right bank of the Río Urubamba. We walked 38 km of trails and surveyed 49 km by canoe.

Sector 3: Río Ucayali

We encountered titi monkeys at 13 localities along the Río Ucayali and we heard them at two. The situation along this river is different from that reported in the literature (Hershkovitz 1990; Aquino and Encarnación 1994). At four localities on the right bank of the Río Ucayali, in its southern reaches, we encountered 16 titis that were similar to the reddish titi monkeys along the Río Inuya, which we identified as *C. toppini*. At one point (near latitude 10°2'50"S), this species was replaced by a different titi that had a white stripe on the forehead, reddish underparts, a brownish back, and a tail with the terminal half whitish. We observed this species at four localities (22 individuals) and it was reported at an additional locality on the same side of the river. The species was identified as *Callicebus discolor* (*sensu lato*).

We found no evidence of titi monkeys in the area just north of the Río Tambo, on the left bank of the Río Ucayali. It was not clear to us if this was a natural absence or that the species had been extirpated. We encountered more titis, matching the phenotype of *Callicebus discolor* that we had also observed on the other river bank, at three localities (nine individuals) to the north of this area. We walked 44 km of trails surveyed 39 km by canoe. The results are summarized in Figure 7 and Table 1.

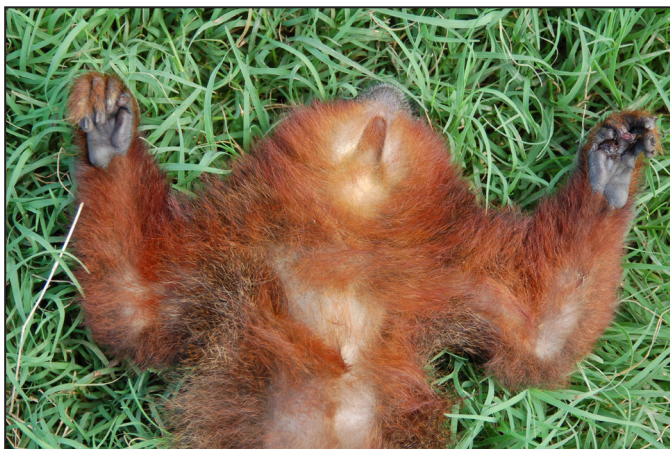
Discussion

The goal of this study was to identify the different species of *Callicebus* in the Atalaya region and to determine their distributions. During the expedition we encountered three species, including one which was new and undescribed. The three species are discussed here and we indicate their hypothetical distributions.

Callicebus toppini Thomas, 1914

Callicebus toppini. Thomas, O. 1914. *Ann. Mag. Nat. Hist.*, 8th ser., 13: 480. Toppin's titi. Type locality. Río Tahuamanu, N. E. Peru [sic], near Bolivian boundary. About 12°20'S, 68°45'W. Synonym: *Callicebus cupreus acreanus* Vieira, C. da C. 1952. *Pap. Avuls. Dept. Zool.*, São Paulo (11): 23. Acre titi. Type locality. Brazil: Iquiri, Territory of Acre, upper Río Purus.

The reddish, dark-tailed titi monkeys that we encountered on the right (eastern) side of the Río Urubamba and the upper Río Ucayali did not match *C. cupreus* (Fig. 8), *C. discolor* or *C. brunneus* that have been reported in recent taxonomic revisions (Hershkovitz 1990; Van Roosmalen *et al.* 2002) as occurring in the central and southern part of Peru. After studying the literature and the holotype at the British Museum



Figures 1–3. (left column) Lateral and frontal views of the head, and ventral view of the specimen of *C. toppini* collected on the right bank of the Río Urubamba (specimen deposited in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42399). Note the reddish hairs on the ears, thin black line on the forehead and yellowish crown. Photographs by Proyecto Mono Tocón.



Figures 4 and 5. (above) Dorsal views of the specimen of *C. toppini* MUSM 42399 collected on the right bank of the Río Urubamba. Photographs by Proyecto Mono Tocón.



Figure 6. (above) The infant of *C. toppini* is uniformly reddish-agouti dorsally, comparable to the coloration of infants of *C. cupreus*. Specimen collected on the right bank of the Río Urubamba (deposited in the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42400). Photograph by Proyecto Mono Tocón.

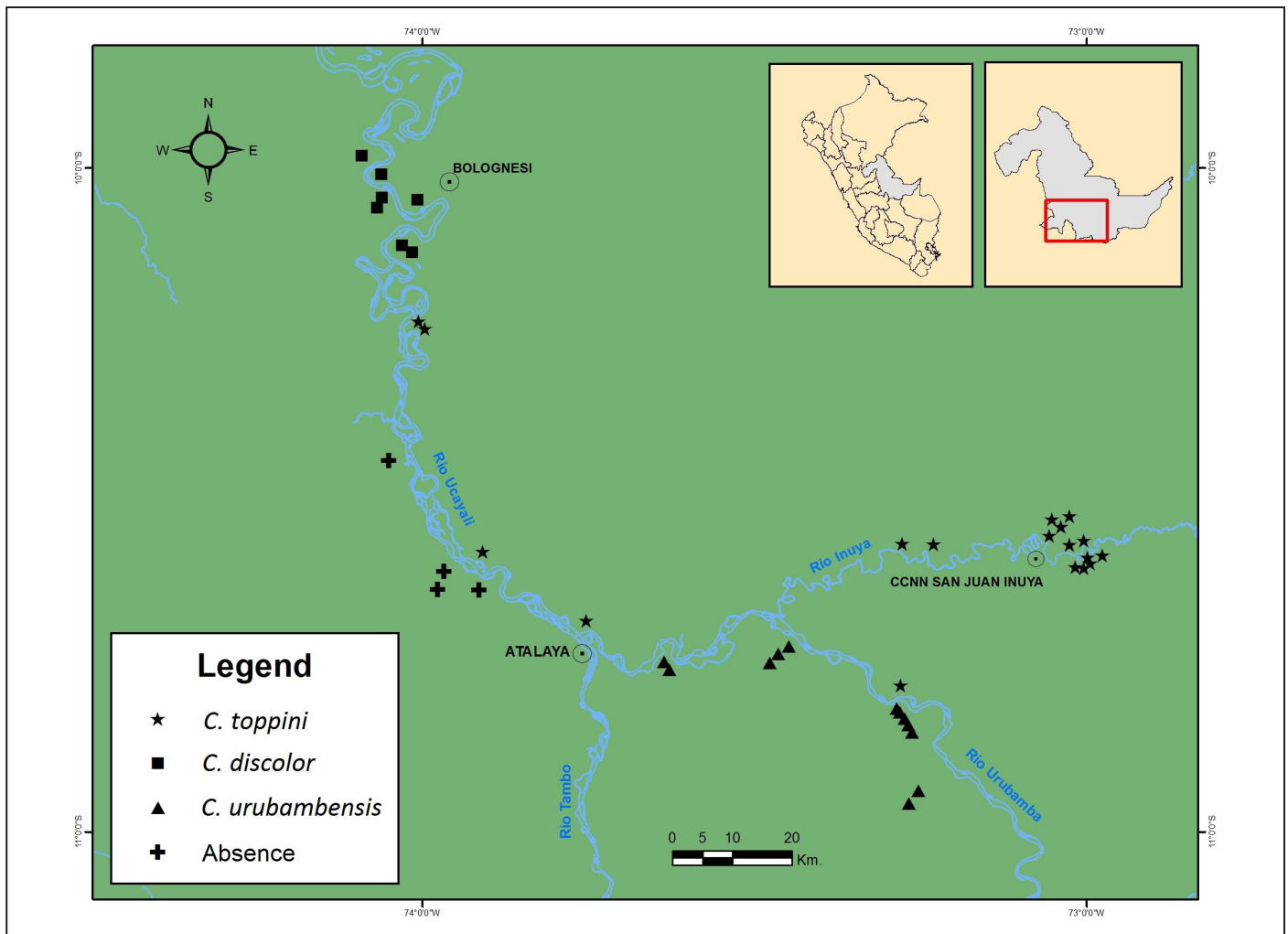


Figure 7. Localities of *Callicebus* species observed during the field survey.

Table 1. Localities, number of individuals seen and identification of *Callicebus* observed during the field survey.

Locality	River / Margin		Altitude (m)	Taxon	Number of individuals seen	Coordinates	
Río Ucayali	Ucayali	Right	180	<i>C. discolor</i>	4	10°02'50"S	74°00'26"W
Quebrada Shebonillo	Ucayali	Left	208	<i>C. discolor</i>	5	10°02'13"S	74°03'34"W
Quebrada Shebonillo	Ucayali	Left	178	<i>C. discolor</i>	2	10°02'26"S	74°03'35"W
Betijay	Ucayali	Right	175	<i>C. discolor</i>	*	10°02'08"S	74°02'25"W
Río Ucayali	Ucayali	Right	187	<i>C. discolor</i>	7	10°00'09"S	74°04'30"W
Río Ucayali	Ucayali	Left	173	<i>C. discolor</i>	2	09°59'15"S	74°05'02"W
Río Ucayali	Ucayali	Right	199	<i>C. discolor</i>	5	10°06'16"S	74°01'42"W
Río Ucayali	Ucayali	Right	173	<i>C. discolor</i>	6	10°06'21"S	74°01'30"W
Río Sepa	Sepa	Left	264	<i>C. urubambensis</i>	4	10°57'20"S	73°15'50"W
Río Sepa	Sepa	Right	296	<i>C. urubambensis</i>	5	10°56'26"S	73°15'19"W
Penal del Sepa	Urubamba	Left	267	<i>C. urubambensis</i>	3	10°48'45"S	73°17'15"W
Penal del Sepa	Urubamba	Left	269	<i>C. urubambensis</i>	3	10°48'47"S	73°17'12"W
Penal del Sepa	Urubamba	Left	268	<i>C. urubambensis</i>	3	10°48'49"S	73°17'10"W
Penal del Sepa	Urubamba	Left	258	<i>C. urubambensis</i>	3	10°48'45"S	73°17'14"W
Penal del Sepa	Urubamba	Left	280	<i>C. urubambensis</i>	3	10°48'50"S	73°17'08"W
Takile	Urubamba	Left	253	<i>C. urubambensis</i>	2	10°43'03"S	73°26'47"W
Takile	Urubamba	Left	267	<i>C. urubambensis</i>	4	10°43'20"S	73°27'08"W
Takile	Urubamba	Left	227	<i>C. urubambensis</i>	1	10°43'13"S	73°27'03"W
San José	Urubamba	Left	306	<i>C. urubambensis</i>	2	10°44'31"S	73°38'12"W
San José	Urubamba	Left	301	<i>C. urubambensis</i>	2	10°44'29"S	73°38'18"W

Table 1 continued on next page

Table 1. (continued)

Locality	River / Margin		Altitude (m)	Taxon	Number of individuals seen	Coordinates	
San Juan/Inuya	Inuya	Right	267	<i>C. toppini</i>	2	10°34'27"S	73°00'22"W
San Juan/Inuya	Inuya	Right	256	<i>C. toppini</i>	3	10°34'44"S	73°01'36"W
San Juan/Inuya	Inuya	Right	331	<i>C. toppini</i>	1	10°33'13"S	73°03'22"W
San Juan/Inuya	Inuya	Right	282	<i>C. toppini</i>	3	10°31'51"S	73°02'58"W
San Juan/Inuya	Inuya	Right	308	<i>C. toppini</i>	1	10°31'57"S	73°02'25"W
San Juan/Inuya	Inuya	Right	301	<i>C. toppini</i>	1	10°31'58"S	73°02'30"W
San Juan/Inuya	Inuya	Left	252	<i>C. toppini</i>	1	10°34'10"S	73°00'20"W
San Juan/Inuya	Inuya	Left	274	<i>C. toppini</i>	3	10°34'26"S	73°00'22"W
San Juan/Inuya	Inuya	Left	265	<i>C. toppini</i>	1	10°34'19"S	73°00'19"W
San Juan/Inuya	Inuya	Right	315	<i>C. toppini</i>	4	10°34'36"S	72°59'06"W
San Juan/Inuya	Inuya	Left	265	<i>C. toppini</i>	4	10°34'35"S	72°59'36"W
Río Inuya	Inuya	Right	250	<i>C. toppini</i>	2	10°35'04"S	73°14'38"W
Río Inuya	Inuya	Left	241	<i>C. toppini</i>	3	10°34'38"S	73°16'52"W
Quebrada Chicosillo	Ucayali	Right	216	<i>C. toppini</i>	2	10°40'54"S	73°45'11"W
Río Ucayali	Ucayali	Right	208	<i>C. toppini</i>	5	10°35'27"S	73°55'12"W
Río Ucayali	Ucayali	Right	188	<i>C. toppini</i>	4	10°13'43"S	74°00'38"W
Río Ucayali	Ucayali	Right	196	<i>C. toppini</i>	5	10°13'47"S	74°00'34"W
Río Urubamba	Urubamba	Right	260	<i>C. toppini</i>	3	10°47'25"S	73°16'43"W
Sabaluya	Urubamba	Right	240	<i>C. toppini</i>	*	10°41'05"S	73°42'07"W

* no observation, but presence reported by local communities

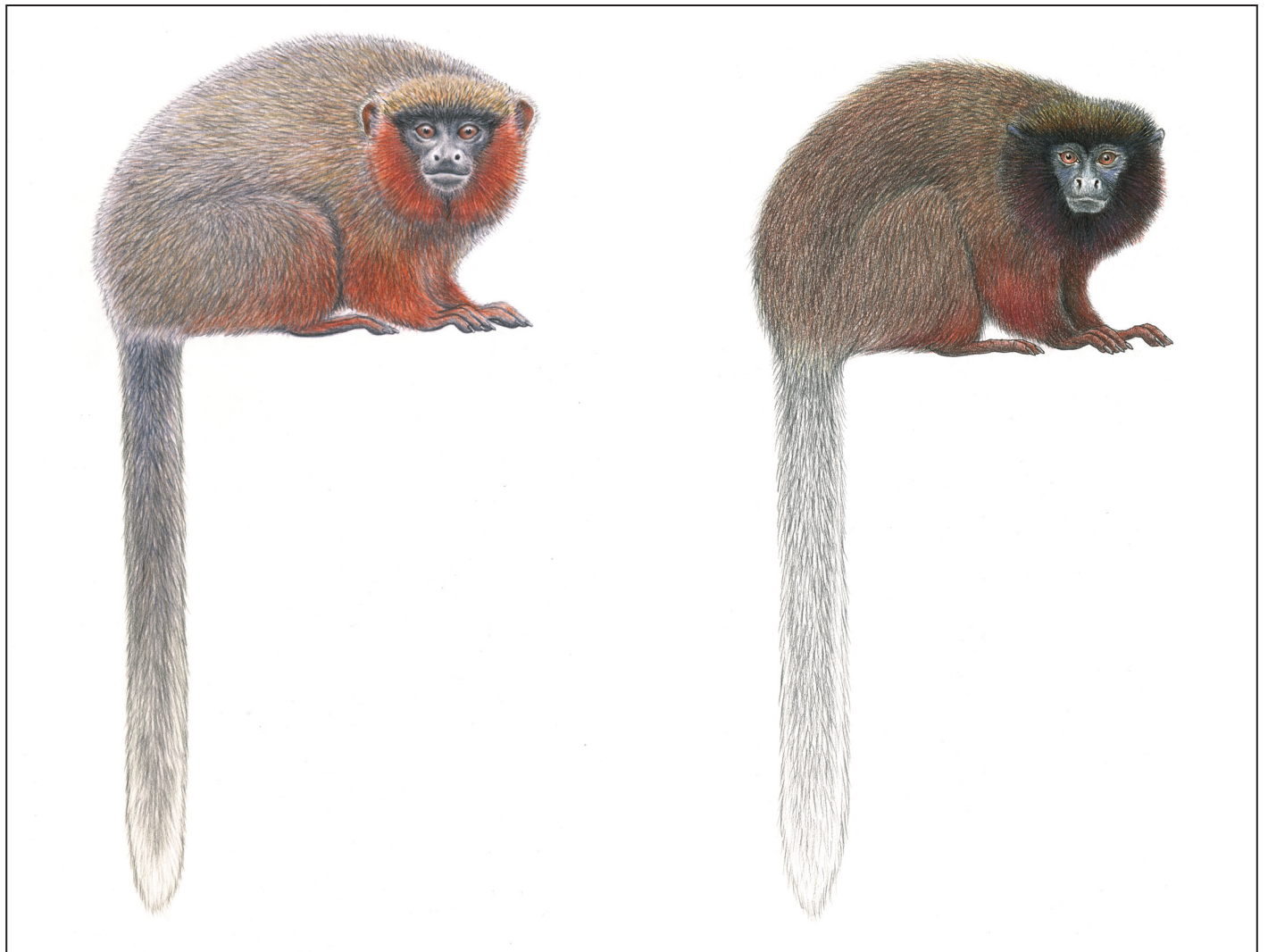


Figure 8. Toppin's titi, *Callicebus toppini* (left) compared to the coppery titi *Callicebus cupreus* that has a fluffier tail that is more whitish throughout its length (on the right). Some *C. cupreus* are as orange as *C. toppini*, but always have a whitish tail. Illustrations by Stephen D. Nash.

(Natural History) in London (Figs. 9–11), we identified the observed and collected reddish animals as *Callicebus toppini*.

This species was described by Thomas (1914; p.480) as follows: “Allied to and of the same grizzled brown color as *C. cupreus*. Crown-hairs similarly tipped with buffy, but along the front edge of the hairy part of the forehead the hairs are black, thus forming an indistinct blackish frontal band. Belly and terminal part of limbs red, as in *cupreus*, but on the hind legs the red is rather more extended, coming up to cover the knee. Hairs on ears dark reddish brown, tail hairs mixed



Figures 9–11. Holotype of *Callicebus toppini* in the British Museum (Natural History). Collection no. BM 19.14.3.3.3. Photographs courtesy of the British Museum (Natural History) Picture Library.

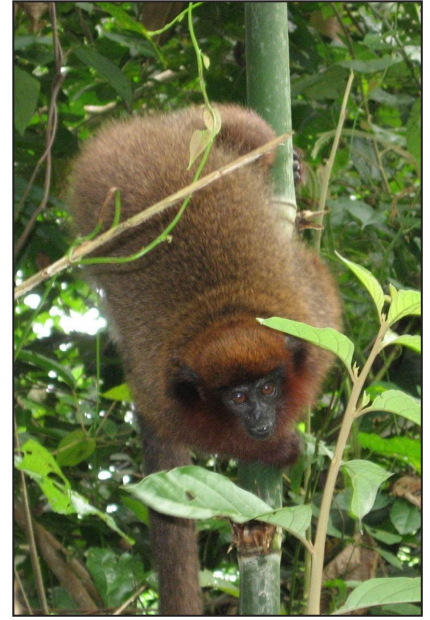
grey and blackish, as in *cupreus*, but those on the proximal two-thirds are tipped with black, not with white or buffy as in the other species of this group.” The type locality is the Río Tahuamanu, in south-eastern Peru (Fig. 24).

Herschkovitz (1963) first considered *C. toppini* to be a junior synonym of *C. brunneus*, but after examining more specimens, including the holotype, in his 1990 review he synonymized it with *C. cupreus*. Partly based on the examination of the AMNH specimens from the Atalaya area, he included the Río Inuya in the range of *C. cupreus*. The AMNH specimens from the Atalaya region all have dark tails with a whitish tip, and match well with the original description and the holotype of *C. toppini* (J. Vermeer pers. obs.).

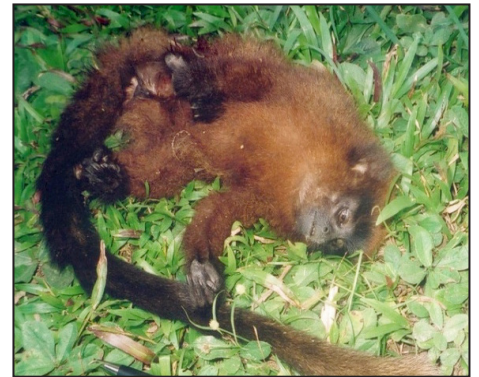
A comparable dark-tailed taxon, *acreatus* Vieira, from Iquiri, Acre, Brazil, closely resembles the holotype of *C. toppini*, and we consider it to be a junior synonym, as did Cabrera (1957). Examination of pictures of animals from the eastern part of Manu (and our observations of live animals), Los Amigos, Río Camisea and the Tambopata National Reserve in Peru, from Acre in Brazil and from the Pando in Bolivia (see also Rowe and Martinez 2001; Martinez and Wallace 2013; Porter *et al.* 2013) indicates that this whole area is occupied by *Callicebus toppini*. There may be some intraspecific variation in coloration, mainly on the ventrum, and the amount of black hairs on the forehead, ears or hands (Figs. 12–23). In our opinion, the variation seen is not geographically consistent or significant enough to consider the presence of different species.

Table 2. Cranial measurements (mm) of the collected *C. toppini* specimen adult male MUSM 42399, deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima. After Kobayashi (1995).

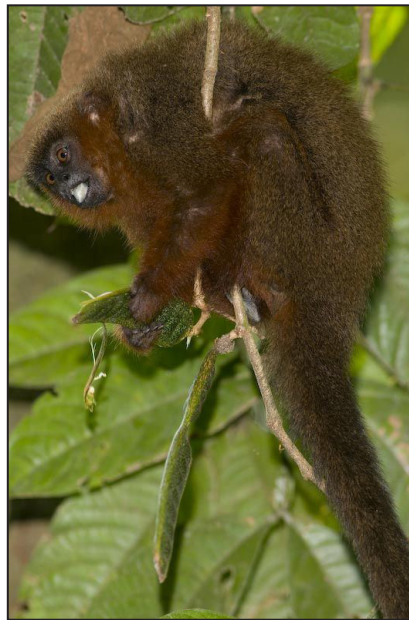
Cranial measurement	Adult male
Nasion – Rhinion	9.2
Rhinion – Prosthion	11.39
Nasion – Prosthion	20.6
Left maxillofrontale -Right maxillofrontale	3.81
Left frontomale orbitale -Right frontomale orbitale	29.85
Left zygomaxillare superior -Right zygomaxillare superior	27.45
Left frontomale orbitale - Left zygomaxillare superior	11.15
Left zygomaxillare superior -Left zygomaxillare inferior	14.52
Greatest width across outer margins of orbit	34.29
Left zygion - Right zygion	37.95
Greatest width across narrowest part in postorbital portion	30.45
Left euryon - Right euryon	33.97
Prosthion - Bregma	44.47
Nasion - Bregma	29.08
Bregma - Lambda	30.13
Prosthion - Lambda	57.96
Basion - Bregma	33.63
Left zygomaxillare inferior -Right zygomaxillare inferior	32.3
Left kondilion laterale - Right kondilion laterale	32.01
Left koronion - Right koronion	37.22
Infradentale -Left kondilion laterale	38,93
Infradentale - Gnathion	12.97
Greatest length between left koronion and base of mandibular	32.31



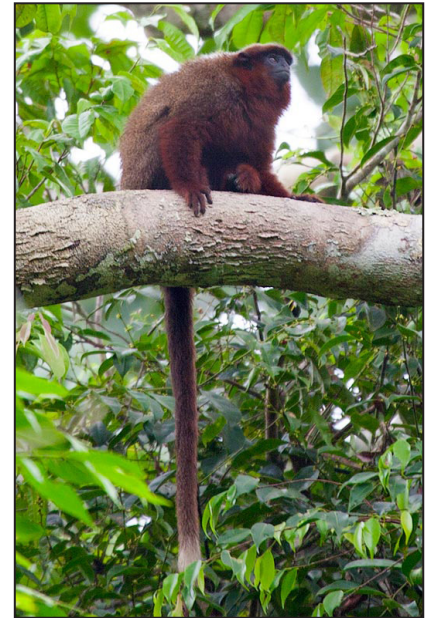
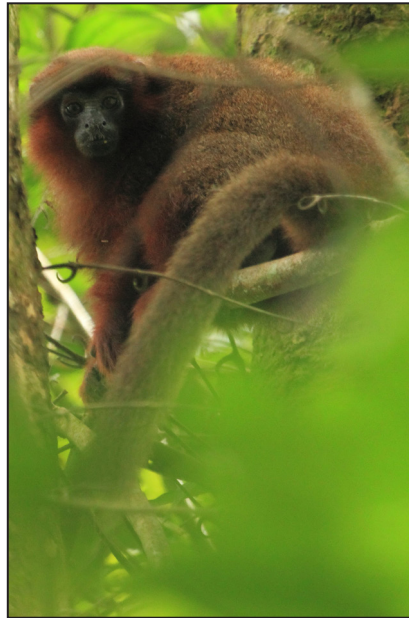
Figures 12–14. *Callicebus toppini* from three different localities. From left to right: Manu National Park, on the border of the upper Río Madre de Dios, Peru (photo by Mauro Mozzarelli); Los Amigos, north of the Río Madre de Dios, Peru (photo by Job Aben); and Tambopata Research Center, left margin of the Río Tambopata and south of the Río Madre de Dios, Peru (photo by Inés Nole Bazán). For localities, see Figure 24.



Figures 15–17. *Callicebus toppini* from two localities. On the left a titi from the left side of the Río Inuya, Peru (photo by Proyecto Mono Tocón); in the middle a male from the Los Amigos Biological Station (CICRA), north of the Río Madre de Dios, Peru (photo by Cédric Girard-Buttoz), and on the right a titi killed by hunters near Los Amigos (photo by Jenna Lawrence). The latter two have very dark hands and feet compared to other animals on the pictures (including other animals from the same locality, Fig. 13). For localities, see Figure 24.



Figures 18–20. *Callicebus toppini* from the Tambopata Research Center, left bank of the Río Tambopata, south of the Río Madre de Dios, Peru (photos from left to right by: Brett Cole, Roland Seitre and Peter Eekelder). For localities, see Figure 24.



Figures 21–23. Three more *Callicebus toppini* from Brazil and Bolivia. From left to right: Zoobotanical Park of the Federal University of Acre, Río Branco, Acre, Brazil (photo by J. C. Bicca-Marques); Río Branco, Brazil (photo by Tomaz Nascimento de Melo), and Manuripi, Pando, Bolivia (photo by Erwin van Maanen). For localities, see Figure 24.

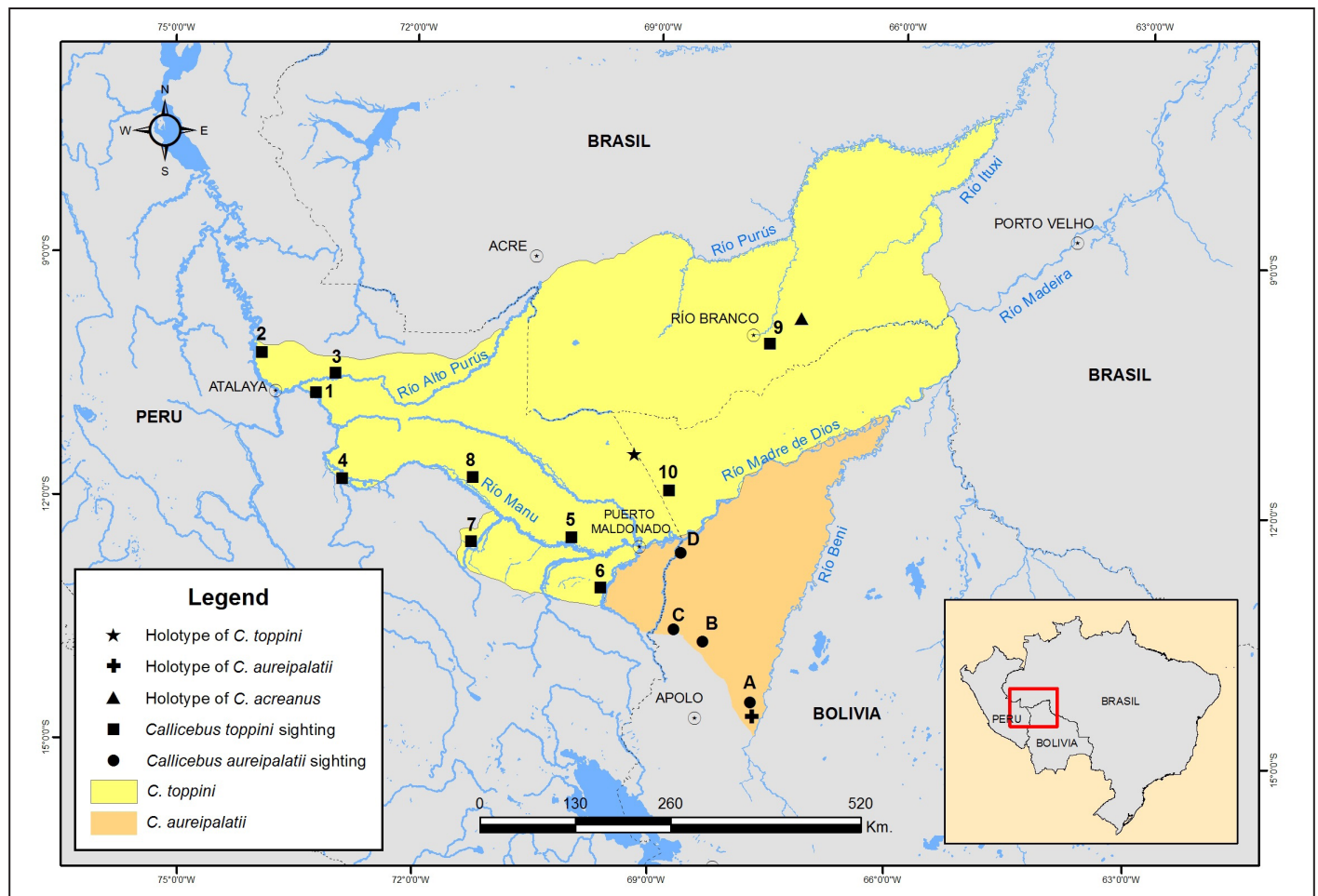


Figure 24. Hypothetical distributions of Toppin's titi *Callicebus toppini* and the Madidi titi *Callicebus aureipalatii*, based on observations, photographs, examination of museum specimens and literature cited in the text. Locality 1: Río Urubamba, Peru (this study); 2: Río Ucayali, Peru (this study); 3: Río Inuya, Peru (this study); 4: Río Camisea, Peru (pictures provided by T. Gregory); 5: Los Amigos, Peru (Figs. 13, 16, 17, and many other pictures); 6: Tambopata Research Center, Peru (Figs. 14, 18, 19, 20, and many other pictures); 7: Manu National Park, upper Río Madre de Dios, Peru (Fig. 12, and pers. obs.); 8: Manu National Park, Cocha Cashu, Peru (pictures provided by John Bunce and Inés Nole Bázan); 9: Río Branco, Acre, Brazil (Figs. 21, 22); 10: Manuripi, Bolivia (Fig. 23); A: Río Tuichi, Bolivia (Wallace *et al.* 2006); B: Río Undumo, Bolivia (Wallace *et al.* 2006); C: Upper Río Madidi, Bolivia (Wallace *et al.* 2006); D: Green Bolivia, Bolivia (Martinez 2010).

The situation around the Los Amigos Biological Station (CICRA) warrants some more attention. Besides the common *C. toppini* (Fig. 13), there are some reports of darker animals (Figs. 16–17), which could be just a local color variation, as mixed groups are common. Interestingly, of seven pairings studied, all males were dark and the females were distinctly redder (J. Lawrence, pers. comm.). Sexual dichromatism has never been reported in Amazonian *Callicebus*; extreme intraspecific phenotypic variation is common in *C. oenanthe* (Proyecto Mono Tocón, unpubl. data), but there is no indication of sexual dichromatism. Martinez and Wallace (2013) reported similar animals from northern Bolivia with dark hands that do not match the holotype of *C. toppini*. Buchanan-Smith *et al.* (2002) and Christen (1999) observed titi monkeys in northern Bolivia with very reddish/orange on their backs, while others were medium to dark brown. *Callicebus toppini* has a grayish to brownish back, but it is difficult to interpret the observations of the animals with the orange backs. It is clear that more research is necessary in this area.

The validity of *C. aureipalatii* remains unclear. The animal that we collected near the Río Urubamba resembles

very much the holotype of *C. aureipalatii* figured in the publication of the original description (Wallace *et al.* 2006). However, *C. aureipalatii* is reported to be different from the animals of Pando, Bolivia (Martinez and Wallace 2013; Porter *et al.* 2013). Molecular genetic investigation is needed to show that this species is not just a color variant of *C. toppini*.

It is interesting to note that a titi monkey from the south bank of the Río Manuripi, Pando, Bolivia, had a karyotype of $2n = 48$ (Minezawa *et al.* 1989). It was identified as *C. brunneus*, but as there are only reports of reddish animals from the Pando (Cameron *et al.* 1989; Martinez and Wallace 2013; Porter *et al.* 2013; Erwin van Maanen pers. comm. to JV), the titi in question could have been *C. toppini*. Considering that *C. cupreus* and *C. discolor* (*sensu lato*) have a karyotype of $2n = 46$ (Hershkovitz 1990; Bueno *et al.* 2006), this could explain the occurrence of *C. toppini* and *C. discolor* along the Río Ucayali where there is no evidence of a hybrid zone or any geographical barrier. The same is possibly true for *C. toppini* and *C. cupreus* in Peru and Brazil.

In summary, we conclude that the reddish titi monkeys living in south-eastern Peru, south-western Brazil and

north-western Bolivia belong to the species *Callicebus toppini*, and we therefore reinstate it. The Río Urubamba seems to be its western geographical barrier. The species is replaced along the Río Ucayali by *C. discolor* and possibly *C. cupreus*, but the exact northern limits are unknown. The eastern barrier is probably the Río Ituxi (where it is parapatric with *C. dubius*), the southern barriers are the Río Tambopata and Río Madre de Dios. If we consider *C. aureipalatii* as a junior synonym of *Callicebus toppini*, its most southerly locality is the Hondo Valley (Martinez and Wallace 2013), while its eastern boundary is the Río Beni (Martinez and Wallace 2013). For convenience, the species have been separated in Figure 24. More research, in the field and in museums, is necessary to determine the exact limits

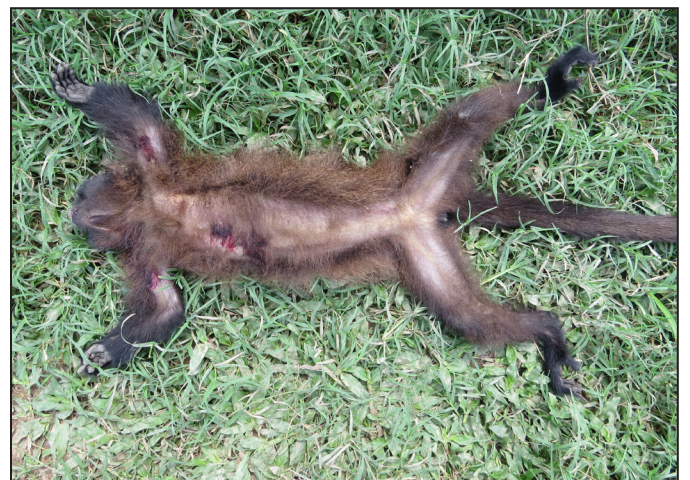
of the distribution of *C. toppini*. Museum specimens labelled as *C. cupreus* and *C. brunneus* should be re-examined to determine which are actually *C. toppini*.

***Callicebus urubambensis* sp. nov.**

The dark brown specimens labeled as coming from “Mouth Río Inuya, Río Urubamba” and “Boca Río Urubamba”, collected by the Olalla brothers and presently in the collection of the American Museum of Natural History, were identified by Hershkovitz (1990) as belonging to *Callicebus brunneus*. However, after observation in the wild, a study of museum specimens and an analysis of the literature, we propose that these animals represent an undescribed species.

Holotype: Adult male, skin and skull. Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42398. Collectors: Jan Vermeer and Julio C. Tello; Proyecto Mono Tocón. Obtained from a hunter on 29 November, 2013, on the left bank of the Río Urubamba (10°48'50"S, 73°17'08"W, altitude 280 m) (Figs. 25–28).

Paratypes: 1) Nulliparous female; skin (forearms missing), skull and complete skeleton. Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima,



Figures 25–28. The holotype of *C. urubambensis* collected on the left bank of the Río Urubamba (specimen deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42398). Photographs by Proyecto Mono Tocón.



Figure 29. The Urubamba brown titi monkey *Callicebus urubambensis* (left) compared to the, more grizzled, brown titi *C. brunneus* (right) with a varying amount of black on the head. Illustrations by Stephen D. Nash.

collection no. MUSM 15911. Collected on 12 September, 1999, by B. D. Patterson at Quebrada Aguas Calientes, left bank of the upper Río Madre de Dios, 2.75 km east of Shintuya ($71^{\circ}16'08''\text{W}$, $12^{\circ}40'50''\text{S}$). 2) Subadult male; skin, skull and complete skeleton. Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 15912. Collected on 12 September, 1999, by S. Solari at Quebrada Aguas Calientes, left bank of the upper Río Madre de Dios, 2.75 km east of Shintuya ($71^{\circ}16'08''\text{W}$, $12^{\circ}40'50''\text{S}$).

Type locality: Peru: near the Colonia Penal del Sepa, on the right bank of the Río Sepa, a western tributary of the Río Urubamba ($10^{\circ}48'50''\text{S}$, $73^{\circ}17'08''\text{W}$). Altitude 280 m.

Synonyms: *Callicebus brunneus* in part (Hershkovitz 1963, 1988; Kobayashi 1995; not Wagner 1842).

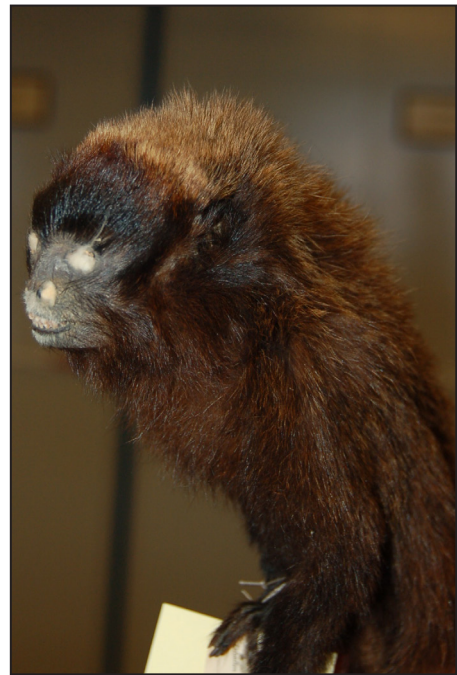
Diagnostic characters: Forehead with a jet-black band extending to behind the ears. Ears black, covered with long black hairs. Hairs of the cheeks brownish-agouti with long black tips, directed forwards and giving the cheeks, from a

distance, a black color. Chin brown agouti. Facial skin black with black hairs on the cheeks and many white hairs on the nose and around the mouth. Pupils black and irises light brown. Dorsal and lateral side of the body, including the upper arms and the legs, brownish-agouti. Crown the same color as the back. Hands and inner side of the forearms black. Outer side of the forearms black up to the elbow, mixed with a small amount of agouti hairs. Feet black, knees darker than the rest of the leg, giving them a blackish hue. Lateral side of the body, inner side of the upper arms and legs brown-agouti, paler colored than the back. Basal half of the tail almost black, mixed with some brown agouti hairs, becoming lighter towards the end, with a greyish tip.

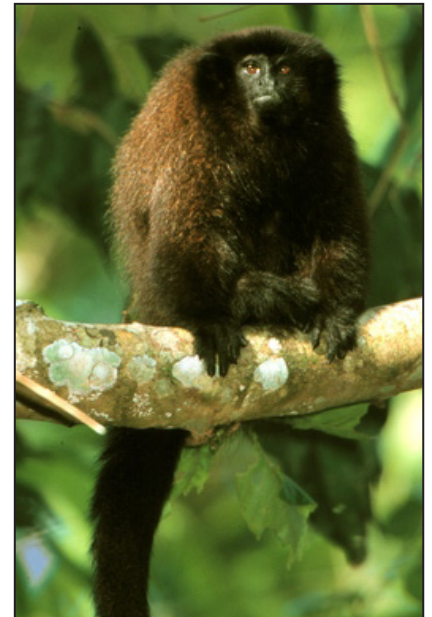
Paratype 15912 differs in having the forearms less black, with more brown-agouti hairs and a few lighter colored hairs on hands and feet. The same variation is also seen in the six AMNH specimens from the Río Urubamba. We did not observe any variation in the 35 individuals that we



Figure 30. View of the heads of *C. urubambensis* (left) and *C. brunneus* (right). Illustration by Stephen D. Nash.



Figures 31 and 32. The lectoparatypes of *C. brunneus* (NMW-ST122 on the left; NMW-B3453 on the right), preserved in the Naturhistorisches Museum in Wien, Austria. The species is more brownish than *C. urubambensis*, has no black forearms and less black around the face. The hairs on the back of the head have yellowish tips. Photographs by Proyecto Mono Tocón.



Figures 33–35. Three *C. urubambensis* from different localities. Individuals shown on the left and in the center: left bank of the Río Urubamba, near the Colonia Penal del Sepa, Peru (Photographs by Proyecto Mono Tocón); specimen on the right: Amazonia Lodge, on the left bank of the upper Río Madre de Dios, Peru (Photograph by Kevin Schafer).

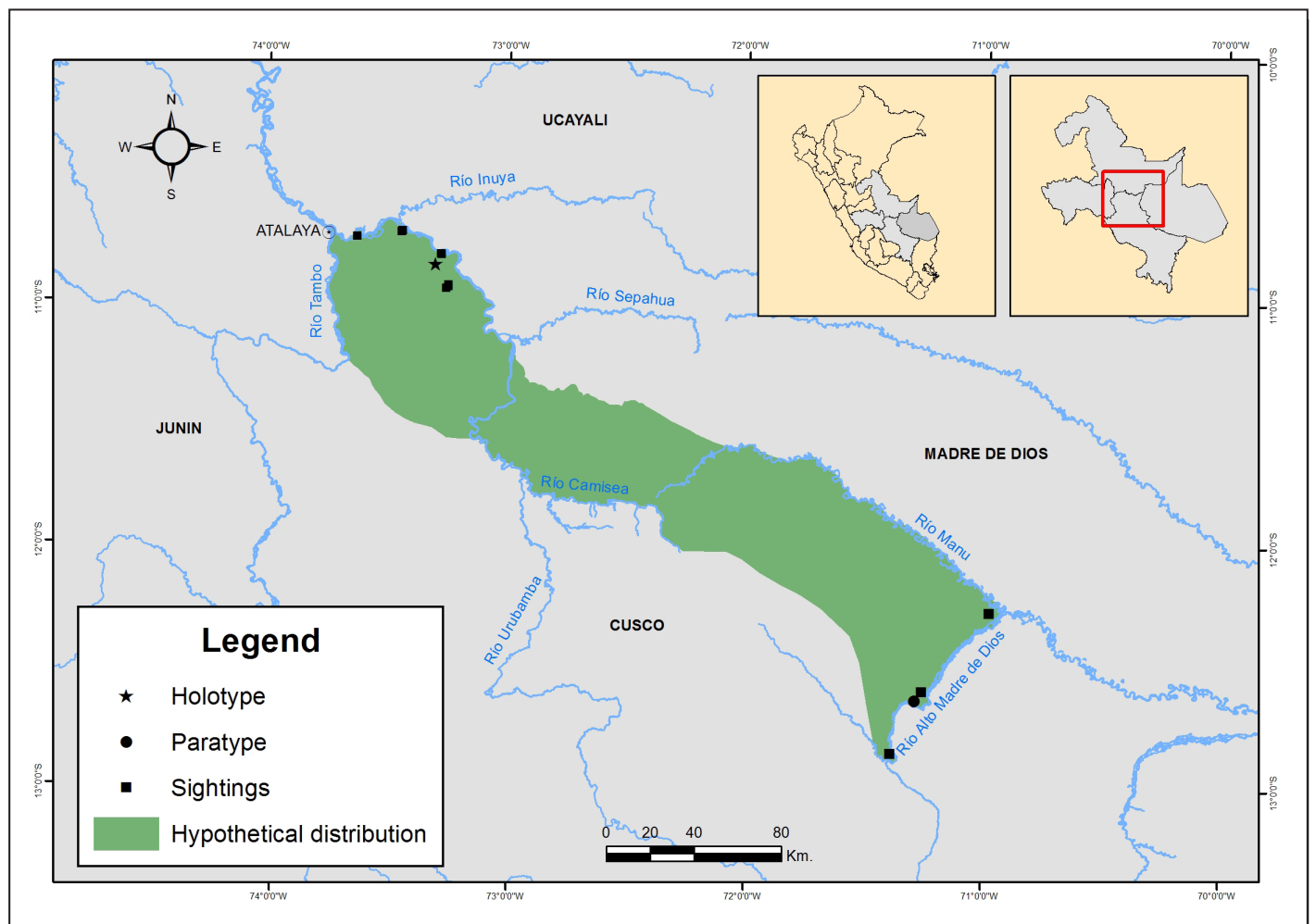


Figure 36. Hypothetical distribution of *Callicebus urubambensis*. Northern sightings during this study, south-eastern sightings along the upper Río Madre de Dios mentioned in the text.

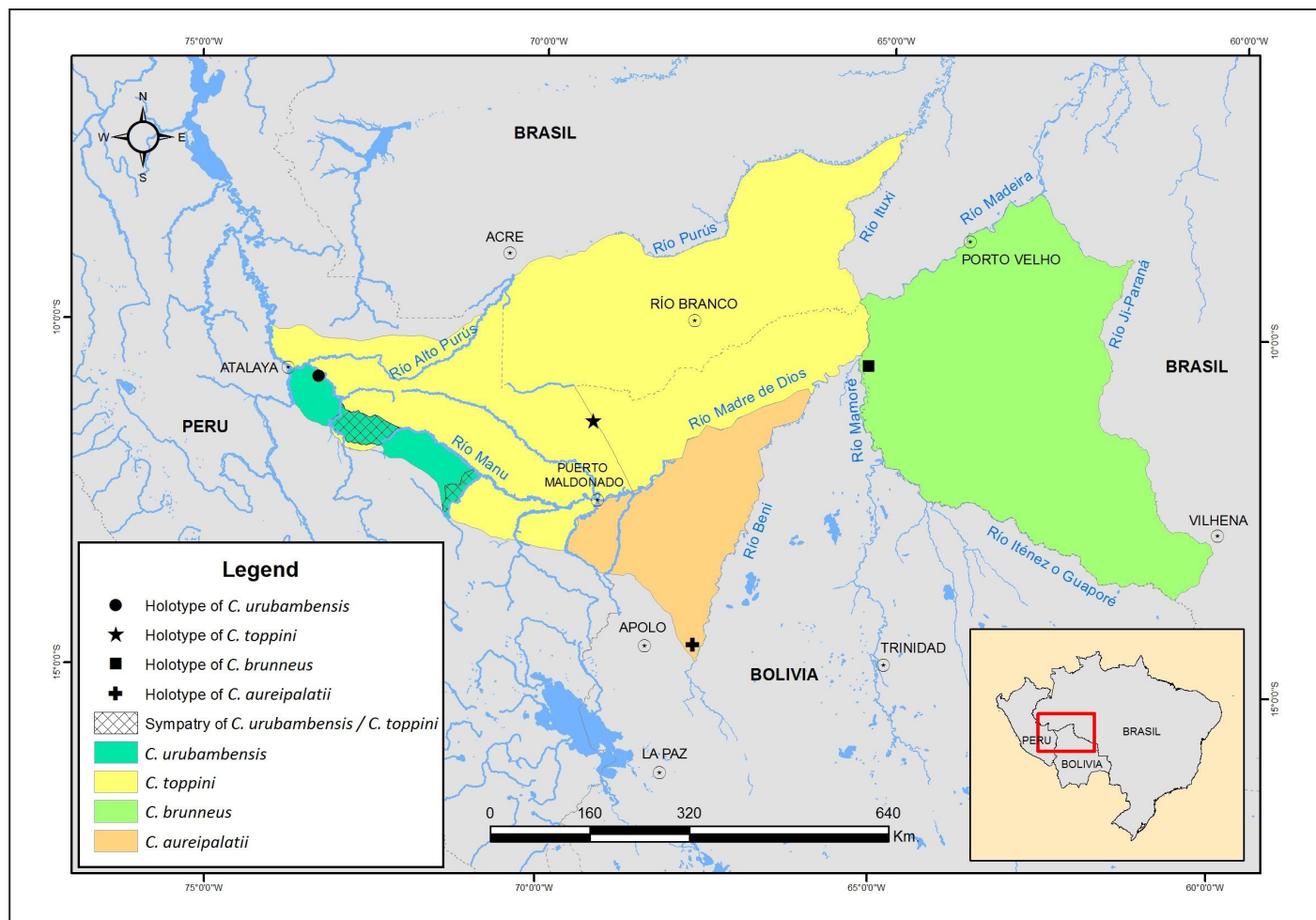


Figure 37. Hypothetical distributions of *Callicebus urubambensis*, *C. toppini*, *C. brunneus*, and *C. aureipalatii*. There is little reliable information on the distribution range of *C. brunneus*; this map is based on Ferrari *et al.* (2000) and Porter *et al.* (2013).

encountered, but it should be noted that it is very difficult to see the details of these dark monkeys in a dark forest.

Comparisons: Distinguished from the partially sympatric *Callicebus toppini* by its dark color and brownish underparts. Along the Río Tambo it is probably allopatric with *Callicebus discolor* from which it is easily distinguished by its black forehead and brown color. It is distinguished from the Brazilian *Callicebus brunneus* (Wagner) by the coloration of the head (Fig. 30). In *C. urubambensis*, the occiput and the sides of the face are the same brown color as the back. In *C. brunneus*, there is a dark brown band behind the jet-black frontal blaze, separating it from the yellowish occiput. The yellowish coloration extends towards the neck, where it becomes the same agouti-brown color as the back and the sides of the body. The cheeks of *C. brunneus* are dark brown, conspicuously darker than the sides of the body.

There is some variation in the coloration of the lecto-(para)-types of *C. brunneus*, but none has the black forearms of *C. urubambensis* (Figs. 31 and 32). There is a geographical gap of more than 600 km between the most eastern observation of *C. urubambensis* and the most western confirmed sighting of *C. brunneus*. Genetic studies could elucidate the taxonomic relationship between the two species.

Measurements of the holotype: Head-and-body length 300 mm; Tail length 400 mm; Foot length 85 mm; Hand length 50 mm; Arm length 120 mm; and Hindleg length 170 mm.

Etymology: This species is named after the Río Urubamba, Peru, where it was discovered.

Vernacular name: The species is locally known as “mono tocón.” We propose the name Urubamba brown titi monkey.

Geographical distribution: We encountered *C. urubambensis* at 12 localities on the left bank of the Río Urubamba. We did not observe it on the right bank of that river or on the left bank of the Río Tambo. The paratypes came from the Quebrada Calientes, on the left bank of the upper Río Madre de Dios, on the eastern border of Manu National Park (71°16'08"W, 12°40'50"S). A photograph of *C. urubambensis* was taken near the Amazonia Lodge, also on the left bank of the upper Río Madre de Dios (71°22'10"W, 12°51'57"S) (Figs. 33–35), while the species was also observed further downriver, near Pantiacolla Lodge (71°14'31"W, 12°39'36"S) and Yine Lodge (approx. 70°55'45"W, 12°16'03"S) (J. Vermeer, pers. obs.). Despite the presence of many researchers and tourists in the Tambopata Nature Reserve and the Los Amigos Biological Station further to the east, there is no evidence that *Callicebus urubambensis* occurs east of the upper

Table 3. Cranial measurements (mm) of holotype of *C. urubambensis* MUSM 42398 and paratype MUSM 15912. After Kobayashi (1995).

Cranial measurement	Holotype MUSM 42398	Paratype MUSM 15912
Nasion – Rhinion	9.61	10.42
Rhinion – Prosthion	11.16	8.12
Nasion – Prosthion	20.81	20.43
Left maxillofrontale - Right maxillofrontale	3.59	3.11
Left frontomolare orbitale - Right frontomolare orbitale	28.31	29.59
Left zygomaxillare superior - Right zygomaxillare superior	25.69	26.04
Left frontomolare orbitale - Left zygomaxillare superior	13.12	10.47
Left zygomaxillare superior - Left zygomaxillare inferior	11.70	13.87
Greatest width across outer margins of orbit	33.99	34.00
Left zygion - Right zygion	37.08	37.39
Greatest width across narrowest part in postorbital portion	29.86	29.51
Left euryon - Right euryon	33.97	33.28
Prosthion - Bregma	45.19	45.54
Nasion - Bregma	28.38	27.42
Bregma - Lambda	29.35	29.37
Prosthion - Lambda	58.37	60.45
Basion - Bregma	31.19	32.85
Left zygomaxillare inferior - Right zygomaxillare inferior	30.73	28.34
Left kondilion laterale - Right kondilion laterale	31.38	32.62
Left koronion - Right koronion	34.22	36.27
Infradentale - Left kondilion laterale	37.62	40.98
Infradentale - gnathion	9.84	10.8
Greatest length between left koronion and base of mandibular	31.39	38.34

**Figures 38–39.** Skull of the holotype of *C. urubambensis* collected on the left bank of the Río Urubamba (specimen deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, collection no. MUSM 42398). Photographs by Proyecto Mono Tocón.

Río Madre de Dios, and all available photographs indicate that the titi monkey in those areas is the generally misidentified *C. toppini*.

Although we know that rivers are not absolute geographical barriers for titi monkeys, especially in areas where rivers constantly change their course, we used large rivers to indicate the distributions of the species (Fig. 36). We estimate that the range of *Callicebus urubambensis* includes the lowland forest area between the right bank of the Río Tambo and the left bank of the Río Urubamba, and the lowland forest between the left bank of the Río Manu and the left bank of the upper Río Madre de Dios. The species' distribution is further restricted by the presence of mountain ridges to the west and south. The situation near the upper Río Urubamba needs further investigation. On both sides of the Río Camisea there are confirmed records only of *C. toppini* (T. Gregory, pers. comm.). However, somewhere there, there must be a connection between the western and eastern part of the distributions of *C. urubambensis*, unless in recent history the species has been replaced in that area by *C. toppini*. The species has been observed to live in sympatry with *C. toppini* in the eastern part of its distribution, on the left bank of the upper Río Madre de Dios (J. Vermeer, pers. obs.) (Fig. 37).

Systematics: Hershkovitz (1990) and Kobayashi (1995) divided the titi monkeys into species groups. Considering the resemblance in coloration, we would be tempted to place *C. urubambensis* in the same group as *C. brunneus*, which Hershkovitz (1990), Kobayashi, (1995) and Van Roosmalen *et al.* (2002) have in the *moloch* group. Van Roosmalen and Van Roosmalen (2014), on the other hand, placed it in the *cupreus* group. Considering, however, the coloration of neighboring species, we propose that it aligns with the *donacophilus* group (Kobayashi 1995). Following the “metachromism bleaching theory” (Hershkovitz 1988; Van Roosmalen and

Van Roosmalen 2014), *C. urubambensis* would be close to the archetypical taxon of this species group. The dark forehead, forearms, hands and feet show that the species underwent considerable eumelanin saturation, but the process switched to pheomelanin bleaching when members of the species group radiated northwards (*C. oenanthe*, which itself shows pheomelanin bleaching northwards in its restricted range) and south-eastwards (*C. modestus* to *C. olallae* to *C. donacophilus* to *C. pallescens*).

Conservation: The Urubamba brown titi is hunted for food, especially where all the larger primates have been exterminated. As it lives near villages, it is an easy prey for hunters and young boys with slingshots. However, considering its relatively large range with low human presence, there is no immediate threat for this species. It is protected in Manu National Park, and is common along the Río Urubamba (see also Aquino *et al.* 2013).

Callicebus discolor (*sensu lato*)

We provisionally identify the white-browed titi monkeys along the Río Ucayali as belonging to *Callicebus discolor* (*sensu lato*; but see Vermeer *et al.* 2011 for a discussion on that name) (Figs. 40–42). To be more specific, the animals match closely the *Callicebus subrufus* described by Elliot in 1907. This variation of the white-browed titi monkey is recognized by its rufous back, white ears and the basal half of the tail being black. The hands of many animals are very light colored, but not white. However, similarly colored titis have been reported from Ecuador and it seems that *C. discolor* is a highly variable species, just like *C. oenanthe* (pers. obs.); therefore we should probably list *C. subrufus* as a junior synonym of *C. discolor* (*sensu lato*).



Figures 40–42. Three white-browed titi monkeys, *C. discolor* from different localities. On the left: left bank of the Río Ucayali, Peru (Photograph by Proyecto Mono Tocón); in the middle and on the right: different localities on the right bank of the Río Ucayali, Peru. Photographs by Proyecto Mono Tocón. Notice that the latter animal has a small infant on its flank, possibly only one day old.

Taxonomic key to the *Callicebus* species of southern Peru.

- | | | |
|----|--|------------------------|
| 1 | Forehead with whitish transverse band..... | <i>C. discolor</i> |
| 1' | Forehead without a whitish transverse band..... | 2 |
| 2 | Upper and under parts brown; lower arms and legs black..... | <i>C. urubambensis</i> |
| 2' | Upper parts grayish brown, under parts reddish; lower arms and legs reddish..... | 3 |
| 3 | Tail whitish gray..... | <i>C. cupreus</i> |
| 3' | Tail dark with whitish tip..... | <i>C. toppini</i> |

According to Hershkovitz (1990), Aquino and Encarnación (1994), and Van Roosmalen *et al.* (2002), *C. discolor* is restricted to the left (western) side of the Río Ucayali. Hershkovitz (1990, p.63) even questions the provenance of two museum specimens in the AMNH (Río Inuya, east bank of the Ucayali) as being “on the wrong side of the Río Ucayali boundary of the *discolor* range.” We encountered the species on both sides of the river. This is not surprising, as the Río Ucayali is a river that constantly changes its course. It is possible that on the right bank of the Río Ucayali the white-browed titi is restricted to a narrow strip along the river, and that further inland it is replaced by another species, possibly *C. toppini* or *C. cupreus*. Lacking time, we were unable to determine this.

In order to locate the titis, we often played their vocalization from the Emmons *et al.* (1998) recordings. According to the authors, the recording we used was of *Callicebus moloch brunneus*, but considering the taxonomic history described above, this could also be another species. In many cases, individuals of *C. toppini* and *C. urubambensis* responded to the recordings. The white-browed titi monkey did not respond. When we recorded their vocalizations and played them to other groups of the same species, they did respond. This could indicate that titi monkeys can distinguish interspecific differences in vocalizations and do not (always) react to the vocalizations of a different species. Such a “linguistic barrier” could prevent interbreeding between different species. It would be interesting to investigate if the differences in vocalizations could be used to identify species or relationships between different species, just as is the case with some other primate species (Zimmermann 2009; Meyer *et al.* 2012).

Final considerations

To better understand the distributions and taxonomy of titi monkeys in Peru, research should continue further north and eastwards. The northern distributional limit for *C. toppini* and the southern limit for *C. cupreus* need to be established. It would also be interesting to know more about the distribution of *C. discolor* on the right bank of the Río Ucayali. Titi monkeys are often difficult to identify in the forest, especially the darker species, and more museum specimens would help us with understanding the diversity of this genus. Considering the hunting in the region, it should not be difficult for

researchers to obtain skins, skulls and skeletons from local hunters and deposit these materials in museum collections, without promoting (illegal) hunting.

With the addition of these two species, Peru has seven titis; two of them endemic, *C. oenanthe* and *C. urubambensis*. The genus *Callicebus* now comprises 34 species, and, as mentioned, more are likely to be described in the near future. *Callicebus*, as such, is the primate genus with the most species. As indicated by A. Kitchener (in litt.) reasons for this may be behavioral—small, monogamous groups, in small territories, which limit dispersal—and evidently a result of fluvial dynamics, so marked in the white-water rivers of the western Amazon such as the Ucayali, Amazonas-Marañón, Juruá, and Purús and their tributaries. Hershkovitz (1988) emphasized that changes in the courses of the rivers can isolate small populations or bring together two species previously isolated, resulting in hybridization. The large number of species is of course a consequence of our taxonomy, based almost entirely on morphology, pelage color and patterns, and distributions. Long overdue is a phylogenetic analysis of the genus to elucidate the emergence and composition of the different inferred lineages that are currently expressed only as species groups (Hershkovitz 1990; Kobayashi 1995; Groves 2001). Depending on the phylogenetic history and the ages of the different lineages, it may be appropriate to divide *Callicebus* into two or more genera, as was resolved recently in the capuchin monkeys (Lynch Alfaro *et al.* 2012).

Genetic studies of Peruvian primates are hindered by illogical national legislation; it is not difficult to receive a permit to collect dead animal material, but virtually impossible to obtain a permit for materials that will be used for molecular genetic analysis; often the same thing. A better understanding of the taxonomy would help the national government with the development of effective conservation strategies. It is hoped that this frustrating situation will change soon.

Finally, we refer to the discussion (pp.129–130) of the excellent taxonomic revision of the saki monkeys by Marsh (2014). Marsh’s observations about the taxonomic confusions permeating *Pithecia* are also relevant for *Callicebus*. Studies on *Callicebus* distributions are confused by erroneous identifications of observed animals. We hope that with our publication we have contributed to a better understanding of titi monkey taxonomy and distribution in Peru. For this study we

received help from people all over the world who provided their photographs for comparison. There are still many gaps in our knowledge of the taxonomy and distribution of titi monkeys in southern Peru and the rest of South America. We call on all researchers, in Peru and other countries, to share their observations and pictures of titi monkeys with us and the *Callicebus* database <www.callicebus.nl>.

Acknowledgments

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