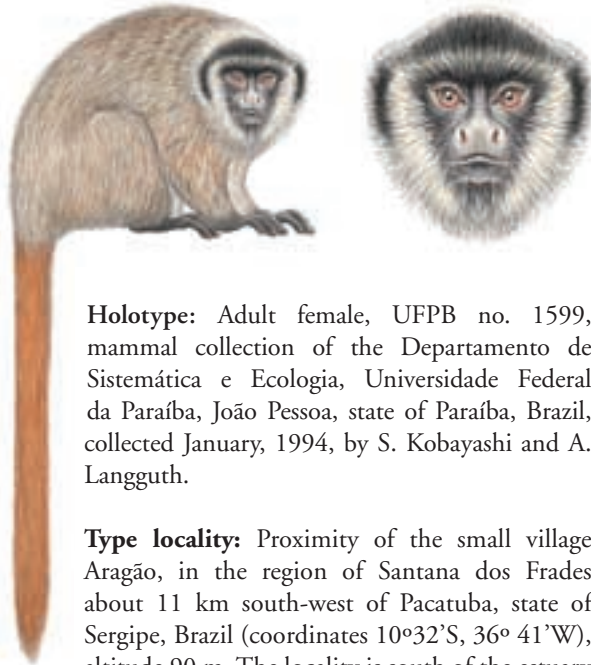


***Callicebus coimbrai*
Kobayashi & Langguth, 1999**



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 10°32'S, 36° 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 Itanhý, 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 interflaves 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 interflaves. 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 interfluvium delineated by the lower Rio Uíra-Curupá and the lower Rio Andirá amidst the much larger interfluvium 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 interfluvium 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 interfluvium south of Rio Tapauá and north of Rio Pauini, 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 interfluvium 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 interfluvium and has already passed the headwaters of the Rio Coarí into *S. m. pluto*'s last stronghold, the Rios Solimões/Coarí/Purús interfluvium 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, *Callicebus 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 Maturá, 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 Sucundurí, 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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