ISSN 1413-4703

NEOTROPICAL PRIMATES

A Journal of the Neotropical Section of the IUCN/SSC Primate Specialist Group

Volume 21
Number 1
July 2014

MARGOT MARSH BIODIVERSITY FOUNDATION

SSC Species Survival Commission

CONSERVACIÓN INTERNACIONAL Colombia

Neotropical Primates

A Journal of the Neotropical Section of the IUCN/SSC Primate Specialist Group

Conservation International
2011 Crystal Drive, Suite 500, Arlington, VA 22202, USA

ISSN 1413-4703 Abbreviation: *Neotrop. Primates*

Front cover: Adult male *Pithecia hirsuta*, Caparú Biological Station, Colombia. Photo by R.A. Mittermeier.

This issue of *Neotropical Primates* was kindly sponsored by the Margot Marsh Biodiversity Foundation, 432 Walker Road, Great Falls, Virginia 22066, USA, and the Los Angeles Zoo, Director John R. Lewis, 5333 Zoo Drive, Los Angeles, California 90027, USA. Printed in Bogotá DC, Colombia on July 25, 2014.

A Taxonomic Revision of the Saki Monkeys, *Pithecia* Desmarest, 1804

Laura K. Marsh[1]

[1]*Global Conservation Institute, Santa Fe, New Mexico, USA; lkmarsh@global-conservation.org*

Abstract

For more than 200 years, the taxonomy of *Pithecia* has been floating on the misunderstanding of a few species, in particular *P. pithecia* and *P. monachus*. In this revision, historical names and descriptions are addressed and original type material is examined. For every museum specimen, all location, collection, and museum data were recorded, and photographs and measurements of each skin, skull, mount, or fluid specimen were taken. The revision is based on work conducted in 36 museums in 28 cities from 17 countries in North America, South America, Europe, and Japan, resulting in the examination of 876 skins (including mounts and fluids), 690 skulls, and hundreds of photographs taken by the author and by colleagues in the field of living captive and wild sakis of all species, and through internet searches. Per this revision, there are 16 species of *Pithecia*: five currently recognized, three reinstated, three elevated from subspecies level, and five newly described.

Key Words: *Pithecia*, saki, taxonomy, revision, new species, *P. pithecia*, *P. monachus*

Resumen

Por más de 200 años, la taxonomía de *Pithecia* ha estado flotando en la confusión de unas pocas especies, en particular *P. pithecia* y *P. monachus*. En esta revisión, los nombres históricos y descripciones son abordadas y el material tipo original es examinado. Para cada espécimen de museo, todos los datos de localidad, colección y museo fueron registrados, y fotografías y medidas de cada piel, cráneo, montaje, o especímenes conservados en fluido fueron tomadas. La revisión está basada en trabajo llevado a cabo en 36 museos en 28 ciudades de 17 países en Norte América, Sur América, Europa, y Japón, resultando en la examinación de 876 pieles (incluyendo montajes y fluidos), 690 cráneos, y cientos de fotografías tomadas por la autora y por colegas en el campo, de individuos vivos en cautiverio o estado silvestre de todas las especies de *Pithecia*, y mediante búsquedas en internet. Con base en esta revisión, hay 16 especies de *Pithecia*: cinco actualmente conocidas, tres reclasificadas, tres elevadas del nivel de subespecie y cinco nuevas descritas.

Palabras Clave: *Pithecia*, saki, taxonomía, revisión, nueva especie, *P. pithecia*, *P. monachus*

What gets us into trouble is not what we don't know, it's what we know for sure that ain't so.
Mark Twain

Introduction

The saki monkeys of the genus *Pithecia* are a poorly studied group of Neotropical primates. Found throughout tropical forests of South America from the Guiana Shield, west to the foothills of the Andes in Ecuador and Peru, south to northern Bolivia, and throughout the Amazon Basin in Brazil as far east as Altamira on the Rio Xingu, these secretive, fast moving, medium-sized monkeys (called "flying monkeys" in many languages) have eluded researchers for decades. There have been few long-term field studies, thus creating a huge knowledge and conservation gap for these unusual animals.

Sakis are the smallest of the pitheciines, but are larger than other non-prehensile-tailed platyrrhines (*Aotus*, *Saimiri*, *Callicebus*, and the Callitrichinae). Adults weigh in at 1.5–4.0 kg, with a wide range in total body length (250–980 mm) and tail length (255–545 mm) reflecting the diversity among the taxa (Buchanan *et al.*, 1980; Mittermeier *et al.*, 1981; L.K. Marsh, unpubl. data). Their tails are often 1:1 with the body length, but in many species tails are longer by >100 mm (based on museum specimen data) for both males and females. Size dimorphism is not striking but, depending on the species, females tend to be smaller in weight and overall size. Sakis are characterized by their long, coarse, fluffy hair that easily piloerects when they are approached in the wild, making them look bigger than they actually are. The hair on the tail tends to be longer than on the back, but this varies among species, and the tail hair also "puffs up" as a threat. Hair on the trunk is always longer than that on the forearms and hind limbs, and underbellies are very lightly covered or bare. Coronal hairs are directed forward as a hood, and, depending on the species, overlap the facial region making them appear to have "bangs." Both males and females have distinct throat glands for scent marking, with varying development depending on the species; some males have obvious neck folds and others only a bare skin patch (Brumloop *et al.*, 1994; Setz and Gaspar, 1997). Sakis are frugivore/seed predators, but they eat insects such as army ants, as well as spiders, and other arthropods (Buchanan *et al.*, 1980; Defler, 2004; pers. obs.). Locomotion consists of quadrupedal walking/running, climbing, and leaping (Youlatos, 1999; Defler, 2004). They vocalize in grunts, chirps, whistles, and low calls, but can be exceptionally quiet when sneaking away from a perceived threat such as a field researcher (pers. obs.).

All species tend to prefer mature forest that includes variations of flooded forest—*várzea* (white-water flooded forest) and *igapó* (black-water flooded forest)—palm swamp (*Mauritia* swamp for some), and terra firma forest (Rylands, 1987; Rylands and Mittermeier, 2009). They can be found in disturbed habitats and in fragments with secondary forest, but as seed predators of large forest tree species (notably of the family Lecythidaceae), they tend to be in higher densities in mature forest (Norconk 2003). One possible explanation for their very large geographic distribution as a genus and as individual species is their ability to use a range of forest types, from várzea to igapó to terra firma (Ayres and Clutton-Brock, 1992).

Previous Taxonomy

There has been a great deal of confusion in *Pithecia* taxonomy. The most recent revision was by Hershkovitz (1987). Later publications (e.g., Rylands *et al.*, 2000; Groves, 2001; Defler, 2004) reiterate Hershkovitz's work (Table 1). Hershkovitz (1987) defined five species with three of them polytypic. They were arranged into two groups as follows:

1) *Pithecia pithecia* Group –
Guianan region: *P. pithecia pithecia*, *P. pithecia chrysocephala*, and

2) *Pithecia monachus* Group –
Amazonian region: *P. monachus milleri*, *P. monachus monachus*, *P. irrorata irrorata*, *P. irrorata vanzolinii*, *P. aequatorialis*, *P. albicans*.

Hershkovitz was compelled to force everything in the genus into this construct, thus missing key differences in what prove to be distinct species, including those that may be different enough that they should not be grouped together (e.g., *irrorata*, *aequatorialis*, or *albicans*). An interpretation of the specimens identified in Hershkovitz (1987) is in Table 2, elaborating the difficulty and confusion he faced while studying these animals.

For Hershkovitz and others, *Pithecia* was a succession of allopatric species with no overlap or chance for mixing. In reality throughout the range, *Pithecia* species likely show sympatry with other members of the genus, or are parapatric with hybrid zones between them. The use of groupings and subspecies has been suspended in this publication until detailed studies on genetics, behavior, morphology, current distribution, and evolutionary relationships have been completed with the guidance of this new taxonomy. Only then can comparable studies be performed and subspecies accurately determined (Groves, 2004).

Early taxonomists

Early taxonomists (1700s through the turn of the 20th century) had a hard time describing sakis because they were so unusual. One of the common mistakes made in describing them was the use of the term "beard," as members of the genus *Pithecia* do not have beards. Since *Pithecia* was originally included with *Chiropotes* (the truly bearded sakis), this mistake was common. More often than not, what the early taxonomists were referring to in *Pithecia* as a "beard" was their chest ruff, distinct in several species. It is a shame that *Pithecia* shares the colloquial name of "saki" (a Quichua term for *Pithecia*) with *Chiropotes*, as the native term

for *Chiropotes* is *cuxiú* (coo-shiu). Perhaps if we make a distinction in the common names for these two, we will stave off confusion later.

Early taxonomists and collectors also had no idea about the behavior of *Pithecia* in the wild. Gray in 1870 called them "gregarious, slow, sad, voracious, and vociferous" (p.59). And while it was clear Gray never saw sakis in the wild, Bates (1892) had seen one as a pet:

> "The Parauacú is a timid inoffensive creature, with a long bear-like coat of harsh speckled-grey hair. The long fur hangs over the head, half concealing the pleasing diminutive face, and clothes also the tail to the tip, which member is well developed, being eighteen inches in length, or longer than the body. […] The Parauacú is also a very delicate animal, rarely living many weeks in captivity; but any one who succeeds in keeping it alive for a month or two, gains by it a most affectionate pet. One of the specimens of *Pithecia albicans* now in the British Museum was then living on the property of a young Frenchman, a neighbour of mine at Ega. It became so tame in the course of a few weeks, that it followed him about the street like a dog. My friend was a tailor, and the little pet used to spend the greater part of the day seated on his shoulder, whilst he was at work on his board. It showed, nevertheless, great dislike to strangers, and was not on good terms with any other member of my friend's household than himself. I saw no monkey that showed so strong a personal attachment as this gentle, timid, silent little creature" (p. 336).

Sclater (1879) probably understood best: "We know very little of [*Pithecia*] habits in the wild state, although it appears that they are normally silent" (p.174). It has been my experience with captive sakis of various species that they are indeed quite calm, gentle, and allow themselves to be petted by humans.

The Trouble with Sakis

Many erroneously labeled types have been placed in the museums that house *Pithecia* specimens. There are a number of reasons for this, including the historic methods of specimen collection and the lack of field observations; the age of individuals placed as types and the longevity of sakis in the wild; misunderstanding of females and their anatomy; and the business of "transitional" males.

Historic collection of specimens

Until the latter half of the 20th century, the taxonomist in question might have gone to the country of interest for collecting, but he likely remained behind any real expedition into the forest in favor of a nearby town or city. He would have a team of local hunters or collection experts culling the animals for him, and more often than not, sakis were among the wildlife plunder as opposed to animals of targeted interest. Thus, many specimens have location designations such as "Cayenne," "Iquitos," "Manaus," "Sarayacu," or other similar towns even if the animals are from much further afield or from the other side of a river. This leads to more than one species being described for a site and does not necessarily account for actual distribution. For instance, the abundance of types in French Guiana and from Cayenne in particular likely represents the number of French explorers at the time more than the diversity of the region. Worse, early explorers (1700–1800s) would simply label locations as "Tropical America," "South America" or "Brasils," which may or may not have actually meant the country of Brazil, as "Brasils" was a generic term for South America 100–200 years ago.

Even some of South America's most prolific collectors, the Olalla brothers, may not have been as reliable as we would wish to believe by their specimen tag information. Wiley (2010), in an excellent tracing of the history of the Olalla family's work collecting birds in Peru and Brazil, recounts the then (1965) curator for Field Museum Emmet R. Blake's impression of the men: "Blake's impression was that Carlos [Olalla] was suspect, but that Alfonso [A.M. Olalla] was 'not given to actual skullduggery, although generally he didn't bother to indicate which side of a river his [specimens] came from [...] he simply didn't know any better.' Blake went on to say that '[Philip] Hershkovitz ... bears me out on this and has had exactly the same trouble with monkeys borrowed from the AMNH that you are having with some of our Olalla birds. In fact, Philip [Hershkovitz] admits that in his younger collecting days he also was less than precise in specifying localities as related to the banks of rivers' " (p.5).

Traditional taxonomists, including Hershkovitz, almost always made their determinations once the samples were back in the home museums. Out of context and far from the forests where the sakis lived, they gave names to juvenile males and all ages of females as though they were adult males of a new species. It has only been in the last decade that information for determinations has been so readily available to a taxonomist in the form of digital photography, international cross-referencing, easy communication with colleagues around the world, and photos of living animals—in the wild and captivity—throughout the range. In the past, memory, notes, verbal descriptions, the occasional painted plate, or later film photography (which relied heavily on the development process) were the principal ways to determine and compare species.

Taxonomists working from their home museums, particularly 100–200 years ago, worked almost blind when describing saki specimens. If they had not been to Paris, London, or Munich to see the actual specimens placed there by Étienne Geoffroy St.-Hilaire, John Edward Gray, or Johann Baptist von Spix, then comparative descriptions often began with apologia for not having seen the types, but they would press on regardless having maybe read about them or seen, at some moment, a painting of one. This kind of "doing the best one could" in taxonomy was prevalent through the turn of the

20th century and speaks volumes to the perpetual confusion having to do with the age and sex of animals brought in. Without having seen the animals in the wild or living in any way, it was nearly impossible for early taxonomists to accurately describe them. After nearly two paragraphs of both apology and cross reference to what he had read about *Pithecia*, W. H. Flower in 1862 described a female that came to the British Museum as "securely adult," but he confessed that the dimensions of his specimen were "rather inferior" to either Spix's description of *P. hirsuta* or Gray's of *P. irrorata*. I examined the very same specimen myself (BMNH No. 1863.6.15.3), and found it to be a small juvenile female.

The age of individuals

I had the opportunity to examine available saki skulls in addition to reference skins, mounts, and fluids during the course of this revision. And while I only performed the most cursory of examinations (i.e., tenpoint measurements and photographs; see "Methods"), I noted the relative age-class of individuals based on general tooth wear, canine development, and cranium suturing. I was repeatedly surprised going

Table 1. Classifications of *Pithecia* from nominal species to Hershkovitz (1987), Rylands *et al.* (2000), Groves (2001), and this paper.

Nominal Species	Hershkovitz (1987)	Rylands *et al.* (2000)	Groves (2001)	This paper
Simia monacha É. Geoffroy St.-Hilaire, 1812	*P. monachus monachus*	*P. monachus monachus*	*P. monachus monachus*	*P. monachus*
P. monachus É. Geoffroy St.-Hilaire, 1812	*P. monachus monachus*	*P. monachus monachus*	*P. monachus monachus*	*P. monachus*
P. hirsuta Spix, 1823	*P. monachus monachus*	*P. monachus monachus*	*P. monachus monachus*	*P. hirsuta*
P. inusta Spix, 1823	*P. monachus monachus*	*P. monachus monachus*	*P. monachus monachus*	*P. inusta*
P. guapo Schinz, 1844	*P. monachus monachus*	*P. monachus monachus*	*P. monachus monachus*	Type not seen
P. milleri J.A. Allen, 1914	*P. monachus milleri*	*P. monachus milleri*	*P. monachus milleri*	*P. milleri*
P. napensis Lonnberg, 1938	*P. monachus monachus*	*P. monachus napensis*	*P. monachus napensis*	*P. napensis*
P. monachus É. Geoffroy St.-Hilaire, 1812	*P. aequatorialis* Hershkovitz, 1987	*P. aequatorialis*	*P. aequatorialis*	*P. aequatorialis*
P. monachus É. Geoffroy St.-Hilaire, 1812	–	–	–	*P. isabela* sp. nov.
P. monachus É. Geoffroy St.-Hilaire, 1812	–	–	–	*P. cazuzai* sp. nov.
P. irrorata Gray, 1842	*P. irrorata irrorata*	*P. irrorata irrorata*	*P. irrorata irrorata*	*P. irrorata*
P. irrorata Gray, 1842	*P. irrorata vanzolinii* Hershkovitz, 1987	*P. irrorata vanzolinii*	*P. irrorata vanzolinii*	*P. vanzolinii*
P. irrorata Gray, 1842	–	–	–	*P. rylandsi* sp. nov.
P. irrorata Gray, 1842	–	–	–	*P. mittermeieri* sp. nov
P. irrorata Gray, 1842	–	–	–	*P. pissinattii* sp. nov.
P. albicans Gray, 1860	*P. albicans*	*P. albicans*	*P. albicans*	*P. albicans*
Simia pithecia Linnaeus, 1766	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia*
Simia leucocephala Audebert, 1797	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia*
Simia rufiventer É. Geoffroy St.-Hilaire, 1812	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. chrysocephala*
P. adusta Olfers, 1818	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	Type not seen
P. nocturna Olfers, 1818	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia*
P. saki Muirhead, 1819	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	Type not seen
P. rufibarbata Kühl, 1820	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	Type not seen
P. ochrocephala Kühl, 1820	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia*
P. capillamentosa Spix, 1823	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. chrysocephala*
P. pogonias Gray,1842	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. pithecia pithecia*	*P. chrysocephala*
P. chrysocephala I. Geoffroy St.-Hilaire, 1850	*P. pithecia chrysocephala*	*P. pithecia chrysocephala*	*P. pithecia chrysocephala*	*P. chrysocephala*
P. monachus lotichiusi Mertens, 1925	*P. pithecia chrysocephala*	*P. pithecia chrysocephala*	*P. pithecia chrysocephala*	*P. chrysocephala*

back through the data at the disparity in what appeared to be adult skins—based on size, facial color, pelage, or reproductive status—that they had older juvenile or subadult skulls. This certainly lead to some confusing early taxonomic determinations, including the fraught *P. monachus* type in the Muséum National d'Histoire Naturelle in Paris, which is a long-faded juvenile male based on canine size and body size of the overall mount (cf. *P. monachus*).

Based on skull morphology, some females (among museum specimens) that appeared to have been lactating, or at least were preserved with noticeable, elongated nipples, that may or may not have had distended vulva associated (see "*Pithecia* Females," below), often were juveniles. According to Pereira and Fairbanks (1993), age of reproduction correlates to juvenile mortality and adult longevity. In primates whose females reproduce younger, there tends to be less juvenile mortality and longer-lived adults. Skins that had signs of reproductive maturation characteristics, such as well-developed throat glands in males or nipples in females, often did not have skulls that were fully adult. It appears that *Pithecia* may live longer in the wild and have a longer window of reproduction than may have been determined previously, but this clearly needs further investigation.

Table 2. Interpretation of Hershkovitz (1987): specimen number call-outs and comparisons with this paper. AM = Adult male, AF = Adult female, JM = juvenile male, JF = juvenile female. Hershkovitz (1987) is first appearance; many used several times.

Museum	Specimen No.	Hershkovitz ref.	Hershkovitz det.	LKM det.
FMNH	88862	Figure 8	*P. m. monachus* (AM)	*P. monachus* (AM)
FMNH	71806	Figure 8	*P. m. monachus* (AF)	AMNH, not FMNH with that number *P. napensis* (AF)
FMNH	46176	Figure 8	*P. p. pithecia* (AM)	*P. pithecia* (SAM)
AMNH	94132	Figure 8	*P. p. pithecia* (AF)	*P. chrysocephala* (JM)
FMNH	46172	Figure 11	*P. monachus* (AF)	typo FMNH 46176: *P. pithecia* (M)
FMNH	91806	Figure 13	*P. monachus* (AF)	typo AMNH 71806: *P. napensis* (AF)
UCMVZ	157795	Figure 13	*P. monachus* (AM)	*P. napensis* (SAM)
AMNH	93255	Figure 14	*P. pithecia* (JF)	9325x series in FMNH, but no skull in either AMNH or FMNH with this number
FMNH	86995	Figure 15	*P. monachus* (AF)	*P. aequatorialis* (JF)
FMNH	79387	Figure 15	*P. pithecia* (AM)	*P. chrysocephala* (SAM)
FMNH	87000	Figure 16	*P. m. monachus* (AM)	*P. isabela* sp. nov. (AM)
FMNH	86993	Figure 16	*P. aequatorialis* (SAM)	*P. aequatorialis* (SAM)
	Art	Figure 17	*P. monachus*	unknown – amalgam
	Art	Figure 17	*P. irrorata irrorata*	unknown – amalgam
	Art	Figure 18	*P. monachus*	unknown – amalgam
PHOTO		Figure 24	*P. m. milleri* (AF)	*P. milleri* (AF)
PHOTO		Figure 25	*P. i. irrorata* (AM)	*P. mittermeieri* sp. nov. (AM)
PHOTO		Figure 26	*P. i. irrorata* (AM)	*P. irrorata* (AM)
FMNH	122796	Table VI	*P. monachus* (AM)	*P. isabela* sp. nov. (AM)
FMNH	70638	Table VI	*P. monachus* (AM)	*P. milleri* (AM)
FMNH	79635	Table VI	*P. monachus* (AM)	Typo 70635: *P. milleri* (AM)
FMNH	70641	Table VI	*P. monachus* (AM)	*P. milleri* (AM)
FMNH	122797	Table VI	*P. monachus* (JF)	*P. isabela* sp. nov. (JF)
FMNH	70636	Table VI	*P. monachus* (JF)	*P. milleri* (JM)
FMNH	93251	Table VI	*P. pithecia* (AM)	*P. pithecia* (SAM)
FMNH	93252	Table VI	*P. pithecia* (AM)	*P. pithecia* (SAM)
FMNH	95504	Table VI	*P. pithecia* (AM)	*P. pithecia* (AM)
FMNH	95508	Table VI	*P. pithecia* (AM)	*P. pithecia* (JM)
FMNH	95509	Table VI	*P. pithecia* (AM)	*P. pithecia* (AM)
FMNH	95510	Table VI	*P. pithecia* (AF)	*P. pithecia* (AF)
FMNH	93250	Table VI	*P. pithecia* (JF)	*P. pithecia* (JF)
FMNH	93253	Table VI	*P. pithecia* (JF)	9325x series in FMNH, but not in either AMNH or FMNH
FMNH	95511	Table VI	*P. pithecia* (JF)	*P. pithecia* (JF)

Studies of comparative cranial morphology struggle in that, as with genetics, they tend to mix species together. For instance, in Marroig and Cheverud (2004, 2009) and Marroig *et al.* (2003) skulls used for comparison, according to the few reported specimen numbers and location maps, lumped several species. In Figure 2 of their 2004 paper, the *P. monachus* sample comprised animals in Brazil from Benjamin Constant south along the Río Yavari into Río Galvez (*P. monachus*), southwest of the Río Ucayali (*P. inusta*), as well as one from northern Peru (no number, but likely *P. aequatorialis* or *P. napensis* by location), and one in Colombia (*P. milleri*). They encountered a similar problem with *P. irrorata*, where none of the animals per the map (or few samples mentioned) are actually *P. irrorata* (see the species sections in this paper). I observed sagittal cresting in some skulls, but it was not necessarily something that could be used to determine species differences. It is quite possibly more associated with the kinds of foods available in the region and what is being consumed rather than a species trait, although some species, like *P. monachus*, appear more structurally prone to it.

Comparisons of skull morphology must be made with care and the understanding that the differences in age can make a skull in the same species appear to be quite different if it truly is an older adult versus a subadult. The key in my opinion is twofold to understanding saki skulls: 1) The slope of the braincase and face in the articulated skull, particularly as the animal ages, but especially when comparing adults, and 2) the wideness at the back of the mandible—while not perfect across all species, the mandible is wide in young sakis and becomes more constricted as the animal ages. In females, again for some but not all species, the older mandibles are wider than their counterpart adult males, which have mandibles that tend to be more constricted. Infants, juveniles, and some subadults seem to have "bubble heads," but as the animal matures the braincase narrows and stands up higher, depending on the species.

Hershkovitz lamented, "Consistent size, and cranial or dental differences between species of the *P. monachus* group have not been found" (p.410). I suspect this is due not only to the morphological age variation in the skulls, but the fact that he combined several species together in a single taxon. His lamentation is further corroborated in that across museums there were proportionally more juvenile specimens than adults, and far more females than males for most species, except perhaps *P. pithecia*, which was the closest to equal proportions. Additionally, the older the individual, the more likely the coloration matures to portray the true "type" pattern (see "*Transitional males*" below). As seen in older captive animals, chromatic characteristics may change the appearance dramatically as facial and body hair falls out, or is added, depending on the species.

Pithecia *females*

Another issue that contributes to errors in *Pithecia* taxonomy is that females of most species can be quite similar, especially as preserved specimens. Many (and in some cases all) females in the museums that I have worked in have been mislabeled as male *P. monachus*. Hershkovitz (1987) stated the problem accurately: "Contributing to the confusion was the failure by all authors to recognize sexual dimorphism in facial pilar pattern. This was further complicated by incorrect sexing, as indicated on collectors' skin labels of a large number of the preserved specimens I examined in the various museums" (p.409). He went on to say, "Failure to recognize sexual dimorphism among sakis has been the greatest stumbling block for sorting the species. The striking similarity between females of all species persuaded some taxonomists to treat all as members of the *Pithecia monachus* group and even some females of the *P. pithecia* group as conspecific; irrespective of significant differences between the males, that of male *Pithecia pithecia* excepted" (p.415). Hershkovitz himself suffered from this confusion leading to his mass lumping of species. Hershkovitz also admitted that it is really sexual dichromatism more than dimorphism that differentiates the sexes, if not species.

The problem was perpetuated with live animals in captivity up through the 1960s where the males of *P. pithecia* were often placed with males of *P. monachus* because *monachus* was considered "the female" and *pithecia* "the male" (C.P. Groves, pers. comm.). In the current worldwide captive population I suspect that most of the "white-faced sakis" are likely hybrids; the most common being *P. pithecia* males (or a hybrid male) housed with a *P. chrysocephala* female (Fig. 1).

Figure 1. A mixed, breeding pair at Elmwood Park Zoo: *P. chrysocephala* female and *P. pithecia* male. Photo Elmwood Park Zoo.

Something that is very confusing among the females is their genitalia. I finally understood what I was seeing in numerous specimens after viewing several living females of various species: a swollen vulva resembling male testicles (particularly when dried), and a protruding clitoris, which in museum specimens can resemble a penis (Figs. 2 and 3). The swelling varies among specimens, species, and age groups. Very young juveniles often have the swollen vulvar area even in living individuals, suggesting that age of reproductive readiness is within the juvenile class. Since females can also have distinct throat glands like males and often similar coloration, when coupled in an individual with male-like genitalia and no obvious teats, it is no wonder there is confusion!

Figure 2. Examples of female sexual swelling in museum specimens and living sakis: (a) Adult female *P chrysocephala* (BMNH No. 33.12.6.3); (b) juvenile female *P. chrysocephala* (MPEG 6971); (c) subadult female *P. chrysocephala* (MZSP No. 4249); (d) adult female "Jamari Saki" (MPEG No. 21934; Appendix II); (e) free-ranging juvenile female *P. inusta* at Isla de Los Monos, Iquitos; (f) free-ranging juvenile female *P. aequatorialis* at Isla de Los Monos, Iquitos. Photos by L.K. Marsh.

Females can also confuse the casual observer in the wild. In Ecuador, *P. napensis* lives in smaller family groups of two to eight depending on location, where the main pair often has older offspring or a second adult female living with them (pers. obs.). It was my experience tracking unhabituated sakis in the wild that often the adult males would do elaborate "laps" around the forest to distract the threat (observer), while the primary female remained behind on a more obvious branch, often accompanied by another adult or large juvenile female offspring. The females would eventually retreat as well, but not before the untrained observer might dub the pair "*monachus*" assuming their identical coloration meant they were male and female of that species. Hershkovitz maintained, "Chromatic differences between the sexes are absent or insignificant in *P. monachus*, *irrorata*, and *albicans*" (p.415). My experience is different: while some species are less derived, such as *P. hirsuta* and *P. albicans*, in most cases the sexes are easily separated by appearance. Females placed as male type specimens include: *P. rufiventer*/*pogonias* (adult female *P. chrysocephala*, same specimen for both type determinations), *P. lotichiusi* (adult female *P. chrysocephala*), and one of the Spix *P. hirsuta* syntypes is a young juvenile female.

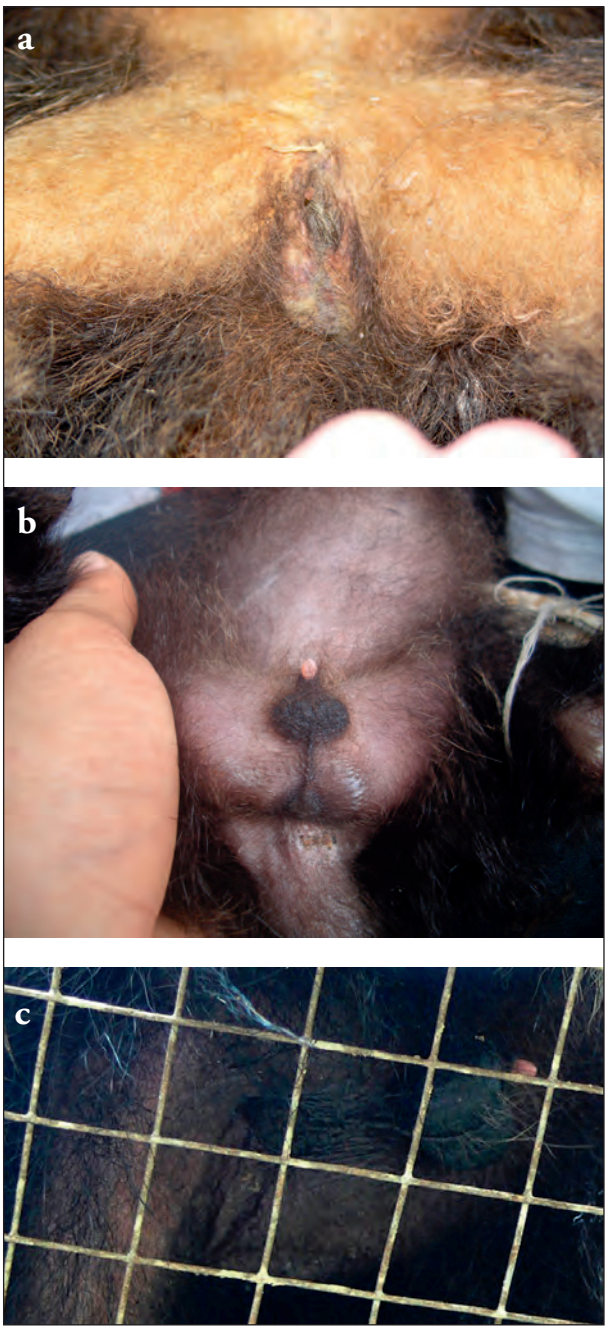


Figure 3. Examples of juvenile male genitalia: (a) *P. chrysocephala* (BMNH No. 12.5.11.2), (b) *P. monachus* pet in Iquitos, (c) free-ranging *P. aequatorialis* at Isla de Los Monos, Iquitos. Photos (a) and (c) by LKM, photo (b) by R. Aquino.

Transitional males

There are several specimens throughout the collections misassigned as adult males of a new species, but are actually juvenile or subadult males that are "transitional." The reason for this is that many of the saki species, and perhaps all to varying degrees, have dramatic "transitional" males where the young male has color characteristics of the adult females or something else entirely. For example, in *P. chrysocephala*, the juvenile to subadult males are grey-agouti, have orange bellies, white bangs, and indistinct orange/black faces—all resembling an odd looking female rather than an adult male (cf. *P. chrysocephala*). By comparison, the fully adult males are silky black, lack stippling or brownish/grey pelage, lack the orange belly, and have solid orange-ochraceous facial disks. This has led to intense confusion in museum specimens, especially those whose genitalia were removed or lost during taxidermy, or which are confusing (see "*Pithecia* females" above). All species have transitional males to some degree and in some cases females as well. The adaptive significance of this coloration is not known.

Likewise the extent and intensity of the ruff in males, while in many cases a species trait, can also vary within species. It seems to change with age, but not always. It would be useful to know whether the color of the ruff, in species which tend to have brighter ruffs, is coincident with breeding status, age, amount of glandular chemical available, or something else. It would also be interesting to know whether any of this kind of passive sexual signaling is at all coincident with female sexual swelling. A lot more work needs to be done on sexual physiology and behavior in general in the genus. Juvenile males placed as adult types: *P. monachus* (see "Discussion" in *P. monachus* section), *P. capillamentosa* (*P. chrysocephala*), *P. nocturna*/*P. ochracephala* (two type descriptions on same mount, Surinamese *P. pithecia*).

Methods

I use the phylogenetic species concept following Groves (2001, 2004) and Rylands and Mittermeier (2009). Since the designation of subspecies is vague and has been assigned in many cases arbitrarily to describe the diversity of Neotropical primates, I have elected to elevate all *Pithecia* to full species status until evidence is provided to delineate

them further (Winston, 1999; Van Roosmalen *et al.*, 2002; Groves, 2004, pers. comm.).

In 2001, I first noticed that the sakis at Tiputini Biodiversity Station, Ecuador, were different (Marsh, 2004), and found that publications about sakis were vague, confusing, or simply repeated information from previous publications (Hill, 1960; Napier and Napier, 1967, 1985; Hernández-Camacho and Cooper, 1976; Moynihan, 1976; Hershkovitz, 1979, 1987; Kavanagh, 1983; Wolfheim, 1983; Soini, 1986; Fleagle, 1988; Emmons and Feer, 1990, 1999; Kinzey, 1992, 1997; Groves, 1993; Schneider *et al.*, 1993, 1995; Bodini and Pérez-Hernández, 1995; Burton, 1995; Rowe, 1996; Reid and Engstrom, 1996; Nowak, 1997; Eisenberg and Redford, 1999; de la Torre, 2000; Rylands *et al.*, 2000; Heymann *et al.*, 2002). To make sense of what I was seeing at Tiputini, I conducted field research throughout Ecuador, visited field sites and wildlife rehabilitation centers in Ecuador, Peru and Brazil, and went to zoos and primate research centers worldwide to see as many living sakis as possible (Table 3).

I also studied collections in 36 museums, where I reviewed 876 skins and fluids and 690 skulls in US, European, and South America (Table 4). For each specimen, whether fluid, skin or mount, I took numerous digital photographs, collected all available information from labels, and field notebooks if available, and went back to any original documents from the original authors, such as É. Geoffroy St.-Hilaire, Spix, Gray, Lönnberg (see references for full list) to get as accurate a fix as possible on some of the more vague type localities. I took twelve photo angles and measured ten aspects of most of the available skulls. I consistently measured: braincase length, braincase width, zygomatic arch width, greatest orbital distance, nasal constriction, orbit width and height, greatest muzzle width, mandible length, mandible height and, when possible, canine length.

To fully corroborate type and museum data with actual animals, I also studied photographs of wild and captive animals throughout South America from a multiplicity of sources, including researchers *in situ* and travelers in areas where sakis live, reviewed the ISIS database for US and European zoos, and worked with the members of the Pitheciine Action Group as well as established taxonomists (C.P. Groves, A.B. Rylands, and A. Kitchener) to validate my findings. Every attempt to use pre-existing types and species names before naming a new species was made. Any new names followed the rules of taxonomic nomenclature (ICZN, 1999; Wilson, 1999).

While some research on the genetics of *Pithecia* has been conducted over the years, I have not used the results here since most of the publications do not have photos or specimen identification of the test subjects, and thus I cannot identify the species used per this revision (but see Martins *et al.*, 1992; Fleck *et al.*, 1999; Voss and Fleck, 2011). Because most of the studies have followed Hershkovitz (1987) and assumed that *P. monachus*, for example, represented a species that covered the vast majority of the Amazon, I am afraid that (to use a metaphor) apples were compared to elephants and the data may not be entirely meaningful as currently published (see "Discussion" for more on this topic).

Conservation Status

Pithecia, like all South American primates, suffer from the effects of region-wide habitat disturbances, including fragmentation of their habitats (Marsh, 2003; Marsh and Chapman, 2013) and hunting. Sakis are hunted throughout their range for subsistence, pets, trophies (e.g., as a tourist trade commodity in Ecuador as "shrunken heads," pers. obs.), and their tails used as "feather dusters" or their skins for hats (Mittermeier, 1977, 1991; Peres, 2000, 2001; Bodmer *et al.*, 2001; de Thoisy *et al.*, 2005; Aquino *et al.*, 2009). Work done by Mittermeier in the 1970s in Suriname detailed the culled biomass and consumption preference of *Pithecia* as compared to the rest of the primate community (Mittermeier, 1977). He discovered that while *Pithecia* was considered a preferred food by 26.7% of the combined indigenous population, they were rare in the regions where he worked, difficult to hunt, small for the (meat) payoff, and proportionally were one of the least hunted of the primates in the country (Mittermeier, 1977). In Ecuador, the Amazonian Quichua do not prefer *Pithecia* meat, although they will eat it if available. They say that the meat is "toxic," and that it cannot be fed to young children or to dogs as they will become ill or even die (pers. obs.). And while *Pithecia*, as a group, are hunted throughout their distribution, it is the cumulative effects of all combined human-induced pressures that ultimately will decide each population's conservation status.

To date, *Pithecia* as a genus is considered Least Concern (IUCN 2010), but the IUCN Red List of Threatened Species classifies only *P. pithecia, P. monachus, P. irrorata, P. aequatorialis*, and *P. albicans*, as per Hershkovitz (1987). *Pithecia albicans* is listed as Vulnerable with populations decreasing, but this was a best-guess estimate by L.K. Marsh in 2007 as part of the IUCN SSC Primate Specialist Group Red-Listing workshop. In actuality, there is very little data on any of the taxa in the wild. Examples are: *P. pithecia*, which has been studied the longest with the most publications, but in particular by Norconk and associates[1], and others (e.g., Mittermeier and Van Roosmalen, 1981; Oliveira *et al.*, 1985; Vié *et al.*, 2001; Riveros and Ferreira, 2001; Lehman *et al.*, 2001; Cunningham and Janson, 2006, 2007); *P. chrysocephala* (see Rylands, 1992; Setz, 1993; Setz and Gaspar, 1997; Setz *et al.*, 1999; Gilbert and Setz, 2001; Gilbert, 2003); *P. napensis* (called "*aequatorialis*" by DiFiore *et al.*, 2007); *P. aequatorialis* (see Aquino *et al.*, 2009); *P. albicans* (see Johns, 1985, 1986, Peres 1993); and a handful of other species (Heymann and Bartecki, 1990; Heymann *et al.*, 2002; Frisoli, 2009; Palminteri and Peres 2012).

1 http://www.personal.kent.edu/~mnorconk/suriname.html; http://www.personal.kent.edu/~mnorconk/venezuela.html.

Table 3. Living *Pithecia* in captivity or the wild (not including US zoos) studied for this publication.

Status	Country	Location	Site	Species
Wild	Ecuador	Yasuní Biosphere Reserve 0°40'32"S, 76°24'19"W	Estación Científica Yasuní de la Pontificia Universidad Católica del Ecuador	*P. napensis*
Wild	Ecuador	Yasuní Biosphere Reserve 00°37'05"S, 76°10'19"W	Tiputini Biodiversity Station	*P. napensis*
Wild	Ecuador	Sucumbios 0°13'34"S, 75°52'34"W	Cuyabeno National Reserve	*P. milleri*
Wild	Ecuador	Yasuní Biosphere Reserve 0°28'09"S, 76°45'25"W	Yarina Tourist Lodge	*P. napensis*
Wild	Ecuador	Yasuní Biosphere Reserve 0°32'54"S, 76°02'30"W	Yuturi Tourist Lodge	*P. napensis*
Wild	Ecuador	Orellana 0°27'49"S, 76°43'59"	Comuna Pamiwa Kocha	*P. napensis*
Wild	Ecuador	Pastaza 0°27'49"S, 76°43'59"W	Shiripuno River Lodge/Research Station	*P. napensis*
Captive	Ecuador	Río Arajuno 1°04'41"S, 77°32'16"W	AmaZOOnico Rescue Center	*P. milleri*
Captive	Ecuador	Guayllabamba, Quito	Zoológico de Quito	N/A
Captive	Colombia	Leticia, Amazonas 3°49'43"S, 70°12'23"W	Maikuchiga Primate Rescue, Amacayacu National Park[1]	*P. hirsuta*
Wild	Brazil	Manaus, Amazonas 2°30'00"S, 60°0'00"W	INPA BDFFP[2]	*P. chrysocephala*
Captive	Brazil	Manaus, Amazonas	Universidade Federal do Amazonas	*P. rylandsi* sp. nov
Captive	Brazil	Rio de Janeiro	Jardim Zoológico do Rio de Janeiro	*P. mittermeieri* sp. nov. (M) *P. rylandsi* sp. nov. (F)
Captive	Brazil	Rio de Janeiro	Centro de Primatologia do Rio de Janeiro	*P. albicans* *P. mittermeieri* sp. nov.
Captive	Brazil	Sao Paulo	Parque Zoológico do São Paulo	*P. albicans* *P. chrysocephala*
Captive	Brazil	Ananindeua, Pará	Centro Nacional de Primatas	*P. rylandsi* sp. nov.
Captive	Peru	Lima	Parque de las Leyendas	*P. inusta*
Captive	Peru	Huachipa, Lima	Parque Zoológico de Huachipa	*P. isabela* sp. nov. *P. inusta* (hybrid)
Captive	Peru	Iquitos	Zoológico de Quistococha	N/A
Captive	Peru	Iquitos	Proyecto Peruano de Primatología, "Manuel Moro Sommo" Primate Center	N/A
Free- ranging	Peru	Iquitos	Pilpintuwasi Rescue Center	*P. aequatorialis* *P. isabela* sp. nov.
Free-ranging	Peru	Iquitos, Pto. Indiana	Isla de los Monos	*P. aequatorialis* *P. monachus*
Captive	France	Paris	Ménagerie du Jardin des Plantes	N/A
Captive	Switzerland	Zürich	Zoo Zürich	*P. pithecia*
Captive	Germany	Frankfurt	Zoo Frankfurt	*P. pithecia (*M) *P. chrysocephala* (F)
Captive	Sweden	Djurgården, Stockholm	Skansen	*P. pithecia*
Captive	Scotland	Edinburgh	Edinburgh Zoo	*P. pithecia* (M) *P. chrysocephala* (F)
Captive	England	London	London Zoo	*P. pithecia*

[1] Photos from Rhett Butler (Flickr) and Xyomara Carretero

[2] Biological Dynamics of Forest Fragments Project (BDFFP), confirmed by Brian Lenz, visited by LKM

Table 4. Museums visited or studied for this revision, including facilities that did not have any specimens available, but were checked for completeness. "No. of specimens" is the total number of skins, mounts, fluids, or frozen samples for *Pithecia* studied in the collection.

Museum	Location	No. of specimens	No. of skulls	Types	Notes on types
North America					
County Museum of Natural History (CMNHLA)	Los Angeles, California	3	0		
American Museum of Natural History (AMNH)	New York City, New York	183	8 1	*P. milleri* (holo- topo-) *P. rylandsi* sp. nov. (holo-) *P. inusta* (key) *P. monachus* (key) *P. napensis* (key)	Allen (1914) Marsh‡ Marsh Marsh Marsh
Smithsonian Institution Natural History Division (SMITH)	Washington, DC	24*	6	*P. aequatorialis* (holo-) *P. rylandsi* sp. nov. (para-) *P. isabela* sp. nov. (holo-, para-) *P. irrorata* (key) *P. milleri* (key) *P. monachus* (key) *P. napensis* (key)	Hershkovitz (1987) Marsh Marsh Marsh Marsh Marsh Marsh
The Field Museum (FMNH)	Chicago, Illinois	72	5 1		
U.C. Berkeley Museum of Vertebrate Zoology (MVZ)	Berkeley, California	6	4		
South America					
Universidad Politécnica Nacional (POLI)	Quito, Ecuador	7	3		
Museo de Ciencias Naturales	Quito, Ecuador	0	0		
Universidad Católica	Quito, Ecuador	0	0		
Universidad de San Francisco	Quito, Ecuador	0	0		
Museo Amazónico (AMAZ)	Quito, Ecuador	1	0	*P. inusta* (para-) *P. monachus* (key)	Spix (1823) Marsh
Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (UNSM)	Lima, Peru	4^	1		
Museo de Zoología de Universidad Nacional de la Amazonía Peruana (UNAP)	Iquitos, Peru	0	3 7		
Proyecto Peruano de Primates, R. Aquino Collection	Iquitos, Peru	4	0	*P. vanzolinii* (holo-, para-) *P. rylandsi* sp. nov. (para-) *P. irrorata* (key) *P. mittermeieri* sp. nov. (para-)	Hershkovitz (1987) Marsh Marsh Marsh
Museu de Zoologia, Universidade de Sao Paulo (MZUSP)	São Paulo, Brazil	79	111	*P. mittermeieri* sp. nov. (para) *P. pissinattii* sp. nov. (para-)	Marsh Marsh
Instituto Nacional Pesquisas da Amazônia (INPA)	Manaus, Brazil	9	9	*P. cazuzai* sp. nov (holo-, para-)	Marsh
Museu Paraense Emílio Goeldi (MPEG)	Belem, Brazil	102	8 1	*P. cazuzai* sp nov. (para-) *P. irrorata* (key) *P. mittermeieri* sp. nov. (para-)	Marsh Marsh Marsh
Museu Nacional Rio de Janeiro (MNRJ)	Rio de Janeiro, Brazil	57	3 7		
Centro Nacional de Primatas (CENP)	Belem, Brazil	3	0		
Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAVH)	Bogotá, Colombia	10	8	*P. milleri* (key)	Marsh

continued on next page

Table 4. *continued*

Museum	Location	No. of specimens	No. of skulls	Types	Notes on types
Museo de Historia Natural, Universidad de los Andes (MHNA)	Bogotá, Colombia	3	3		
Instituto de Ciencias Naturales Universidad Nacional de Colombia (ICN)	Bogotá, Colombia	8	4		
Colección Manuel Ruiz-García, Pontificia Universidad Javeriana	Bogotá, Colombia	0	11		
Europe					
British Museum of Natural History (BMNH)	London, UK	85	8 7	*P. irrorata* (holo-) *P. albicans* (holo- para-) *P. pogonias* (holo-) *P. hirsuta* (key) *P. pissinattii* sp. nov. (holo-, para-) *P. inusta* (key) *P. monachus* (key) *P. napensis* (key)	Gray (1843) Gray (1860) Gray (1842) Marsh Marsh Marsh Marsh Marsh
Museum für Naturkunde (BER)	Berlin, Germany	35	1 6	*P. albicans* (para-)	Gray (1860)
Zoologische Staatssammlung (ZSM)	Munich, Germany	4	2	*P. hirsuta* (holo- syn-) *P. capillamentosa* (holo-) *P. inusta* (N/A)	Spix (1823) Spix (1823) Spix (1823)
Anthropological Institute and Museum (AIM)	Zürich, Switzerland	4	1 7	*P. pogonias* (N/A)	
Naturmuseum Senckenberg (SEN)	Frankfurt, Germany	16	1 4	*P. m. lotichiusi* (holo-) *P. hirsuta*/*P. monacha* (syn-) *P. isabela* sp. nov. (para)	Mertens (1925) N/A Marsh
Naturalis Nationaal Natuurhistorisch Museum (LEID) [formerly Rijks Museum van Natuurlijke Historie (RMNH)]	Leiden, Holland	35	2 6	*P. ochracephala*/ *P. nocturna* (holo-) *P. chrysocephala* (neo-) *P. irrorata* (key)	Temminck (1863) Marsh Marsh
Naturhistoriska Riksmuseet (STOCK)	Stockholm, Sweden	54	5 0	*P. napensis* (holo-) *P. irrorata* (key)	Lönnberg (1938) Marsh
Museum National d'Histoire Naturelle (MNHN)	Paris, France	38	2 1	*P. leucocephala* (holo-) *P. pithecia* (neo-) *P. monachus* (holo- para-) *P. inusta* (neo-) *P. mittermeieri* sp. nov. (holo- para-)	Poiteau (1822) Marsh É. Geoffroy (1812) Spix (1823) Marsh
Royal Scottish Museum (RSM)	Edinburgh, Scotland	4	6		
Museo di Storia Naturale di Firenze (MSNF)	Florence, Italy	4	0		
Naturhistorisches Museum Wien (NHMW)	Vienna, Austria	18	1		
Zoologisches Forschungsmuseum Alexander Koenig (ZFMK)	Bonn, Germany	2	0		
Magyar Természettudomanyi Muzeum	Budapest, Hungary	2	0		

continued on next page

Table 4. *continued*

Museum	Location	No. of specimens	No. of skulls	Types	Notes on types
Asia					
Kyoto University Primate Research Institute (KUPRI)	Kyoto, Japan	0	3		
Total	**36**	**876**	**690**		

‡ All Marsh references are to this paper. "Key" refers to Key Specimens determined by Marsh as important clarifications to type.
*Does not include fluid specimens.
^ The Fleck Lima Collection is at AMNH, accounting for 22 skins and 28 skulls tallied in the AMNH collection.
° Collection now in Lima at UNSM.
N/A = Original type no longer available.
All photos and measurements of specimens in Colombian museums by Xyomara Carretero.
Data from Museo di Storia Naturale di Firenze provided by Dr. Cecilia Veracini.
Data from Naturhistorisches Museum Wien provided by Simon Engelberger and Alice Schuhmacher.
Data from UC Berkeley MVZ provided by Francisco Ponutal.
Data from Zoologisches Forschungsmuseum Alexander Koenig provided by Dr. Gustav Peters.
Data from Magyar Természettudomanyi Muzeum provided by Dr. Gabor Csorba.
Data from KUPRJI provided by Dr. Masanaru Takai.

Perhaps Collar (1997) said it best: "Taxonomy precedes conservation […] without the formal structure of names and an agreed system of usage, there can be no understanding of what exists to be conserved." Prior to this revision, numerous field guides, primate species books, and other primate references simply did not have enough information to determine not only what species was in a region, but also what was a male or female. One example of many are the beautiful paintings in de la Torre (2000), one of which was supposed to be a *P. aequatorialis* male, but in fact is a *P. napensis* female, and the other of a *P. monachus* male does not resemble any saki species, anywhere, and appears to be more of an amalgam of what a presumed *monachus* looks like. Worse, for both scientists working in the region and for tourists, neither *P. aequatorialis* nor *P. monachus* occur in Ecuador.

Thus, it is impossible to determine the conservation status of any of the animals identified in this monograph, except perhaps through inference in areas such as Rondônia where there is severe deforestation and exponential human population growth. A great deal of research needs to be done on existing populations, the limits of their distributions, and the human impacts they face before we can confidently report on their status. Whenever possible, I offer a 'best guess' conservation status, but until we update the IUCN Red List of Threatened Species with corrected data from the field, the status previously posted stands (Version 2010.4. <www.iucnredlist.org>).

NEW TAXONOMIC ARRANGEMENT FOR GENUS *PITHECIA*

For a full history of genus nomenclature, see Hershkovitz (1979, 1987), Groves (2001), and Rylands and Mittermeier (2009). Abbreviations for all museums referenced in this monograph are in Table 5.

Genus *Pithecia* Desmarest, 1804

A thorough reanalysis of the genus *Pithecia* is presented, including species distribution maps, color illustrations of living species, historic plates, photos of type material (skin and skull), gazetteer of all reference materials (Appendix I), and measurements of type material and photos of living animals.

In this revision, there are five original species, three species elevated from subspecific rank, three historic species reinstated, and five newly described species. The total number of *Pithecia* species is 16.

Table 5. Museums and their abbreviations used throughout this publication.

Museums and abbreviations
Anthropological Institute and Museum, Zurich, Switzerland (AIM)
American Museum of Natural History, New York City, New York, USA (AMNH)
British Museum of Natural History, London, UK (BMNH)
Centro Nacional de Primatas, Belém, Pará, Brazil (CENP)
Colección Manuel Ruiz-García, Pontificia Universidad Javeriana, Bogotá, Colombia (CPUJ)
County Museum of Natural History, Los Angeles, California, USA (CMNH)
Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (ICN)
Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia (IAVH)
Instituto Nacional Pesquisas da Amazônia, Manaus, Brazil (INPA)
Kyoto University Primate Research Institute, Kyoto, Japan (KUPRI)
Magyar Természettudomanyi Muzeum, Budapest, Hungary (MTM)
Museo Amazónico, Quito, Ecuador (AMAZ)
Museo de Historia Natural Andes, Universidad de los Andes, Bogotá, Colombia (MHNA)
Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (UNMSM)
Museo de Zoología de Universidad Nacional de la Amazonía Peruana, Iquitos, Peru (UNAP)
Museo di Storia Naturale di Firenze, Florence, Italy (MSNF)
Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG)
Museu de Zoologia Universidade São Paulo, São Paulo, Brazil (MZUSP)
Museu Nacional d'Histoire Naturelle, Paris (MNHN)
Museu Nacional Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ)
Museum fur Naturkunde, Berlin, Germany (BER)
Nationaal Natuurhistorisch Museum Naturalis (frmr. Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (NNMN)
Naturhistorisches Museum Wien, Vienna, Austria (NHMW)
Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRM)
Naturmuseum Senckenberg, Frankfurt, Germany (SEN)
Proyecto Peruano de Primates, Rolando Aquino Collection, Iquitos, Peru (AQ)
Royal Scottish Museum, Edinburgh, Scotland, UK (RSM)
Smithsonian Institution, Natural History Division, Washington, DC, USA (SI)
The Field Museum, Chicago, Illinois, USA (FMNH)
Universidad Politécnica Nacional, Quito, Ecuador (POLI)
University of California, Berkeley Museum of Vertebrate Zoology, Berkeley, California, USA (MVZ)
Zoologische Staatssammlung München, Munich, Germany (ZSM)
Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany

WHITE-FACED SAKI

Pithecia pithecia (Linnaeus, 1766)

Synonymy

1766 *Simia pithecia* Linnaeus, *Systema Naturae* 12th ed. 40. Location unknown.

1789 L' Yarke, Buffon. *Histoire Naturelle Generale et Particuliere, a l'Histoire des Animaux Quadrupedes*, Suppl. Tome Septième, Paris: L'Imprimerie Royale. Location unknown.

1797 *Simia leucocephala* Audebert, *Histoire Naturelle des Singes et Makis*, 6eme fam., 1: 9, plate 2. French Guiana.

1803 *Callithrix pithecia* (Le saki ventre roux) É. Geoffroy Saint-Hilaire. *Catalogue des Mammifères du Museum National d'Histoire Naturelle, Paris*, No. 9. Type no longer exists, female. French Guiana. (see "Discussion").

1812 *Simia rufiventer* / *Pithecia rufiventer* É. Geoffroy Saint-Hilaire. *Recueil d'Observations de Zoologie et d'Anatomie Comparee* (Humboldt expedition), vol. 2, p.358. Type no longer exists. Female. French Guiana. *Nomen oblitum*. (see "Discussion").

1818 *Simia adusta* Olfers. *Journal von Brasilien*, 2: 198. Location unknown. Hershkovitz (1987) substitute name for *Simia pithecia* Linnaeus.

1818 *Simia nocturna* Olfers. *Journal von Brasilien*, 2: 198. No. 39097 at RNH Leiden, subadult male, French Guiana, Cayenne.

1819 *Pithecia saki* Muirhead. *Edinburgh Encyclopedia* 13: 400. British Guiana.

1820 *Pithecia rufibarbata* Kuhl. *Beitrage zur Zoologie und Vergleichenden Anatomie*, p.44. Hershkovitz (1987) notes "holotype juvenile mounted in Leiden," juvenile female. Suriname.

1820 *Pithecia ochrocephala* Kühl. *Beitrage zur Zoologie und Vergleichenden A natomie*, p.44. based on the same specimen as *Simia nocturna* Olfers, 1818, from the Temminck Voyage, subadult male. French Guiana, Cayenne.

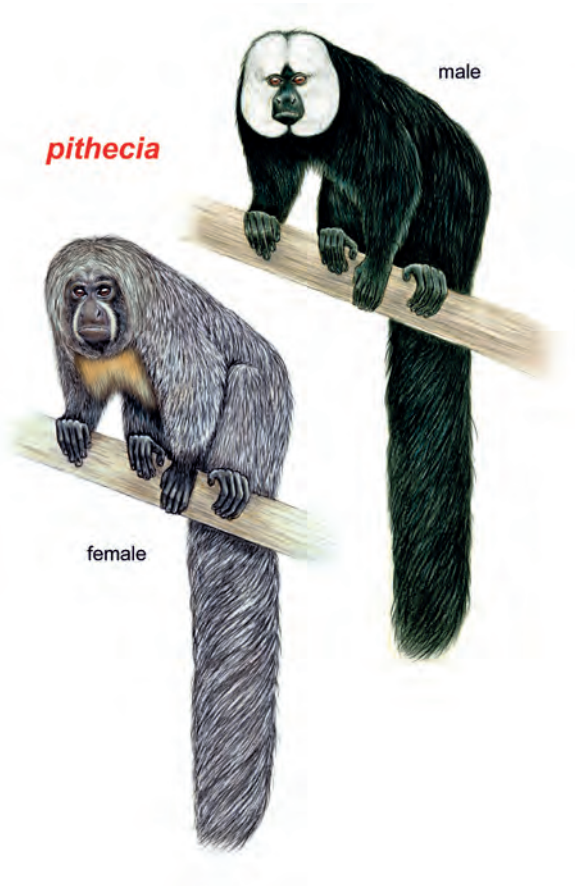
1987 *Pithecia pithecia pithecia* Hershkovitz. *Am. J. Primatol.* 12: 418–419; in part.

Holotype. A type specimen is not known to exist (Hershkovitz, 1987).

Neotype. *Simia leucocephala* mount No. 452, placed in the Museum d'Histoire Naturelle, Paris in 1822 (collector appears to be S. Foiteau) is here designated as a neotype.

Type locality. Cayenne, French Guiana, for the neotype *leucocephala*.

Specimens examined. Two hundred and nine skins and skulls, and dozens of live, captive and wild photos.



Description. *Males*. Fully mature adult males are black with little or no stippling of the dorsal hair. The hands and feet are generally black with no or little hair covering them. Male facial disks are white "half moons" completely covering the circumference of the face, connected in most cases in the midline of the face by a thin black line extending from the top of the forehead to the mid-glabella. The facial skin is black. Males throughout the distribution, but particularly in Suriname and northern Brazil, show "age related" color variations (transitions), where the pelage of juveniles to subadults is similar to that of females: dark brownish to coppery dorsally with grey-brown-cream stippling on hands, feet, and backs (color depending on the location), bright orange chests (which vary in intensity per region), and shaggy, white, fringy, facial hair that becomes dense, short, and thick in full grown males (Fig. 5). *Females*. Varying throughout the distribution, fully mature females are brownish to grayish with some cream or off-white stippling in the dorsal hair, light to bright orange ventral chest hair, and black hands and feet. Females have

distinct white to buffy-orange muzzle lines. The variation in females of this species throughout the range is striking and worth further investigation.

Measurements. Since the neotype is mounted with the skull, the following two tables are generalizations of the species based on available data. Table 6 gives average measurements of adult *P. pithecia* males and females in the museum collections. Table 7 gives examples of cranial measurements for adult male and female *P. pithecia*.

Diagnosis. This saki is one of the most familiar of all sakis as it survives well in captivity, even outside of South America (ISIS 2012, <www.isis.org>). Its success in temperate climates may be due to its more northerly distribution. They are distinct from *P. chrysocephala*, in that the latter has bright orange to dark ochraceous facial disks, and obvious, stiff white to buffy hairs along the lips. Further differentiation is seen in the transitional males of *P. chrysocephala*, which not only look like the *chrysocephala* females, but are very orange in their faces even when young, as compared to the faces of transitional male *pithecia* which are white (see "Discussion").

Distribution. Map 1. Throughout the northern South American countries of Venezuela, Guyana, French Guiana, and Suriname, and in northern Brazil in Roraima, Amapá, and parts of Pará. Those south of this region are *P. chrysocephala*. This does not reflect precise species delineations (e.g., there are cases apparently referable to *P. chrysocephala* in Guyana and to *P. pithecia* south of this initial demarcation), but at present it is not possible to determine if some of these "intermediate" populations are indeed distinct or are color variations of one or the other species (see

Table 6. Average weights and measures for *P. pithecia* adult males and females in museum collections. In parentheses, the number of specimens/range.

Country	Male Total body (mm)	Female Total body (mm)	Male Weight (g)	Female Weight (g)
Brazil*	767 (11/731–832)	748 (8/715–790)	2,057 (3/1720–2500)	1,650 (2/1550–1750)
French Guiana	781 (6/747–850)	768 (4/730–820)	1,725 (2/1649–1800)	N/A
Guyana	815 (8/740–970)	743 (4/715–790)	2,054 (3/1814-2268)	1,588 (1)
Suriname	777 (8/747–805)	730 (4/712–770)	1,925 (3/1769–2100)	1,530 (1)
Venezuela	N/A	N/A	N/A	N/A

All calculations based on available data. Only adults were calculated.
Total body is body length including the head and tail.
*All locations

Table 7. Skull measurements: examples of adult male and female *P. pithecia* in French Guiana and Brazil.

Measurement (mm)	Male* MNHN 1998-233	Female*	Male‡ MPEG 21532	Female‡ MPEG 21533
Length of brain case	76.4	73.6	79.5	78.1
Width of brain case	39.7	40.0	47.0	45.0
Zygomatic arch width	53.5	51.3	57.1	51.8
Orbits – outer	39.9	41.0	43.9	40.0
Nose bridge	5.0	6.6	6.0	7.9
L-orbit inner width	17.0	16.4	17.3	14.2
L-orbit inner height	16.5	17.5	18.2	14.8
Muzzle width	22.2	19.6	22.8	31.2
L-mandible length	50.0	47.4	51.9	47.9
L-mandible height	31.4	26.6	36.1	33.5
Total body length (mm)	750	800	780	740
Weight (g)	1640	N/A	2500	1750

*Male: Museum National d'Histoire Naturelle (MNHN), Paris, No. CG 1998-233, French Guiana, Barrage de Petit-Saut, collected by Jean Christophe Vié, 9 Oct. 1994. Female: MNHN No. CG 2001-1981, French Guiana, Association Kwata.
‡Museu Paraense Emílio Goeldi, Nos. 21532 (M) and 21533 (F), Brazil, Pará, Oriximiná, Cachoeira Porteira, collected by I.E.C.
24 March 1979 and 11 Sept. 1978, respectively. These are some of the animals in the region where the males have white faces with orange cheeks and coppery/black pelage, appearing "intermediate" between *P. pithecia* and *P. chrysocephala*, and females more strongly resemble *P. chrysocephala*.

Map 1. Geographic distribution of *Pithecia pithecia* based on museum specimens and field study sites.

Venezuela
1. Botanical Garden, Orinoco
2. Lago Guri
3. El Manaco, 59 Km SE of El Dorado at Km 74.

Guyana
4. 6.966667, -58.516667
5. Demerara Coast Region
6. Bonnesique Creek (formerly Bonasika River)
7. River Supinaam (by gazetteer Stephens & Traylor 1985)
8. Kartabo (by gazetteer Stephens & Traylor 1985)
9. Kalacoon (by gazetteer Stephens & Traylor 1985)
10. Bartica
11. Rockstone
12. Demerara River
13. Kaieteur Falls
14. Rupununi River

Suriname
15. Kapoeri Creek
16. Matapi
17. Between Matapi Creek and Kabalebo River near Corantijn River
18. Kabalebo River
19. Arrawarra Creek
20. Coppename River, Lolopasi, west bank, across from Foengoe Island
21. Voltzberg area east bank Coppename River
22. Brownsberg National Park, M. Norconk study area
23. Saramacca River, Loksie Hattie
24. Bigi Poika
25. Zanderij
26. Hanover, Weg nearby
27. Paramaribo
28. Perica River
29. Wia-Wia Nature Preserve
30. SW of Moengo
31. Moengotapoe
32. Nassau Gebergte near Marowijne River
33. Brownsberg, general area for R. Mittermeier study (1970s)
34. Lely Gebergte
35. Wilhelmina Mountains, approx. West River
36. approx. 1970s Sipaliwini airstrip
37. Kayser Mountains, approx. M. van Roosmalen study area
38. Kayser Gebergte, current airstrip nearby
39. Zuid River
40. Paloemeu River and Tapanahoni River

French Guiana
41. Maroni River/Crique Maihonni/ Marowijne River
42. approx. St. Laurent du Maroni
43. Saut Sabbat
44. St. Laurent-Kourou Road
45. Saut Tigre
46. Cayenne
47. Ipousin (by gazetteer Stephens & Traylor 1985)
48. Oiapoque
49. Arouani River

Brazil
50. Forte do Rio Branco
51. Rio Caciporé
52. Northern Rio Paru do Oeste, formerly Rio Erepecurú (by gazetteer Paynter & Traylor 1991)
53. Serra do Navio - Amapá
54. Rio Tracajutuba
55. Rio Maracá
56. Rio Jari
57. Porteira
58. Rio Paru do Oeste
59. Oriximiná
60. Obidos
61. Bravo, Lago Flexal, Edo. do Eira/Lara
62. Boiuçú (by gazetteer Paynter & Traylor 1991)
63. Patauá (by gazetteer Paynter & Traylor 1991)

"Discussion"). In Brazil, it occurs north of the Amazon and primarily east-northeast of the Rio Trombetas, extending north to Roraima, east of the Rio Branco. In French Guiana, Suriname, and Guyana, mostly along tributaries that descend to the coast, some further south into the interior at Wilhelmina Mountains, Keyser Gebergte, and Paloemeu/Tapanahoni rivers in Suriname, and the Rupununi River in Guyana. In Venezuela, as far west as Lago Guri in Bolivar State, south of the Río Orinoco. Their distribution in the Parque Nacional Canaima is unknown but likely as they are in northern Roraima. Their distribution further west and south in Venezuela is unknown.

Specific locations. Appendix I. BRAZIL. *Amapá:* Rio Jary – Tapuhy, Cachoeira de Sto. Antônio; Mazagão – Rio Maracá, Moreira, Alto Rio Branco; Terezinha – Rio Amupari, Sinturinha, Teomi, Serra do Navio; Rio Tracajatuba; Rio Villa Nova; Rio Caciporé do Ohcana; Municipality of Oiapoque – Villa Velha do Oiapoque. *Para*: Boiuçú; Bravo – Edo. do Eira; Cabeçeiras do Rio Paru do Oeste – Posto Tirias; Oriximiná – Rio Saracazinho, Cachoeira Porteira; Óbidos – Colônia do Veado; Lago Cuiteña; Patana; Santarém (captive). *Roraima*: Forte do Rio Branco; São Joaquim. FRENCH GUIANA. *Cayenne*: Ipousin – Rio Approuague. *St. Lamount du Maroni*: Mesmond; Saut Macaque sur la Ovaqui; Crique Arouani; Crique Maihonni; Route de Mama a Saint Sabbat. *Sinnamary*: Saut Tigre; Barrage de Petit Saut; Saisie. GUYANA. *Berbice*: Essequibo River – Rockstone. *Bonasica*: Essequibo River – Menarica Creek; Bonnesique Creek. *Demerara*: coast region; Supinaam River. *Mazaruni-Potaro*: Bartica; Kaieteur Falls; Kalacoon; Kartabo; Oko Mountains. *Upper Takutu–Upper Essequibo*: Rupununi River. SURINAME. *Brokopondo*: Sur River – Gania-Kondre-Bovenkondre; Saramacca River – Loksie Hattie, La Poule. *Marowijne*: Tapanahoni River – Paloemeu; Moengotapoe. *Nickerie*: Zuid River – Kayser Gebergte Airstrip; West River – Wilhelmina Mountains; Matapi. *Nassau Geb*: Marowijne River. *Paramaribo*: Zanderij. VENEZUELA. *Bolivar*: El Manaco – 59 Km SE El Dorado, Km 74; La Paragua – Lago Guri (Las Carolinas, Isla Redonda). *Orinoco*: Orinoco Botanical Garden.

Discussion. There has been a great deal of confusion over *P. rufiventer*. It was originally included in the *Catalogue des Mammifères du Museum National d'Histoire Naturelle, Paris*, No. 9 (1803) by É. Geoffroy Saint-Hilaire as *Callithrix pithecia*, "Le saki ventre roux," without a number. As of 2007 in Museum National d'Histoire Naturelle, Paris, there is no type specimen available. There is, however, a stand with a label on it in the type specimen vaults which reads: "#457, Saki a ventre roux, *P. rufiventer*, Guyane, 7-10-1836, male, C.G. 1996-2055." Perhaps this was the stand for the original type (but if the 1836 date is the date of collection and not that of the making of the mount, then it will not be). In I. Geoffroy Saint-Hilaire's (1851) catalogue, under "S[aki] à ventre roux, *P. rufiventer*" (1851: 55) only one specimen is listed as having been accessed prior to that date—a specimen collected in Cayenne in 1819 by M. Martin and clearly not the type specimen. Evidently the type has either been lost, or is yet to be identified in the collection. The first use of the name "*rufiventer*" appears to be by É. Geoffroy Saint-Hilaire in Humboldt and Bonpland's expedition manuscripts (Humboldt *et al*. 1812; p.357) as part of their expedition to the northern and western regions of South America (described as "Brasils" throughout the text, but they never were that far south; see "Introduction"). Adding to the confusion is the label on the type of *P. pogonias* in the British Museum of Natural History (No. 42.4.29.7), which is a *P. chrysocephala* female from Brazil, as: "*P. rufiventer*, Type of *Pithecia pogonias* Gray" (see *P. chrysocephala*: "Discussion"). By location alone (French Guiana, per É. Geoffroy Saint-Hilaire), I have added those *P. rufiventer*s to *P. pithecia.* Most of the specimens labeled as *P. rufiventer* throughout the worldwide museum collections are *P. chrysocephala* females or subadult males from Brazil, or *P. pithecia* females from Suriname, southern French Guiana, or Amapá. Since it has not been in use as a valid taxon since 1899, under the provisions of the Code of Nomenclature (1999: Art.23.9.10), I regard *P. rufiventer* as a *nomen oblitum*.

There is a possibility of either hybrids or new species throughout the distribution of *P. pithecia* if the variations in subadult males and females (in Suriname, in particular) prove not to be simple variations within these age-sex categories of *P. pithecia* and are instead species- or subspecies-defining characteristics. It appears that further north and west to Venezuela, the females are very simple in coloration: grey stippled, shaggy dorsal body hair, orange bellies, and dark grayish-black, mostly uniform faces with white to buffy muzzle lines. In this region, the adult males are generally very black without stippling in the dorsal hairs, with clean white faces. The juvenile and subadult males can be "transitional" in that they resemble females in the grizzling of the dorsal hair and buffy to light orangish bellies, but depending on the region and the age of the individual, the juvenile males can be black with little or no stippling, resembling full adult males.

Moving east and south brings out interesting variations: in areas of Suriname the females are reddish brown and not particularly stippled dorsally; whereas, the subadult males are very stippled with bright orange bellies and white shaggy faces. In contrast to the very white mask of *P. pithecia* males or the dark orange mask of the *P. chrysocephala* males, the sakis in Suriname and southern French Guiana appear intermediate, where males often have more orange in the lower halves of their white facial disks as buffy to orangish "cheeks," or the disk is occasionally entirely light orange in color. Additionally in French Guiana, the animals are smaller and males have distinct lines separating an "outer disk and inner facial disk", similar to that shown in the original illustration for *P. pithecia* (Fig. 4). Many females, juveniles, and subadult specimens from Suriname were described originally as distinct species, as *P. nocturna* and *P. ochrocephala*, but until further work is done on wild

populations to genetically determine if they are distinct in any way or if these specimens are simply off-type coloration from aged curation, they are rolled into *P. pithecia*.

In Brazil, the females more closely approximate those of *P. chrysocephala* than those of *P. pithecia*, and the subadult males are more similar to the Suriname subadult males in coloration. However, in Roraima adult males more closely resemble the *P. pithecia* type. It is interesting to note that Gray (1870) says *P. leucocephala* was from Brazil and that "the forehead is yellow when fresh and white when faded by exposure. M. Geoffroy thinks the colour depends on the size of the specimen" (p.59). This is another of the taxonomic confusions early on where they had *P. chrysocephala* and *P. pithecia* transitional males standing as types, mixed in with adult males of true species. This reinforces the importance of seeing these animals in the wild. Even with such a well-studied group such as *P. pithecia*, we have more work to do.

Figure 4. Likely a painting of the original type, now lost. Original title: "Fox-tailed Monkey, *Simia pithecia*." Plate facing p.169 of *Museum Leverianum: Specimens from the Museum of the Late Sir Ashton Lever*, by George Shaw. Published by James Parkinson, proprietor, 1792–1796.

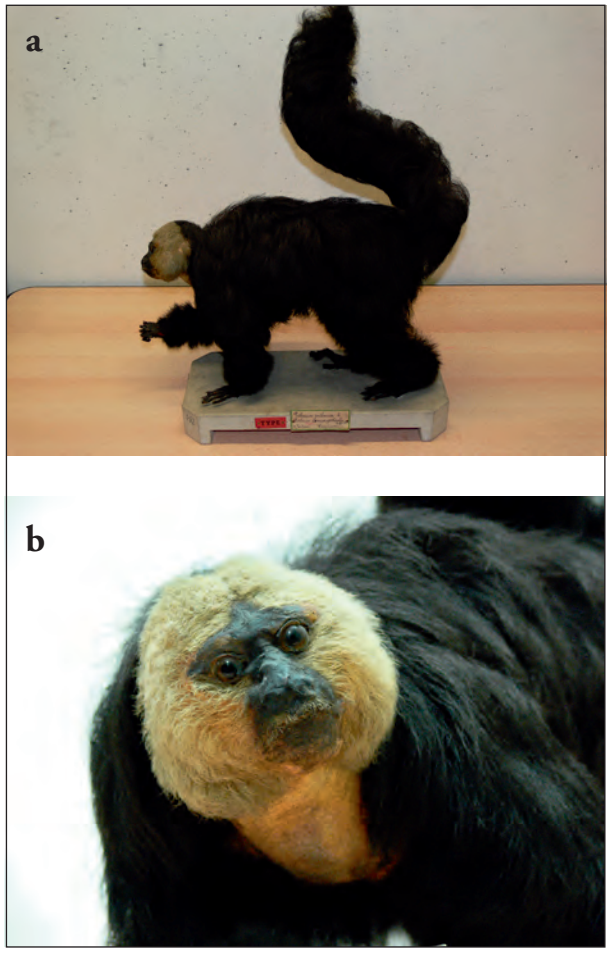


Figure 5. (a) Adult male neotype of *Simia pithecia*, and holotype for *Simia leucocephala*, mount No. 452, Museum d'Histoire Naturelle, Paris. (b) Adult male neotype mount, detail of face.

Figure 6. Wild *Pithecia pithecia* in Venezuela. (a) male, photo by K. E. Glander, and (b) female, photo by M. A. Norconk. Used with permission, all rights retained by Springer Publishers.

Figure 7. Juvenile transitional male. Living captive animal, photo by T. Gregory, Suriname (with permission of T. Gregory).

Figure 8. Juvenile transitional male mount, Leiden Naturalis No. 39097, type specimen for both *Pithecia nocturna* and *Pithecia ochrocephala*, photo by L. K. Marsh.

GOLDEN-FACED SAKI

Pithecia chrysocephala
(I. Geoffroy Saint-Hilaire, 1850)

Synonymy

1823 I. Geoffroy Saint-Hilaire. *Description* Pithecia capillamentosa Spix. *Simarium et Vespertiliarum Brasiliensis Species Novae […] Le Voyage dans l'Interieur du Brasil*, Monaco, Species Novae p.16, pl. 11. Holotype registered by Kraft (1983) at ZSM. This same mount had many determinations, including *P. rufiventer* É. Geoffroy Saint-Hilaire, *P. leucocephala* É. Geoffroy Saint-Hilaire, *Simia pithecia* and *P. pithecia* L. (Townsend); ZSM No. 1, juvenile male (fmr. female). Brazil. *Nomen dubium* (see "Discussion").

1842 *Pithecia pogonias* Gray. *Ann. Mag. Nat. Hist.* Series 1, 10: 256. BMNH No. 42.4.29.7, female. Brazil. *Nomen oblitum* (see "Discussion").

1850 *Pithecia chrysocephala* I. Geoffroy Saint-Hilaire. *Comptes rendus hebdomadaires des séances de l'Academie de sciences*, Paris 31: 875, Brazil.

1850 *Pithecia chrysocephala* I. Geoffroy Saint-Hilaire. *Description des Mammifères Nouveaux ou Imparfaitement Connus de la Collection du Museum d'Histoire Naturelle, et Remarques sur la Classification et les Caractères des Mammifères, Second Memoire: Singes Americains.* Pp.557–559, pl. XXIX of type, Brazil.

1852 *Pithecia chrysocephala* I. Geoffroy Saint-Hilaire. *Catalogue de Primates du Museum d'Histoire Naturelle, Paris*, pl. XXXI, p.876, Brazil.

1925 *Pithecia monachus lotichiusi* Mertens. *Senckenbergiana* 7(1/2): 17. No. 6692, labeled adult female, fmr. adult male. Holotype, Brazil, Manacapurú.

1925 *Pithecia pithecia lotichiusi* Mertens. *Senckenbergiana* 7(3/4): 74. Brazil, Manacapurú.

1939 *Pithecia monacha monacha* Tate. *Bull. Am. Mus. Nat. Hist.* 76: 221. Brazil, Amazonas, Jamundá.

1987 *Pithecia pithecia chrysocephala* Hershkovitz. *Am. J. Primatol.* 12: 417; in part.

Holotype. *P. chrysocephala* plate XXIX in I. Geoffroy Saint-Hilaire's original *Description des Mammifères Nouveaux* for the collection at the Museum d'Histoire Naturelle, Paris (1850) is accepted here and by Hershkovitz (1987) from I. Geoffroy Saint-Hilaire's 1852 publication. I. Geoffroy Saint-Hilaire co-types, mounted skins—one male, one undetermined—reportedly acquired in 1850 by the Museum National d'Histoire Naturelle, Paris, were not there during Hershkovitz's visit (1987), nor were they there as of November 2007.

Neotype. RMNH Leiden (No. 1845(a)): adult male, mount and skull; collected on 15 August 1924 (by unknown), catalogued on 25 May 1930, acquired from the dealers Schlüter & Mass in Halle an der Saale, Germany (C. Smeenk, pers. comm.).

Key specimens. *Pithecia p. chrysocephala* RMNH Leiden (No. 1845(b)): labeled adult female, likely a subadult male, mount and skull; collected on 27 July 1924 (by unknown), catalogued on 25 May 1930, acquired from the dealers Schlüter & Mass in Halle an der Saale, Germany (C. Smeenk, pers. comm.); Manacapurú, Amazonas, Brazil. *Pithecia pogonias* holotype, adult female, skin and skull, British Museum of Natural History (No. 42.4.29.7), Brazil. *Pithecia* (*m., p.*) *lotichiusi* holotype at the Senckenberg Museum, Frankfurt (No. 6692), labeled adult female, likely subadult, collected by W. Ehrhardt, 4 July 1924 from Manacapurú "nake Manaos [sic] mittlerer Amazonas, Brazil."

Type locality. I. Geoffroy Saint-Hilaire stated that the holotype was from "le Brésil, sur les bords du fleuve des Amazones." Neotype from Manacapurú, Amazonas, Brazil.

Specimens examined. One hundred and twenty-three skins and skulls; photos of living wild and captive animals.

Description. *Males.* Overall body coloration is black as are hands and feet, similar to *P. pithecia*, but the facial disk is entirely deep orange or reddish brown. Facial skin is black, bare

around eyes, nose, and chin. Upper lip has thick, stiff cream to light orange hairs. Large juvenile to subadult males in some regions are similar to *P. pithecia* in the same age group where they resemble females (agouti dorsally, including arms, legs and hands, with bright orange chests). Subadult males are more grayish, very mottled compared to females with grey or grey-white agouti, more than just grizzling to make the whole body grayish, but faces are orange to light orange, not fully defined in a disk as they are in adult males. In older juveniles, this facial hair can be quite shaggy to adpressed. The facial pattern can be indistinct and resemble females more closely than males, particularly in younger animals. *Females*. Dorsal pelage with black to brownish base hairs and some streaking overall, but with tan to buffy arms, legs and tail. The agouti pattern is darker and less extreme than subadult males. Hands and feet are black. The skin around the eyes, nose, and chin is bare and pinkish to grey. Facial hair is in a black horseshoe ring meeting at the top in either a white or orangish to buffy star, and the crown hair over the forehead is whitish or pale and distinct from the dorsal pelage. Orange muzzle lines extend from under the eyes. Their chest and belly is dull to bright orange.

Diagnosis. *Pithecia chrysocephala* differs from *P. pithecia* in that males always have bright to dark orange-ochraceous facial disks with contrasting light lips. Females are similar in many ways to *P. pithecia* females, but tend to be distinct with dark to black facial hair, bright orange malar lines, an orange stripe down the forehead in juveniles and a white star in the center on adults. There are similar females in Guyana *P. pithecia* populations.

Measurements. See Table 8.

Distribution. Map 2. Only in Brazil, north of the Rio Amazonas, both sides of the Rio Negro, especially in the lower reaches near Manacapurú, east to Faro along the Rio Nhamundá, where populations on the east side appear to be a mix of both *chrysocephala* and *pithecia* (see "Discussion"). One specimen in the Berlin collection (BER No. 91313) is clearly an adult male, but is written on both tag and skull to be from the Rio Içá, collected by Lako. If this is true, it is much further west than originally thought. However, this skin was probably collected in the 1920s, and it is unclear if *P. chrysocephala* still occurs in the region, or if it ever did. The boundaries of *P. pithecia* and *P. chrysocephala* are unclear further north in the states of Amapá, Roraima, and Pará, and need further investigation.

Specific locations. Appendix I. BRAZIL. *Amazonas*: Rio Ica; Rio Negro – Manaus (Km 165, 170, 190), Apuaú - Bocabau Chueiro/Cuieiras, Acajutuba, Porto Mauá, Igarapé do Bolivia, Yavanari, Iaunari, Tabocal; Kastuaria Mirim - Rio Purus(?); Iranduba; Itacoatiara; Itapiranga; Rio Solimões - Manacapurú; Rio Itabani nee Atabani; Rio Uruba; Silves; Uatumã - UHE Balbina, Vista Alegre, São Sebastião; Aniba - Igarapé Zinho, Rio Angusta; Lago do Serpa; Lago do Canacary. *Pará*: Rio Erepecurú - Cachoeira do Tronco; Rio Amazonas - Faro, Rio Piratucu, Serro do Espelho, Nhamundá.

Table 8. Measurements for *P. chrysocephala* neotype and key specimens. Adult male and subadult male in Nationaal Natuurhistorisch Museum, Leiden (NNML), and adult female in Naturmuseum Senckenberg, Frankfurt (SEN). All collected originally in Manacapurú, Brazil.

Measurement	Male NNML 1845‡	Sub-adult male NNML 1845a‡	Female SEN 6692
Skull (mm)			
Length of brain case	73.5	76.9	71.6
Width of brain case	41.3	40.7	40.1
Zygomatic arch width	45.6*	50.1	46.1
Orbits – outer	39.0	40.9	38.5
Nose bridge	0.47	0.52	0.50
L-orbit inner width	17.3	16.5	15.7
L-orbit inner height	17.8	16.9	15.4
Muzzle width	19.9	23.0	19.8
L-mandible length	43.5	48.9	44.0
L-mandible height	28.7	32.1	29.4
Post-crania (cm)			
Head/body	42	47	44
Tail	37	39	38

*Estimated, right side broken
‡ Numbers assigned by LKM; no mount numbers assigned at time of study (November 2007) at NNML.

Discussion. The confusion in this species lies with females and juvenile/subadult males. Females in both *P. chrysocephala* and the Suriname *P. pithecia* have exaggerated genital swellings with a distended clitoris (see "Introduction: Females"). In preserved skins and mounts this tends to have the appearance of a scrotum and a small penis.

Pithecia capillamentosa. The type of *P. capillamentosa* Spix in the Zoologische Staatssammlung München, Munich, Germany (ZSM, No. 1) is either a small juvenile male *P. chrysocephala* from Brazil, or possibly a juvenile male *P. pithecia* from eastern Brazil, state of Amapá, or even French Guiana as some taxonomists have determined. There are multiple tags on the type in the ZSM: 1) *P. capillamentosa* Spix, *Simia pithecia* Lin., *P. leucocephala*, female or male juv.; 2) *P. leucocephala* Geoff., Brasilien Spix; 3) *P. capillamentosa* Spix, Typus, Cayenne, ?sex; 4) *P. pithecia* L. (Townsend), (?viewed in July) "*Saki pithecia* (J. Saki Lajuru?—hard to read German script), Catalog J. Akademie, 1816; 5) *P. rufiventer* Geoff, (hard to read German script, name of journal) Suppl. I, v. 222, Suppl. V, 101, Annal I, Adult female; 6) *P. capillamentosa* Spix, *Simia. Bras.*, sp. nov. 1823, v. 16, Tab. XI; and 7) a hard to read ZSM tag with what appears to be reference to a (Wagler B- T- hard to read German name), *J. Amphib.* v. 6, ann. 4, v. 7 with no species det. *Pithecia capillamentosa* remained a valid taxon and was referenced by

several authors Elliot (1912), Cabrera (1957), Hill (1960), and Napier and Napier (1967)), but as it is clearly a juvenile and thus a confusing specimen, given the difficulty of distinguishing juveniles of *P. chrysocephala* and *P. pithecia*, the name is best ranked as a *nomen dubium* (as suggested by C.P. Groves, pers. comm.).

Pithecia pogonias. The type of *P. pogonias* in the British Museum (Natural History), London (BMNH 42.4.29.7) is an adult female *P. chrysocephala* resembling those throughout most of the range in Brazil. It is a good specimen, representative of females, with skull, but since the name has not been in use for a valid taxon since 1899, under the provisions of the Code of Nomenclature (1999: Art. 23.9.10), it ranks as a *nomen oblitum* (as noted by C.P. Groves, pers. comm.). It remains, however, a key specimen as an example of a *P. chrysocephala* female.

The type of *P. lotichiusi* in the Naturmuseum Senckenberg, Frankfurt (NMSF 6692), is an adult/subadult female (based on the robustness of the skull), and was named later than *P. chrysocephala*, and thus ranks as a junior synonym. It is retained here as a key specimen.

The original determination for this species per the holotype set forth by I. Geoffroy was as *P. chrysocephala*. Hershkovitz (1987) and others considered it to be a subspecies (*P. p. chrysocephala*) to fit into the two-group scheme. I re-elevate it to species as it is distinctly different from *P. pithecia* in phenotype, skull morphology, and range. There may be hybrid zones throughout the northern range and into Suriname and the Guianas per discussion in the *P. pithecia* section.

The Faro sakis appear to be a mix of both *chrysocephala* males and *pithecia*; it is interesting that there are also some larger juveniles that appear to have whiter, shaggier faces in the collection from that site with very orange-faced adult males. More work in this region needs to be done to determine if these animals are hybrids, a separate subspecies, different species, or color morphs of *chrysocephala*.

Figure 9. Plate XXIX of *Pithecia chrysocephala*, adult male holotype per I. Geoffroy Saint-Hilaire (1850) in *Description des Mammifères Nouveaux ou Imparfaitement Connus de la Collection du Museum d'Histoire Naturelle, et Remarques sur la Classification et les Caractères des Mammifères, Second Memoire: Singes Americains*.

Map 2. Geographic distribution of *Pithecia chrysocephala* in Brazil.

1. Iaunari
2. Manacapurú
3. Acajutuba (approx.)
4. Iranduba
5. Manaus
6. Igarapé do Bolivia
7. Rio Apuaú
8. 105 km north on BR 174 (approx.)
9. Balbina
10. Itacoatiara
11. Lago Serpa
12. Igarapé Aniba (approx.)
13. Silves
14. Tabocal
15. Lago Canaçari
16. Rio Itabani
17. Rio Uatumã
18. São Sebastião do Uatumã
19. Rio Piratucú
20. Faro

Figure 10. Hand-colored lithograph from a drawing by Benjamin Waterhouse Hawkins (1807–1889) of "*Pithecia pogonias* (*P. chrysocephala* female) and the head of *Pithecia leucocephala*", but here depicted as a *P. chrysocephala* male.

Figure 11. Mount of adult male neotype of *Pithecia chrysocephala*. (1845) at Naturalis Museum, Leiden, with skull (a) and two aspects of the skull (b and c). Photos by L.K. Marsh.

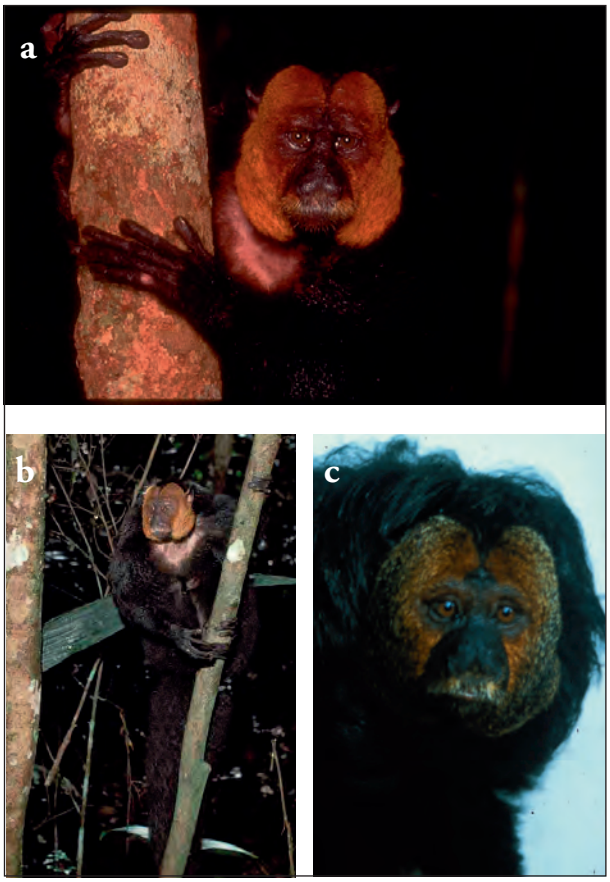


Figure 12. Adult male *Pithecia chrysocephala* in the wild and captivity. Photos (a and b) by L.C. Marigo and (c) R.A. Mittermeier, all Brazil (photos used with permission).

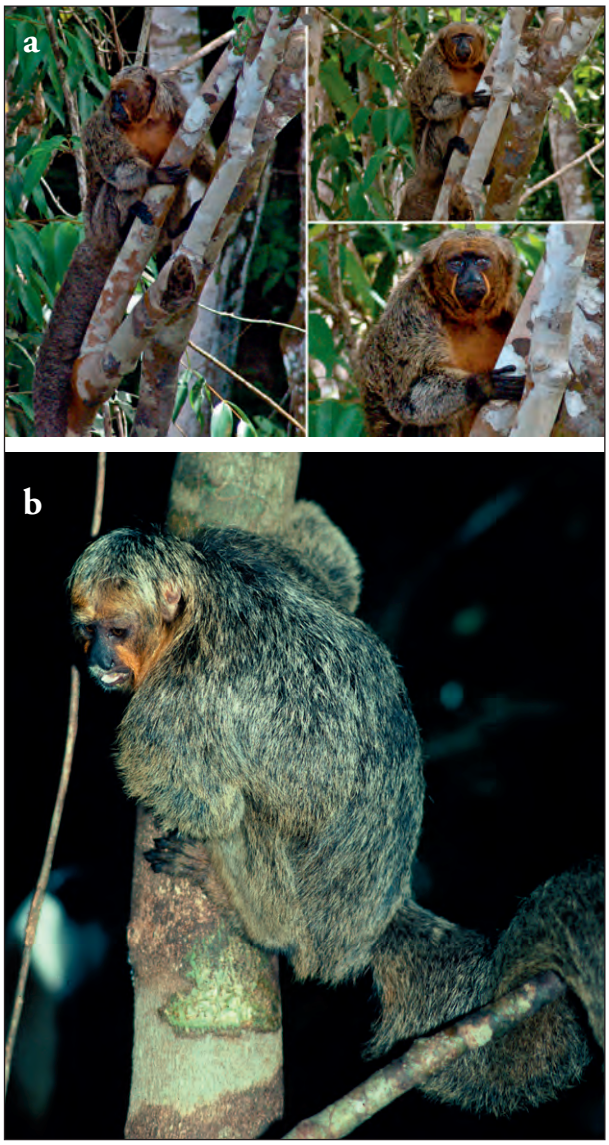


Figure 14. Transitional, large juvenile to subadult *Pithecia chrysocephala*, all near Manaus, Brazil. (a) Subadult male, photos by J. C. Serio Silva, and (b) juvenile male, photo by R.A. Mittermeier (photos used with permission).

Figure 13. Female *Pithecia chrysocephala*. (a) subadult, photo by J.M. Ayres, (b) young adult, Manaus, photo by J. White, and (c) adult, São Paulo Zoo, São Paulo, photo by L.K. Marsh (photos used with permission).

HAIRY SAKI

Pithecia hirsuta (Spix, 1823)

Synonymy

1823 *Pithecia hirsuta* Spix, J. B., von. *Simiarum et Vespertilionum Brasiliensium Species Novae*. F.S. Hübschmann, Munich, pp.14–15, pl. 9. *Pithecia hirsuta*, p.14.

Holotype. Adult male mounted specimen with skull intact (No. 19) at the Zoologische Staatssammlung München (ZSM), Munich, Germany, placed by Spix (1823), and as illustrated in the *Simiarum*. Currently labeled as "syntype" by ZSM.

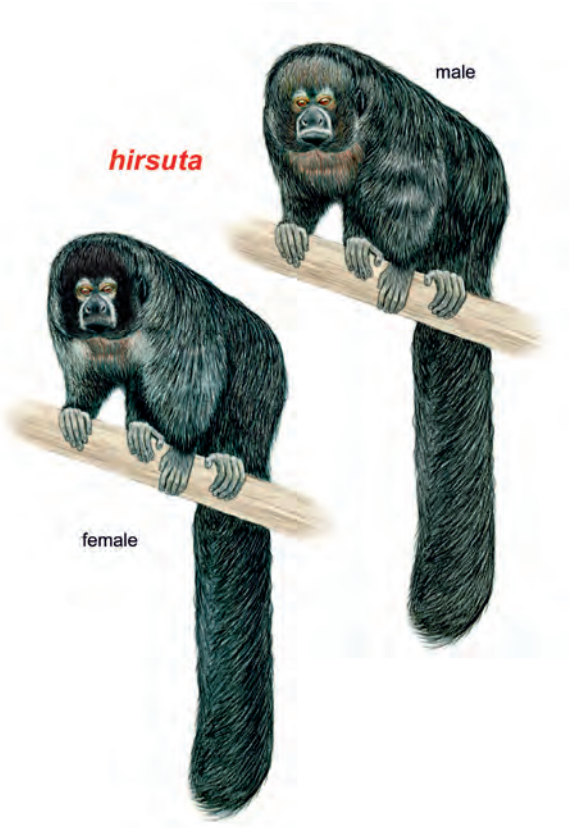
Syntypes. Mounts at ZSM placed by Spix (1823), Nos. 15, adult male, and 14, juvenile female. Described currently by the ZSM as "syntypes."

Type locality. The forests between the Rio Negro and the Rio Solimões, Amazonas, Brazil. As for all Spix types a region is reported, not a specific location.

Key specimens. Skins and skulls for adult males, BMNH Nos. 27.3.6.3 and 27.8.11.23 collected by W. Ehrhardt, 29–30 September 1926 (tag note on 27.8.11.23: "Topotype of *P. inusta* Spix", which is incorrect (cf. *P. inusta* types), and adult-subadult females BMNH Nos. 34.6.14.4 and 34.6.14.5. Subadult male from the Rolando Aquino collection (AQ 29.1.82) now in the Museo de Historia Natural, Lima, Peru (UNMSM).

Specimens examined. Sixteen skins and skulls, including photo references of living animals in Brazil and Colombia. Localities of BMNH adult male specimens: Brazil, near the rios Solimões (Tabatinga, on the frontier with Colombia) and Negro, along the Rio Tonantins (possibly near where the original Spix types were collected). BMNH adult females were collected in Brazil, Rio Içá, "Lago do Caroira" (an oxbow lake on the south side of the river, in the upper reaches, as per Paynter and Traylor [1991]; likely it has a different name today). Rolando Aquino collected a subadult male north-east of the Río Napo, along the left side of the Río Tamboryacu, northern Peru (now in the UNMSM).

Description. The most uniform and the plainest of the sakis with very little dichromatism between adult females and males. Males and females are similar in coloring, where the pelage is black with some stippling, but in most cases the whitish stipple is short and not as abundant as in other species. Both have very white hands, and the tail is longer than the head and body. *Males*. Males with dominantly blackish agouti to brown-agouti head, blackish to brownish



chest hairs, and a black chest ruff. The upper section of the chest from the neck to the ruff is obviously bare where the scent gland is positioned. The lips and malar stripes are clearly visible, white to cream and thick. Small bare spots of pinkish to light-colored skin can be seen above the eyes where the rest of the facial skin is predominantly black. Defler (2004) adds, "Males are slightly larger with longer tails, and have a black scent gland or thickened "bulbous sack" under their necks. Males have black testicles and a bright pink penis." (This accurately describes features of many of the species in *Pithecia* as the penis is pink, the testes are black, and the scent glands can vary in distinctiveness). *Females*. Females have more pelage stippling in general than males, but compared to other sakis it is sparse. Females have the white malar stripes as in males, but lack the white hairs across the lips so evident in the males. The hair around the face is blacker than agouti and not as short and tight against the face as in males. The skin on the face is pinkish around the eyes and above the muzzle and the chin, which is black as it is in the males.

Measurements. See Table 9 for Spix's measurements of the holotype, and Table 10 for two adult male key specimens in the British Museum of Natural History (BMNH).

Table 9. Original measurements of *Pithecia hirsuta* holotype from Spix (1823).

Morphology	Original (in)	mm
Trunci (body)	1'5 ¼"	438.2
Capitis (head)	3½"	88.9
Facici	1½"	38.1
Caudae (tail)	1' 6⅓"	465.7
Humeri	4"	101.6
Ulnae	3¼"	82.6
Palmae (hand)	3"	76.2
Femoria	6"	152.4
Tibiae	5¼"	133.4
Plantae (foot)	4½"	108.0
Angulus Facialis	47°	–
Angulus Cerebralis	44°	–

Table 10. Measurements for key specimens of adult male *P. hirsuta* at the British Museum of Natural History, London.

Measurements	Male BMNH 27.8.11.23	Male* BMNH 27.3.6.3
Skull (mm)		
Length of brain case	78.0	–
Width of brain case	44.4	–
Zygomatic arch width	56.4	–
Orbits--outer	43.9	–
Nose bridge	0.68	–
L-orbit inner width	17.7	–
L-orbit inner height	16.9	–
Muzzle width	24.3	–
L-mandible length	50.04	–
L-mandible height	–	–
Post-crania (mm)		
Head/body	500	480
Tail	430	410
Hindfoot	–	120
Ear	–	31

* Skull available, but was not measured.

Diagnosis. *Pithecia hirsuta* is distinct from *P. monachus* in that it is quite plain, something *monachus* got the reputation for probably because of É. Geoffroy Saint-Hilaire's simplistic and cryptic original description (cf. *P. monachus*). Whereas *P. monachus* adult males have adpressed brown hairs that cover the entire face, and in juvenile males the face can be whitish, *P. hirsuta* juvenile males have a dense agouti ring with contrasting white malar strips and obvious white lips, nearly resembling the adults. The females of the two species are distinct as well: those of *P. hirsuta* have very black facial disks and nearly resemble the male *hirsuta*, only lacking in the white lips, but the female *P. monachus* has soft, shaggy brown and white facial hair with white malar lines.

Distribution. Map 3. *Pithecia hirsuta* is distributed in the "wedge" of rivers formed by the Rio Negro to the east in Brazil, north of the Rio Solimões in Brazil and Peru, north of the Río Napo in Peru, and south of the Río Caquetá in Colombia (the Rio Japurá in Brazil). It is not known how far west they occur or where the boundary with *P. milleri* is, although *P. milleri* is found in La Paya National Park, Colombia, and probably the Zona Reservada Güeppí in Peru. *Pithecia milleri* appears in the Cuyabeno-Aguarico region in Ecuador to the exclusion of *P. hirsuta* (L.K. Marsh, pers. obs.). In Colombia, it occurs in the national natural parks of Amacayacu, Puré, and Cahuinarí for a total of 1,868,380 ha (Defler, 2004 originally referenced as *P. m. monachus*). In Brazil, it is found south of the Rio Japurá and north of the Rio Solimões-Amazonas, but how far to the Rio Negro in the east they are found is unclear as Spix's type locality is imprecise, suggesting only they are from the swathe between the rios Negro and Solimões.

Specific locations. Appendix I. BRAZIL. Amazonas: Rio Negro/ Solimões – Tabatinga, Rio Tonantins; Rio Içá – Lago do Caroira. COLOMBIA. *Amazonas*: Río Igara-Paraná – La Raicilla Ravine, La Chorrera; Amacayacu National Natural Park; Río Cahuinari; Bravo Ravine; Río Cotuhe; San Jose del Encanto. Puré National Park: Caño Mateo, Caño Arapa, Caño Esperanza, Quebradón El Ayo; Curare–Los Ingleses Indigenous Reserve: Caño Curare, Caño Agua Blanca, Caño Zumaeta; Camaritagua Indigenous Reserve / Vereda Madroño: Caño El Boliviano. PERU. *Loreto*: Río Napo (north) - Río Tamboryacu.

Discussion. The Spix specimens are losing hair, but their corresponding illustrations were drawn when the types were fresh are useful as combined type information. All of the Defler (2004) information used for *P. monachus monachus* accurately describes *P. hirsuta*. *P. monachus* does not occur north of the Amazon River (cf. *P. monachus*). AMNH 71802, collected by A.M. Olalla on 21 November 1925 is credited with the location of "Boca Río Curaray," as part of the expedition that was indeed in the area in previous months. It is likely, as it appears to be a *P. hirsuta* male, that it was collected on the other side of the Rio Napo near that location.

Figure 15. Spix (1823), plate IX, *Pithecia hirsuta* holotype and corresponding museum mount (ZSM No. 19). Images courtesy R. Kraft, ZSM.

Map 3. Geographic distribution of *Pithecia hirsuta*.

Peru

1. Río Tamboryacu
2. Olalla brothers collection area (approx.), Nov. 1925

Colombia

3. Río Igará-Paraná, La Chorrera, 20 km downstream of La Raicilla Ravine (approx.)
4. Río Cahuinari
5. Amacayacu National Park
6. Río Cotuhe, Bravo Ravine (approx.)
7. Río Cara-Paraná
8. Río Cotuhe, Tarapaca
9. 2°08'S, 69°48'W Caño Mateo, Puré National Park
10. 2°19'S, 69°44'W Caño Arapa, Puré National Park
11. 1°50'23''S, 69°43'39''W, Caño Esperanza, Puré National Park
12. 1°35'S, 69°30'W, Quebradón EL Ayo, Puré National Park
13. 1°20'5''S, 69°49'22''W, Caño Curare, Curare-Los Ingleses Indigenous Reserve
14. 1°19'36''S, 69° 46'02''W, Caño Agua Blanca, Curare-Los Ingleses Indigenous Reserve
15. 1°24'42''S, 69°34'58''W, Caño El Boliviano, Camaritagua Indigenous Reserve / Vereda Madroño
16. 1°22'19''S, 69°58'04''W, Caño Zumaeta, Curare-Los Ingleses Indigenous Reserve

Brazil

17. Rio Tonantins
18. Tonantins
19. Lago do Caruará (location by Hershkovitz 1987)
20. Tabatinga

Figure 16. *Pithecia hirsuta* Spix, Schwarzbärtiger Mönchaffe, hand-painted plate by Johann Andres Fleischmann (1835) for the Royal Bavarian Art Institute of Private Piloty & Löhle, Munich, and corresponding syntype mount (ZSM No.15). Images courtesy of R. Kraft, ZSM.

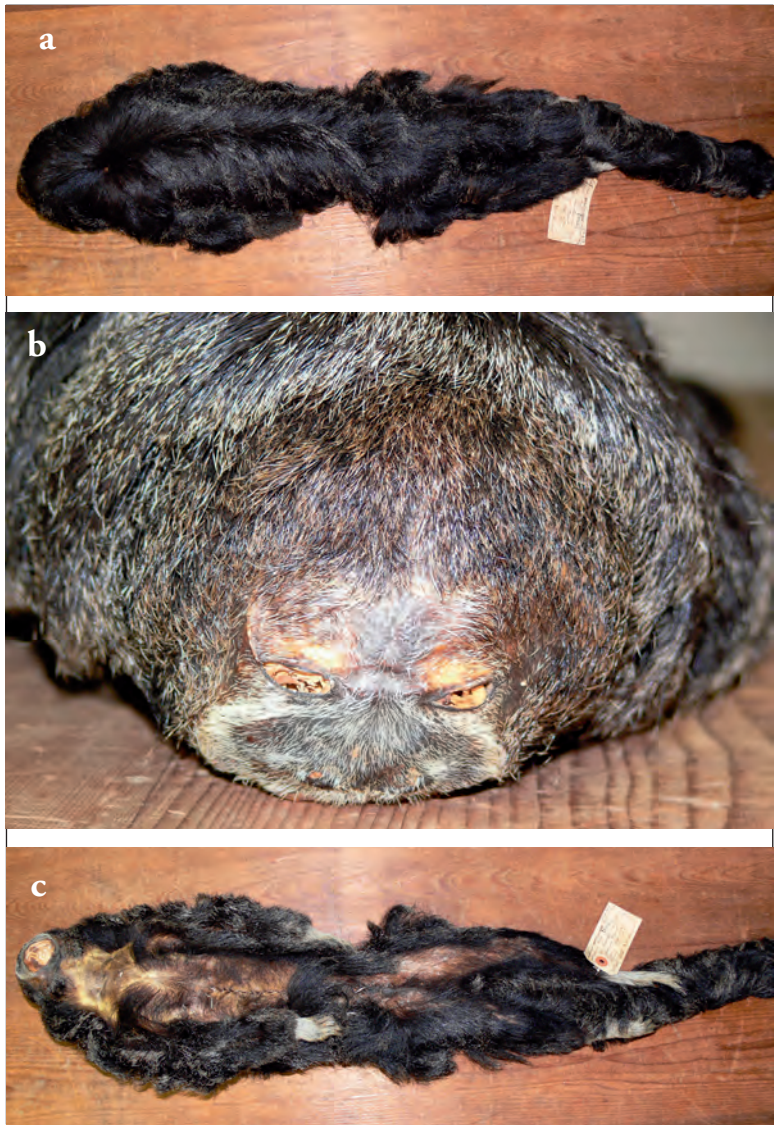


Figure 17. Adult male key specimen, full body and details, BMNH No. 27.8.11.23. Photos by L. K. Marsh.

Figure 18. Living male and female *Pithecia hirsuta* from Colombia. (a) adult male, photo by R.A. Mittermeier, (b) adult female pet in Amacayacu National Natural Park, 2009, photo by X. Carretero. Photos used with permission.

MILLER'S SAKI

Pithecia milleri (J. A. Allen, 1914)

Synonymy

1914 *Pithecia milleri.* J.A. Allen, New South American Monkeys. *Bull. Am. Mus. Nat. Hist.* 43: 650.

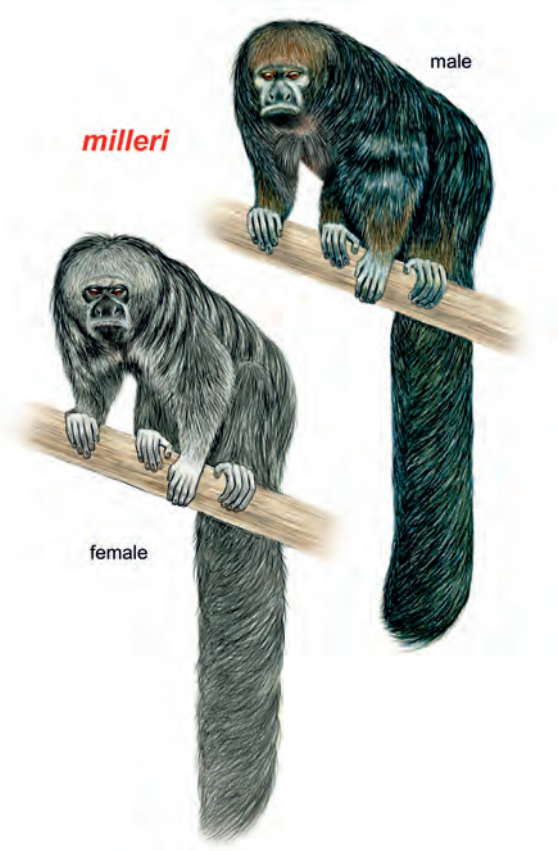
1987 *Pithecia monachus milleri* Hershkovitz. *Am. J. Primatol.* 12: 424–425, in part.

Holotype. Adult male in the American Museum of Natural History, New York, USA, No. 33876 collected by Leo Miller, 8 July 1912 (Collection No. 878), for whom the species was named (Allen, 1914).

Topotype. Juvenile male, No. AMNH 33877, collected and designated by Leo Miller, 9 July 1912, determination by J.A. Allen.

Type locality. Colombia, Department of Caquetá, near Morelia (alt. 700 ft) at the head of the Río Fragua.

Key specimens. Adult male, FMNH No. 70635, collected by P. Hershkovitz, 3 Jan.1952, determination by Hershkovitz as *P. m. milleri*, Colombia, Caquetá, Florencia, Montañita, 400 m. Adult female, IAVH No. 0601, collected by H. Chiriví and J. A. Mora, 8 March 1973 from Colombia, Putumayo, Puerto Leguízamo, Caucaya stream, Miguel Velásquez farm, jungle entering by Limoncocha, north-west of Puerto Leguízamo. Note: "Breast with milk, infant capture. Group of five individuals in a swamp area."



Specimens examined. Thirty-five skins and skulls, wild and captive photo references including those observed and photographed by L. K. Marsh in Cuyabeno, Ecuador.

Description. In overall pelage, males and females are more grizzled than *P. hirsuta*, and females in particular are noticeably grayer in the face and pelage. *Males.* As per Allen's (1914) description of the male type: "Upperparts, limbs and tail black, the hairs with long pale yellowish [white] tips; face sparsely clothed with short whitish hairs; front half of head mars brown, the hairs short and course; underparts thinly haired, foreneck naked; hairs dark brown with whitish tips on the throat and belly and with yellowish brown tips over the pectoral region; hands yellowish white, feet whitish grizzled with black." Subadult and juvenile males have the soft, very brown "mars" coloration of the type as described by Allen, but it is more adpressed in adults making a denser brown band around the face. Males have white hairs along the malars and lips as in *hirsuta*, but also have white under the eyes and often above as well, which is present in *hirsuta* but not as obvious. Overall pelage is much more grizzled than in *hirsuta*, including darker "sleeves" on the forearms where there are patches of brown infused in the black; likewise in the "cuffs" of the hindlimbs. The ruff is not obviously brown or lighter, but can range, as in *hirsuta*, from a lighter tan to black. *Females*. Faces are shaggier and whiter in general, sometimes with a distinct white band across the forehead. Longer, shaggier white malar lines, and indistinct white across the lips. Also with whitish hands and feet, less distinct in general than *hirsuta*.

Diagnosis. Males and females are dichromatic and more distinct from one another than *P. hirsuta* males and females. *Pithecia milleri* is distinct from *P. hirsuta* with males much more grizzled throughout the pelage, and much browner faces and forearms than *P. hirsuta*. *Pithecia milleri* females are grayer overall than *P. hirsuta* females, but particularly gray in the face contrasting with the very black *P. hirsuta* female faces.

Measurements. See Table 11, including original measurements from Allen (1914).

Distribution. Map 4. In Colombia, *Pithecia milleri* is distributed from the foothills up to 500–700 m surrounding Florencia, east to the area of La Macarena, and south of the Río Caquetá to at least Puerto Leguízamo. It is unclear where the boundary with *P. hirsuta* lies beyond Mecayá. According to Defler (2004), it occurs in La Paya National Natural Park (422,000 ha), Colombia. South of the Río Putumayo it extends into Ecuador north of the Río Napo, but it is unclear how far it occurs east between the Napo and Putumayo. It is possible since Miller's sakis have been recorded in Cuyabeno, Ecuador, that they could be found across the border west into Peru in the Zona Reservada Güeppí, north of the Napo. To date, there have been no records of them in that region.

Specific locations. Appendix I. COLOMBIA. *Caquetá*: Río Peneya; Río Caquetá - El Infierno - Puerto Santander; La Murelia; Florencia - Montañita; La Tagua - Tres Troncos. *Meta*: La Macarena National Natural Park. *Putumayo*: Caucaya Stream - Puerto Leguízamo - Miguel Velasquez Farm/ Limoncocha; San Antonio - Mocoa; Puerto Limón - Indigenous Reservation El Picudo - Villa Garzón; Río Mecaya; Caquetá River - El Hacha Stream (between Putumayo and Caquetá). ECUADOR. *Sucumbios*: Río Aguarico - Lagarto Cocha; Shushufindi; Cuyabeno - Laguna Garza, Laguna Grande, lodges, Río Cuyabeno.

Discussion. *Pithecia milleri* was described as a distinct species separate from *P. monachus* by Allen, but Defler (2004) and Hershkovitz (1987) treated it as a subspecies of *P. monachus*. It is here elevated back to a species. An Olalla specimen, AMNH (No. 71816) collected 25 January 1926, was misplaced by Hershkovitz (1987) as being a female from Peru at "Boca Lagarto Cocha", and perhaps he was the one who changed the tag on the specimen from "Ecuador" to "Peru." While it is not entirely incorrect to place it in Peru as the location is near the border with that country, with further investigation, Wiley (2010) discloses: "The Río Lagarto Cocha is a small tributary of the Río Aguarico, itself a tributary of the Napo. The current international boundary between Ecuador and Peru follows the lower Aguarico and the Lagarto Cocha. […] Carlos Olalla's letter stated that it took three days to canoe up the Río Aguarico to reach the Lagarto Cocha. […] Carlos had nothing to say

Table 11. *Pithecia milleri* holotype AMNH 33876, topotype AMNH 33877, and key specimens FMNH 70635 and IAVH 0601.

Measurement	Male AMNH 33876	Male* AMNH 33876	Male FMNH 70635	Female** IAVH 0601
Skull (mm)				
Total length	81.9	82.7	85.7	76.4
Breadth of braincase	43.3	43.7	46.9	41.0
Occipitonasal length	–	75.7	–	–
Basal length	–	63	–	–
Zygomatic breadth	55.5	57	56.9	–
Orbital breadth	43.0	43.2	42.8	–
Nasal breadth mid- orbit	6.3	–	7.5	5.0
Nasals	–	16 × 15	–	–
Postorbital breadth	–	35	–	–
L-orbit inner width	16.6	–	15.8	16.8
L-orbit inner height	17.7	–	19.6	17.6
Breadth of rostrum at canines	26.4	26.0	25.5	–
Palatal length	–	25	–	–
Breadth of palate at M1	–	14	–	–
Maxillary tooth rows	–	19.6	–	–
L-mandible length	52.2	–	61.3	55.6
L-mandible height	41.7	–	41.8	–
Post-crania (mm)		**AMNH 33877‡**	**FMNH 70637^**	
Total length	880	730	819	825
Head-body	480	330	361	420
Tail	400	400	458	405
Hind foot	120	110	120	117.2
Ear	–	–	34	31.5

* Reported in Allen, J.A. 1914. New South American Monkeys. *Bull. Am. Mus. Nat. Hist*. 43: 650.
‡ Juvenile male topotype does not have its associated skull, only basic body measurements.
^ Adult Male FMNH 70637, same location as key specimen male FMNH 70635, but without skull. FMNH 70635 without body measurements.
**Wt. 2102 g. Data on IAVH 0601 from Xyomara Carretero.

about where his party camped or collected at the mouth of the river. Lagarto Cocha, despite its name ("cocha" means lake in Quechua), is a small black-water river, less than 50 m wide that meanders southward through hilly terrain. Recent satellite photos show the mouth of the river at 0°39'18"S, 75°15'41"W, but it appears that this mouth is recent, formerly having been about 2 km SW" (Wiley, 2010, p. 37). While males north-east of the Río Orteguaza appear to be *P. milleri*, the females, at least in museum collections, almost resemble *P. hirsuta* with blacker faces than the more typical *P. milleri* of Ecuador and southwestern Caquetá. As with many saki species, it is possible that the colorations change according to age. Thus, more research is needed on these populations to determine the boundaries with *P. hirsuta*.

Map 4. Geographic distribution of *Pithecia milleri*.

Colombia

1. La Macarena National Park, Meta
2. Caucayá Airport, Puerto Leguízamo
3. Quebrada Caucayá, Limoncocha, Miguel Velásquez Farm (approx.)
4. Between Leguízamo and La Tagua (approx., K. Watanabe Expedition 1973–74)
5. Tres Troncos (approx.)
6. La Tagua
7. Quebrada El Hacha (approx., Caquetá River Expedition 1960)
8. Río Caquetá, Puerto Santander, El Infierno Farm
9. Montañita
10. Morelia, Caquetá
11. Mocoa
12. Puerto Limón, Villa Garzón, El Picudo Indigenous Reservation
13. La Solita Creek, Solita
14. Vereda La Leona, Valparaiso
15. Río Peneya

Ecuador

16. Río Aguarico, Boca Lagarto Cocha (by gazetteer, Paynter 1993)
17. Cuyabeno National Park, all points within, including Laguna Garza Cocha
18. Cuyabeno Lodge
19. Río Aguarico
20. Sushufindi

Figure 19. Holotype specimen, adult male, full body and details, AMNH 33876. Photos by L.K. Marsh.

Figure 20. Holotype AMNH 33876, skull. Photos by L.K. Marsh.

Figure 21. Adult male *Pithecia milleri* in Cuyabeno National Park, Ecuador. Photos by L.K. Marsh.

Figure 22. Adult female *Pithecia milleri* in Cuyabeno National Park, Ecuador. Photos by L.K. Marsh.

MONK SAKI

Pithecia monachus
(É. Geoffroy Saint-Hilaire, 1812)

Synonymy

1812 *Simia monacha* É. Geoffroy Saint-Hilaire. *Rec. Obs. Zool. Anat. Comp.* (Humboldt expedition). Vol. 2, p.359.

1813 *Pithecia monachus*. É. Geoffroy Saint-Hilaire. *Ann. Mus. Hist. Nat. Paris* 19: 116.

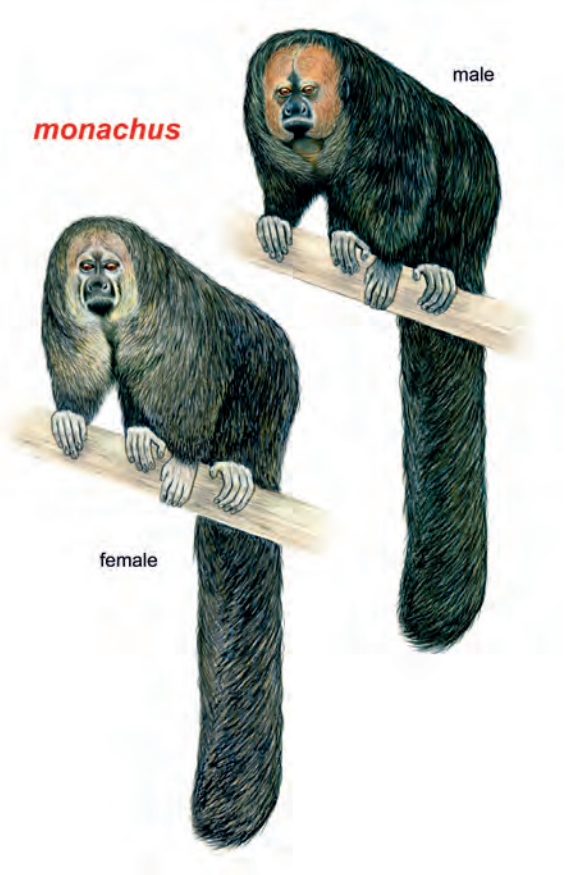
Holotype. Skull-in mount MNHN No. 447, Type 92, 2005-928, juvenile male. Other information on mount: "Cabinet de Lisbonne, Brasil 1808. É. Geoffroy St.-Hilaire 1812, *Ann. Mus. Hist. Nat.* Paris 1. XIX, p.116."

Key specimens. *Males*: AMNH No. 11132, collection no. 210, adult male, skin and skull, collected by D. W. Fleck, 1995–1996 from Peru, lower Río Galvez, eastern side, at Nuevo San Juan. FMNH No. 87002, adult male, skin and skull, C. Kalinowski, January 1957 from Peru, south of the Río Amazonas, Río Maniti, east side, at Santa Cecilia. MPEG No. 1828, adult male, skin and skull, skin and skull, J. Hidasi, November 1960 from Brazil, Rio Javarí, Estirão do Ecuador. *Females*: MNHN No. 448, catalogue no. 1664, subadult female, skull-in mount, collected on the Castelnau et Deville Expedition, 1867 (which could be the mount date, not the expedition date as it was much earlier) from Peru, Río Yavarí, no specific site. FMNH No. 88861, adult female, skin and skull, collected by C. Kalinowski, September 1957, from Peru, Río Yavarí-Mirim, no specific location. AQ 04.6.82, juvenile female, skin only, collected by R. Aquino, 4 June 1982 from Peru, upper Río Orosa on the west side near the confluence of Río Chontay. BMNH No. 27.3.6.4, adult female, skin and skull, collected by W. Ehrhardt, 10 September 1926 from Brazil, upper Solimões, at Santa Rita, likely present-day Santa Rita do Weil.

Type locality. Geoffroy Saint-Hilaire's (1813) type description says, "Habite…le Brésil?" (p. 117). Others have placed it with Spix's *Pithecia hirsuta* north of the Rio Solimões, but the type specimen itself has an indeterminate locality.

Specimens examined. Eighty-one specimens, skins, skulls, and photos of living animals from Peru: ríos Yavarí-Mirim, Lago Preto, Tamashiyacu-Tahuayo by M. Bowler, Quebrada Blanco, Río Tahuayo by E. W. Heymann, ríos Tapiche and Tahuayo by various tourists; in Colombia, Leticia area by Juan Manuel Renjifo Rey and Glenn Perrigo, and captives or pets by R. Aquino, L. K. Marsh, and tourists in area of Iquitos.

Description of holotype. Because of the vast confusion about this specimen in particular, I here give detailed



information about it for future investigators. Geoffroy Saint-Hilaire (1813) wrote: "Pelage varié par grandes taches de brun et de doré: poils bruns en grande partie et des l'origine, et roux-dorés vers l'estremité: chevelure rayonnante de l'occiput et aboutissant au vertex" (p. 116). He did not provide measurements of this animal, nor an illustration in his publication of it. His description can be applied to several species of *Pithecia*, both male and female, but mysteriously does not describe the type that was presumably placed by him. The original text from Kühl (1820) repeats in Latin basically what Geoffroy Saint-Hilaire described, but it too in no way describes the specimen that is there now. It does, however, read like it might describe the subadult "transitional" males (see Description, below): "Pilis longissimis, densissimis, ab apice inde bruneis, apicibus tantum extimis ochraceis; ad capitis latera autem et sinciput adpressis, paucioribus, pallide cinerascente ochraceir; in fronte media longitudinaliter haud divisis, occipitis radiantibus, confertissimis. Manuum pilis brevibus, adpressis. Species omnium minima. In Museo Parisiensi" (p. 45). And Gray in 1870 describes *monachus* in the catalogue for the BMNH as black, grey-washed; hairs very long, harsh,

white-tipped; head and crown of male yellow, of female white" (p. 59), which is significantly closer (but see Discussion, below).

If the type specimen is used as the definitive reference, then the one presently in the Paris vaults is quite different from all original references. Gray (1860) refers to the *P. monachus* type as "from a very young specimen in bad shape" (p. 230) and in 1870 Gray repeats: "The specimen described by Geoffroy was young and in very bad shape," which sadly does correctly reflect the current type. However, J.A. Allen (1914) vaguely described *P. monachus* as having a "forehead and crown white," which approximately agrees with the type as it appears today.

Thus, the problem with the Paris type is many-fold: it is a small juvenile, it was in poor condition as far back as 1860, over time it faded from sunlight hitting the front of the specimen possibly changing the defining coloration (previous curation had the types in clear glass cases for public viewing without regard to natural light or protection from fading, C.P. Groves, pers. comm.), and it could be a female. Hershkovitz (1987) cited the type as "MNHN Paris, No. 447, sex indeterminable, mounted specimen, skull in skin" (p. 423). If the type is in fact from Brazil, there are juveniles with a white band around the face within the *monachus* range. The confusion remains as far as the type is concerned as there are both young juvenile males and females in that region with white bands around their faces. As an example, MPEG 30768 from Atalaia do Norte, Rio Javarí, Brazil, is labeled "male", but it is a juvenile female (Figure 33). It is clear from this study that the holotype has value for historical purposes only, not for taxonomic reference.

Description. There is a great deal of variation in the color of the juveniles, both male and female, and the adults. It appears, based on skull morphology, that these sakis in particular live a long time, and their coloration changes over time. In particular, older adult males tend to have some of the most pronounced sagittal crests of all the saki species.

Males. Adult male dorsal pelage is black with very little stippling overall. The forearms and across the chest tend to have longer whitish tips, with the chest ruff having dark roots, but light tan to orangish tips. Juvenile and subadult males are more grizzled in general, with the ruff more obvious and stippling across the arms at chest height make the ruff seem more extensive. The hair from the whorl on the nape of the neck does not extend as far forward over the face as in some sakis, and is darker with less stippling, especially in subadult males. Both adult and juvenile males have black wrists. The hands and feet are mottled black and white, growing whiter with age, but the hairs are subterminally black. The adult males' faces are very brown, and are darker the older they get. The hair is adpressed especially in older animals, with a definite crease up the forehead ending in a star or "pit" between and just above the eyes. In the skulls of older animals, there is a pronounced sagittal crest. Malar lines are white and vary in width depending on age as the white below the cheek line can blend to the malars. There are fine white hairs along the upper lip as well. The facial skin of the muzzle is black with fine whitish hairs sometimes present. In subadult males, the face is white with only a band of brown up the centerline of the forehead. As these animals age, they are similar to adult female *P. inusta*, and become "two-tone" where the top band of their faces is brown and the bottom white. In some males, the white diminishes to just wide malar lines, and in others it remains white at the lower part of the face. Juvenile males, depending on age, have a white head-band with some brown forming down the center. In very young males, the brown can be nearly across the forehead with the rest of the face white. One of the striking features in older males is the multifolded glandular throat sack, which is more pronounced in this species than any other saki. *Females.* The overall pelage of females is similar to that of males in that it is black with some stippling throughout. Females in general tend to be slightly more grizzled, especially in the forearms. The hair of the nape whorl extends forward further than in males, but gradually so, it is not as noticeably abrupt as in males. Young, breeding age females can have very loose brownish to whitish mottled faces. Older females have soft, loose dark brown foreheads with shaggy white below, looking "two-toned". Malar lines are shaggy and white and in older females can blend in with the white lower cheek hair. The ruff on females is darker brown or black, with occasionally lighter tips, that are less extensive than in males. They have less extensive throat glands. In older females, hands and feet are whiter than those of males.

Measurements. None for the type specimen. Table 12 for key specimens of the species.

Diagnosis. Unlike *inusta*, older adult male facial hair appears more as a band around the face, with some hair filling in toward the muzzle, rather than the face finely covered entirely in hair. Also distinct is the glandular throat sack, and clearly bifurcated forehead muscles on either side of a notable sagittal crest seen in the skulls of some individuals. Faces are much darker brown overall in adult males in *P. monachus* than *P. inusta*, and adult female *monachus* tend toward the brown-topped forehead with the white below, as opposed to the nearly entirely white of adult female *inusta*.

Distribution. Map 5. In general found in the interfluvial areas between the rios Solimões, lower to middle Ucayali, and lower Yavarí in Peru extending south to at least Sarayacu/Serra do Divisor, and the lower reaches of the rios Javarí to Juruá in Brazil. In Peru: Río Tahuayo region including the Reserva Comunal Amishiyacu-Tahuayo and Quebrada Blanco, north to Río Maniti and Río Orosa, Río Yavarí-Mirim and Río Yavarí region, including, Quebrada Esperanza, Río Galvez, north-east to San Fernando, and Leticia/Tabatinga. Tourist photos and specimens of sakis in the ríos Tahuayo and Tapiche are possibly of subadult males or even of *P. inusta* males. If these animals prove different, it

may be because of introgression from *P. inusta* in the Río Ucayali watershed coming up from the south (cf. "Discussion" below). In Brazil: Benjamin Constant, Santa Rita do Weil, Atalaia do Norte, and Estirão do Equador.

Specific locations. Appendix I. BRAZIL. *Amazonas*: Rio Javari – Estirão do Equador, Atalaia do Norte; Benjamin Constant – Mata Esperança do Município, Rio Quixito – Seringal, Boa Vista (Gondino), José Veiga; Santa Rita; Tabatinga. PERU. *Loreto*: Río Yavari; Río Yavari Mirim – Mariscal Ramon, San Fernando, Quebrada Esperanza, Lago Preto; Río Maniti – Maynas, Santa Cecilia; Pebas; Río Amazonas – Orosa, Río Chontay; Río Galvez - Nuevo San Juan; Río Tahuayo – Quebrada Blanca, Tahuayo Lodge, Tamashiyacu; Río Tapiche – Puerto Punga, San Salvador; Iquitos.

Discussion. The "*Monachus* Mess" has been snowballing for almost 200 years. I read all available early references regarding the description of *monachus*, including É. Geoffroy (1812, 1813), Kühl (1820), Spix (1823), Gray (1860, 1870), Elliot (1913), J.A. Allen (1914), Lönnberg (1938), and Tate (1939). All of them were confused and conflicting about what Geoffroy meant. Spix (1823) simply ignored *monachus* altogether, clearly naming and referencing *hirsuta* and *inusta*, animals that can still be identified today (cf. *P. hirsuta* and *P. inusta*). Gray (1870) was not only displeased with the Paris type, but he was also confused about what *monachus* was by rolling it into synonymy, among others: I. Geoffroy's description of *monachus* from the Castelnau Expedition, Spix's *P. hirsuta*, Poeppig's *P. guapa* and Lesson's two *P. nocturna* (both of which are *P. pithecia* transitional juvenile males), and his own *P. irrorata* saying, "the [specimen] in the British Museum, figured in the 'Voyage of the Sulphur,' has the face quite bald. This is now shown to be accidental, as the others, more lately received, have white hairs on the face" (p. 59). We know now that he was right about *irrorata*, that there actually are bare-faced animals, it is not that the hair has been rubbed off (cf. *P. irrorata*).

Lönnberg understood the problems best, and tried to give an historic rationale: "*P. monachus* was named in 1812 by É. Geoffroy St. Hilaire (*Ann. Mus. Nat*. Paris XIX, p. 116). Although the general characteristics of this monkey are indicated, it has not been sufficiently clear which of the existing races or subspecies is to be considered as the typical one. In consequence of this the specific name quoted has sometimes been used in a rather collective sense, and several new names have also been published. Spix introduced two new names 1823 (*Sim et Vesp Bras*), the types of which were fully described and also pictured on plates, so that they with full certainty may be recognized vz. *hirsuta* (i.e., p. 14, Pl. IX) and *inusta* (i.e., p. 15, Pl. X). Both these subspecies are represented in the present collection, and as it is not proved, whether any of these can be regarded as identical with the typical *monachus*, the names of Spix are used."

Like Spix, Lönnberg never attaches any specimens to *monachus*, instead he accurately supports Spix's clearly defined species (and adding a new one of his own, cf. *P. napensis*) leaving us to believe that while Geoffroy indeed was looking at a saki monkey, which saki monkey has been bantered about for generations. Complicating this issue is the fact we have no record of who actually selected the Paris type, nor where it was actually collected. It is exactly as Lönnberg described; that *monachus*, up to this publication, has been used in a "collective sense," a dumping ground, of unknown or unnamed sakis. And based on Hershkovitz's last saki work, he fell prey to the same condition. Hershkovitz (1987) stated, "Consistent size and cranial or dental

Table 12. Measurements for *P. monachus* key specimens.

Skull Measurements (mm)	AMNH 11132 Male	FMNH 87002 Male	MPEG 1829 Male	FMNH 88862 Male	FMNH 88861 Female
Length of brain case	81.6	84.8	86.3	86.9	80.0
Width of brain case	36.8	46.0	44.0	48.2	42.6
Zygomatic arch width	53.0	58.0	57.4	56.8	51.0
Orbits-outer	38.9	41.3	46.2	42.1	39.8
Nose bridge	6.1	7.15	7.0	7.2	6.2
L-orbit inner width	17.5	16.2	17.4	15.6	16.1
L-orbit inner height	18.5	19.4	19.3	18.3	18.4
Muzzle width	24.2	25.4	25.5	26.4	22.8
L-mandible length	52.1	59.1	57.6	61.0	56.5
L-mandible height	38.0	39.1	41.0	40.7	38.1
Post-crania (mm)					
Total	–	875	–	8	864
Tail	–	457	–	4	404
Hind foot	–	126	–	1	118
Ear	–	33	–	3	32

Map 5. Geographic distribution of *P. monachus*.

Brazil
1. Estimated location Rio Juruá (E. Garbe Expedition 1901–02)
2. Santa Rita do Weil
3. Benjamin Constant
4. Atalaya do Norte
5. Rio Quixito
6. Estirão do Equador

Peru
7. San Fernando
8. Boca Río Yavari Mirim
9. Quebrada Esperanza (approx.)
10. Río Orosa
11. Orosa
12. Río Orosa (R. Aquino collection)
13. 3°26'S, 72°46'W
14. Rio Maniti, Río. Cecilia
15. Pto. Indiana
16. Quebrada Blanco
17. Tahuayo Lodge
18. Río Tahuayo, Tamashiyacu
19. Río Yavari Mirim
20. Río Galvez, Nuevo San Juan
21. Río Tapiche, San Salvador
22. Boca Rio Punga, Puerto Punga
23. 6°14'S, 74°01'W
24. Sarayacu

differences between species of the *P. monachus* group have not been found" (p. 410). This problem for him likely arose from the fact that he lumped several different species and sex/age classes into not only the "*monachus* group," but into the *monachus* species itself (cf. Table 2 "Introduction").

The clearest, earliest example of what adult *P. monachus* looks like is Plate 3 in Castelnau *et al.* (1855) depicting an adult male holding an infant with a portrait of a 'female' although the female here is so vague it appears to be more similar to a transitional subadult male or a *P. inusta* female (Figure 23). The animals depicted in it are from Peru. It is of note that Étienne Geoffroy Saint-Hilaire's son, Isidore, is credited with the species determination in this image and was a member of the expedition into Peru and Brazil. It is this image that allowed *P. monachus* to remain as a recognizable species, and is what I used to determine adult key specimens.

One of the distinctive characteristics in the *P. monachus* adult males is their conspicuous, multi-folded glandular throat sack (Figure 28b). It is unclear whether the throat sacks on both males and females are used for scent marking for territory or sexual signaling, although as compared to other New World primates, sakis are not particularly strict territory defenders (pers. obs.). *Pithecia* sexual behavior has been studied (Setz and Gaspar, 1997; Lehman *et al.*, 2001; DiFiore *et al.*, 2007; Norconk, 2006; Thompson and Norconk, 2011; Thompson *et al.*, 2011), but there are no studies on the size of the glandular areas or excretion rate/

volume of male glands in relation to sexual advantage, if there is one. Furthermore, while it is clear that at least some sakis signal mates using lingual gestures (tongue moving rapidly in and out of the mouth; Figure 30) similar to other New World primates (for example, *Alouatta*, pers. obs. for *A. pigra*, Jones [2002] for *A. palliata*), it is unclear whether subadults of *P. monachus* (or any sakis for that matter) initiate sexual partners more frequently with visual cues, such as lingual gestures, as compared to older males with extensive throat glands who may predominantly use scent to attract mates. The function of both visual and olfactory cues in saki sexual behavior needs further investigation in all species.

The deep confusion over *P. monachus* was not just over its appearance, but its location, as Geoffroy confusingly gives us "Le Brésil?" without any further details, and, as has been mentioned, other authors (including Hershkovitz) simply presumed that he meant what Spix later reported for *P. hirsuta*. Hershkovitz (1987) was another in a long line who placed *monachus* thus: "Amazonian region in Ecuador, in Peru the basins of the ríos Huallaga, Ucayali, and Purus in the departments of Amazonas, eastern Huanuco, Pasco, Loreto, and Ucayali, then east into Brazil to the west (left) bank of the Rio Juruá in western Amazonia and Acre; altitudinal range between 50-1500 m above sea level" (p. 423). And while he at least got the right species within those boundaries, other authors presumed this location information to mean that *monachus* was also in Colombia (Defler 2004) and worse, throughout Ecuador, Peru, Bolivia, and Brazil, all the way to the Rio Tapajós (BDGEOPRIM 2002). It is no wonder we have such divergence in genetic results, and in any kind of comparative anatomy for projects involving "*P. monachus*."

With more extensive analysis and considerably more data, it may be shown that *P. inusta* and *P. monachus* are the same species with a huge variation in pelage coloration and skull morphology. Likewise, it may be shown that there are even more species in the Ucayali/Yavarí/Juruá region. The sakis in the lowermost Ucayali, in particular in the ríos Tahuayo and Tapiche, are included in *monachus* for now, although it is unclear if these animals, photographed by tourists in the region, are subadult *monachus* males or are adult *inusta* males. If *inusta* occurs primarily in the Ucayali drainage and *monachus* in the Yavarí/Javarí, there could be a "mixing point" somewhere in the north as well as somewhere around Sarayacu/Serra do Divisor in the south. Regardless, the designations of *P. inusta* and *P. monachus* as distinct in this publication represent an understanding that there are differences in the sakis of that region, that we need to be careful about creating a new "dumping ground" of species such as *monachus* was historically, and that "something is going on" in these populations that is worthy of further research.

Figure 23. *Pithecia monachus* depicted in Plate 3 of Castelnau *et al.* (1855).

Figure 24. *Pithecia monachus* holotype MNHN No. 447. Photos by L.K. Marsh.

Figure 25. Full mount and detail of MNHN No. 448, subadult female, from Río Yavarí, collected on the Castelnau et Deville Expedition, 1867. Photos by L.K. Marsh.

Figure 26. Adult female key specimens, full body and details of: (a) Brazilian *Pithecia monachus*, BMNH 27.3.6.4 from Santa Rita, Solimões, and (b) Peruvian *Pithecia monachus*, FM NH 88861, adult female from Río Yavarí-Mirim. Photos by L.K. Marsh.

Figure 27. Adult male key specimens, full body and details of: (a) Brazilian *Pithecia monachus*, MPEG 1828 from Estirão do Equador on the Rio Javarí, and (b) Peruvian *Pithecia monachus,* FMNH 87002, adult male from the Río Maniti. Photos by L.K. Marsh.

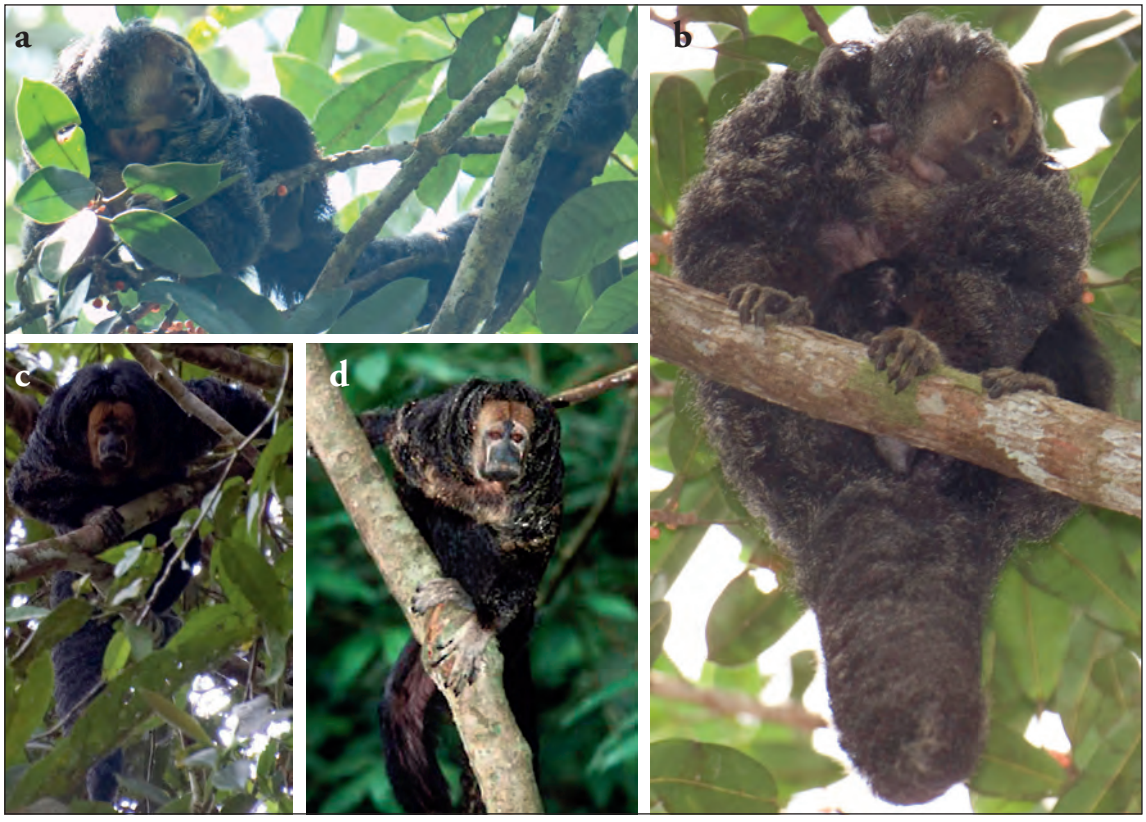


Figure 28. (a–c) Wild adult male *Pithecia monachus*, (d) captive adult male, Iquitos Zoo. Photos by Mark Bowler.

Figure 29. Subadult male *Pithecia monachus* (or possibly adult male *P. inusta*; cf. Discussion) from the Río Tahuayo region. (a) wild male, photo by Mark Bowler; (b) provisioned male, photo by John Agnew.

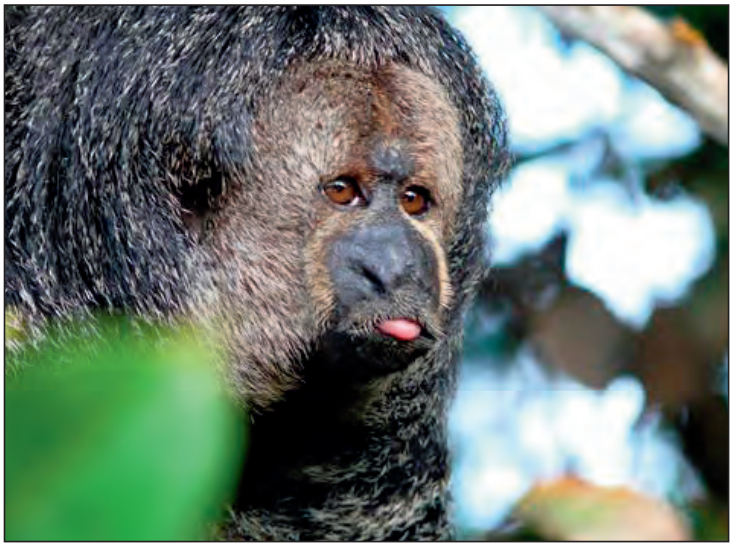


Figure 30. Subadult male *Pithecia monachus* sexually gesturing to a female. Photo by Sally Kneidel.

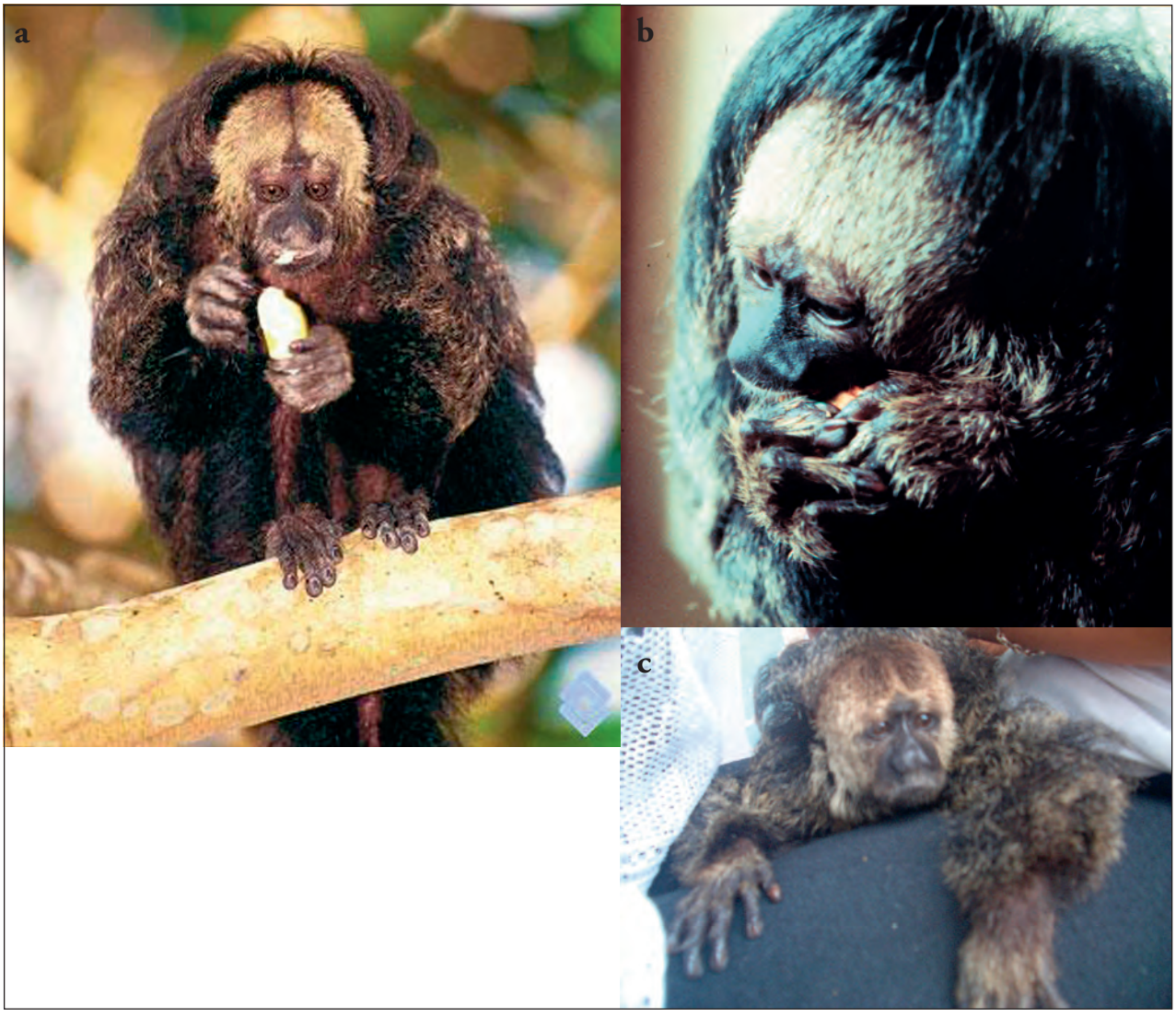


Figure 31. Different ages of transitional males: (a) Living juvenile male *Pithecia monachus* near Leticia, photo by Juan Manuel Renjifo Rey; (b) pet in Quebrada Blanco, Río Tahuayo, Peru, photo by U. Bartecki; and (c) pet in Iquitos, Peru, photo by R. Aquino.

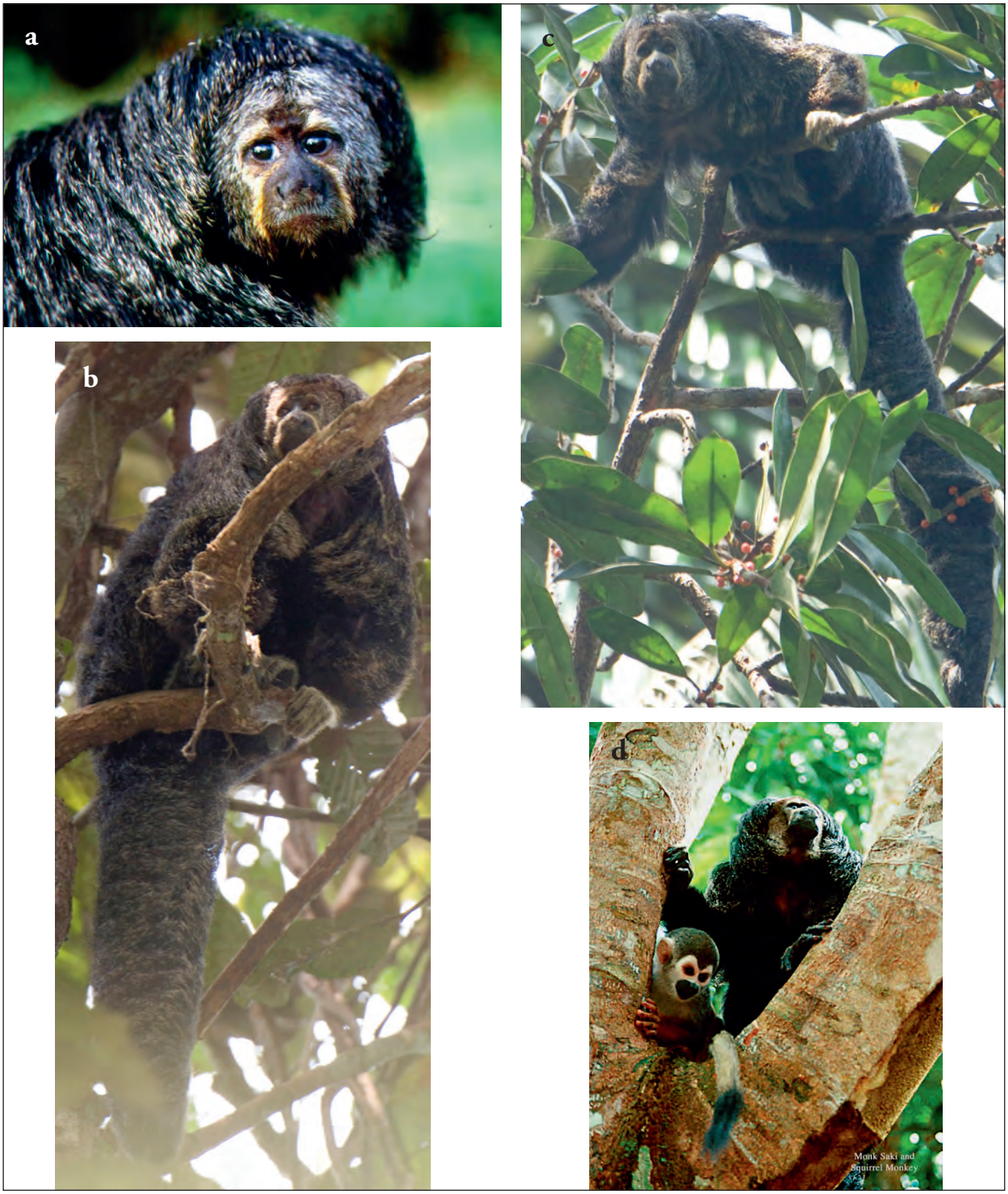


Figure 32. (a) Juvenile female *Pithecia monachus* in the Tamashiyacu-Tahuayo region, photo by E.W. Heymann; (b) adult female *P. monachus* (with squirrel monkey), rescue center near Río Selva, Tabatinga, photo by Glen Perrigo; (c-d) wild *P. monachus* in Peru, breeding (subadult) female, near Boca Río Yavarí-Mirim, photos by M. Bowler.

Figure 33. Various aspects of *Pithecia monachus*, juvenile female, MPEG 30768, from Atalaia do Norte, Brazil.

BURNISHED SAKI

Pithecia inusta (Spix, 1823)

Synonymy

1824 *Pithecia inusta* Spix, J. B. von. *Simiarum et Vespertilionum Brasiliensium Species Novae*. 1823. F. S. Hübschmann, Munich, p. 15–16, pl. 10.

1987 *Pithecia monachus monachus* Hershkovitz, P. *Am. J. Primatol*. 12: 422–424, in part.

Holotype. Plate only (Figure 1), original mounted specimen has been lost or destroyed (R. Kraft, ZSM, pers. comm. 2007).

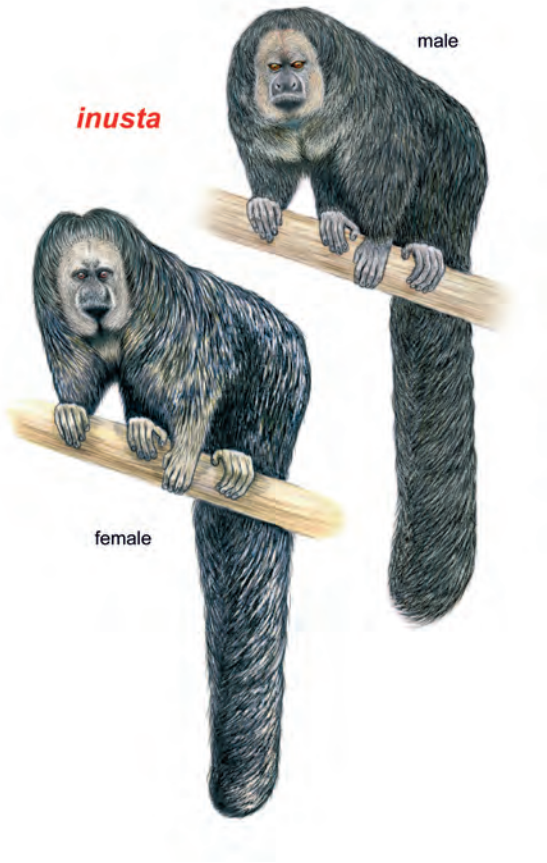
Type locality. Spix (1823) does not specify where the mounted type was collected, not even by country, in his original publication (cf. Discussion below).

Key specimens. MNHN No. 449, subadult male, skull in mount, is similar to the original holotype, this one collected by Castelnau and Deville in 1867 as part of their South American expedition. UNMSM No. 29, skin only, collected by Koepcke in 1949, Peru, near Huanuco, Río Llullapichis, Estación Biológica Panguana. BMNH No. 28.5.2.42, adult male, skin and skull, 18 September 1927, from Peru, upper Río Ucayali, Chicosa, and No. 28.5.2.43, subadult female, skin and skull, 3 August 1927, from Peru, upper Río Ucayali, Cumeria. Both collected at 1500 feet above sea level (457.2 m), and on the Godman-Thomas Expedition (Thomas (1928: 253). And AMNH No. 239853, adult male, skin and skull, collected 28 June 1963 by M. D. Tuttle from Peru, Pasco, Oxapampa Province, Nevati, Mission, 900 feet above sea level (274.3 m).

Specimens examined. Forty-nine specimens, skins and skulls, photos of living sakis by R.A. Mittermeier, J. Vermeer, L.K. Marsh, and tourist photos in the region.

Description. The classic tight, adpressed white faces seen in older museum mounts are confusing at best, as some may be young males and others adult females, the two being very similar. Thus, the following description takes into account the full range of variability among not only adults of this species, but of the females and juvenile age classes. Both males and females have a "diamond" in the center of their foreheads just above the eyes, but in the adult female it tends to be more distinct and less haired than it is in the males.

Males. Dorsal pelage is black with light stippling across the back in juveniles to subadults, more overall in older animals, where the grizzling is short and light initially and increases in length and volume in older males. The ruff is darker brown at the base with light tan tips in younger



animals, but can become brighter with buffy-tannish or nearly orange tips in older males. The chest is otherwise sparsely covered in black hair. The forearms in males are sparsely covered in a pattern that for some looks like a triangle up the arm, where half or more is not stippled at all. Wrists tend to be black or without grizzling. The hands and feet are white, and hind feet can have a distinct dark 'V' on the older animals.

In adults, the face is entirely covered in short, closely pressed tan to off-white hairs with white, short-haired muzzle lines that are more or less distinct as they blend with the rest of the facial hair. The muzzle is bare, with dark skin, and there are scattered short white hairs along the lips. The transitional males have a very tightly pressed white face and this look can last into subadult ages such that quite large animals appear to have solid white faces like older adult females. All older males in general appear to have a line up the forehead likely caused from muscles beneath the skin forming an indented "line". Subadults in the northern reaches of the range (Río Tahuayo/Río Tapiche) have whitish faces with a tan line down the center of the forehead,

over the "indent" (cf. *P. monachus* Discussion); whereas, individuals in the south appear to be more uniform in their burnished color as they get older. There is evidence in some skins that this tan line "spreads out" over the face over time making it the tan-white-burnt color of adults.

Lönnberg (1938) agreed with the original Spix's (1823) description of *P. inusta* saying: "The crown and the forehead, the cheeks from below the eyes and the sides of the head are densely covered with short, very stiff erect hairs which are directed somewhat forwards, or so on the sides more or less downwards, but are not adpressed. The colour of these hairs is somewhat variable, in some the crown is more pale brownish and others more greyish, and in both cases the color fades downwards and on the sides to more or less whitish […] Mustache always whitish, short white hairs on lips" (p.8).

Table 13. Original measurements of *Pithecia inusta* holotype by Spix (1823).

Morphology	Original (ft/in)	mm
Trunci (body)	1'4"	406.4
Capitis (head)	3"	76.2
Facici	1¼"	31.8
Caudae (tail)	1'7"	482.6
Humeri	3¼"	82.6
Ulnae	3⅛"	79.4
Palmae (hand)	2¼"	57.2
Femoria	4⅛"	104.8
Tibiae	6"	152.4
Plantae (foot)	4"	101.6

Females. The dorsal coloring in adult females is very grizzled, often with a light tan colored ruff, and a mostly white to tannish face, similar to males. Forearms tend to be densely covered with white grizzling and white wrist cuffs (lacking in the males). Faces of adult females are similar to males, although they are longer overall and whiter in general. They also do not tend to have the strong muscular indentations up the forehead as in males. Juvenile females have many transitional "looks" from shaggy, loose hair covering the face that is greyish to brownish to turning shaggy white and eventually a closer white/tan that covers the face similarly as in males. The whorl of hair on the nape of the neck extends longer and in more "bangs" in the females than in males, where it appears to be mostly drawn back and not coming as far forward over the face.

Measurements. See Tables 13–15. A mounted, skull-in specimen, UNMSM No. 54E is an interesting example of an adult female (based on the genitalia of the mount), which looks very similar to Paris 449, a mounted, skull-in subadult male. Canine length on UNMSM 54E is: upper left = 7.8 mm and upper right = 7.9 mm.

Diagnosis. The species most similar to *P. inusta* is *P. monachus*, which likely shares part of the northern limits of the range, particularly between the ríos Amazonas/Yavarí in the north-eastern corner of Peru. *Pithecia inusta* is clearly

Table 14. Measurements for *Pithecia inusta* in Peru and the Brazil, Rio Juruá‡ sakis.

Skull (mm)	BMNH 28.5.2.42 Adult male	AMNH 239853 Subadult male	NHRM 2219‡ Adult male	NHRM 2375‡ Subadult male	NHRM 2472‡ Adult female	NHRM 2328‡ Subadult female
Length of brain case	86.0	85.0	90.0	84.0	86.0	86.0
Width of brain case	43.0	45.1	47.0	43.0	45.0	44.5
Occipitonasal length	–	–	78	72.5	76	76.5
Condylobasal Length	–	–	74	65	70	67
Zygomatic arch width	59.3	57.5	61	50	56.5	52
Orbits – outer	43.0	37.6	45.5	40	43	40
Least postorbital width	–	–	34	34	35	35
Nose bridge	6.4	6.1	–	–	–	–
L-orbit inner width	15.5	16.5	–	–	–	–
L-orbit inner height	16.4	18.4	–	–	–	–
Palatal Length	–	–	31	26.5	28.5	25.5
Breadth of palate insideM1	–	–	14	13.5	13	11
Muzzle width	25.1	26.7	27.5	22.5	22.5	23.5
L-mandible length	54.6	50.1	–	–	–	–
L-Mandible height	–	39.4	–	–	–	–
Length of maxillary row of cheek teeth	–	–	19	20	19	19

‡ Measurements reported by Lönnberg (1938).

distinct from *monachus* and all other sakis in the ontogeny of the juveniles, both females and males. Juvenile male *inusta* have closely pressed white faces that cover all of the face, and juvenile females have gray-black, sometimes brownish, faces that become white, whereas juvenile male and female *monachus* tend to be two-toned brown and white, with adult female *P. monachus* often retaining that coloration.

Distribution. Map 6. In Peru, mostly in the Río Ucayali watershed, where collections appear to have been from both sides of the river from Sarayacu south, especially in the upper reaches where it narrows toward the Río Urubamba/Río Tambor split. They are in the foothills along the Río Pachitea below Oxapampa, particularly east of the Pachitea along the Río Llullapichis, Monte Alegre, Puerto Victoria, and Nevati/Mission. See "Discussion" below for sakis in the upper Rio Juruá region in Brazil and the upper Río Pachitea in Peru. Population may reach as far north as the ríos Tahuayo and Tapiche in the lower Ucayali watershed (cf. Discussion, below).

Specific Locations. Appendix I. BRAZIL. *Amazonas*: Rio Juruá – Igarapé do Gordão, Igarapé Grande, João Pessoa. *Acre*: Upper Rio Juruá – Porongaba, Porto Saids. PERU. *Huanaco*: Río Pachitea - Monte Alegre, Tabalosos, Pachitea. *Pasco*: Oxapampa - Nevati Mission, Puerto Victoria; Río Pachitea - Panguana, Río Llullapichis, Río Santiago. *Loreto*: Río Ucayali - Sarayacu; Contamana - Cerro Azul; Cumeria; Masisea - Tushemo; Chicosa. *Ucayali*: Río Ucayali; Río Pisqui; Río Urubamaba; Via Utuginia; Río Inuya; Lagarto.

Discussion. "*Inustus*" in Latin means "burned," and is an apt description of the adult males with their burnished tan-white faces.

Elliot (1913) was the first to include *P. inusta* and *P. hirsuta* as synonyms for *P. monachus* using the Spix locale of *P. hirsuta* for all three, even though neither Spix nor Geoffroy give location information for either *inusta* or *monachus*: "The type of *P. inusta* Spix is in the Munich Museum and can in no way be separated from *P. monacha*. It is full grown in good condition and came from the forests of the Tonantins affluent of the Solimões River near Tabatinga" (p. 290) (see "The Monachus Mess," in *P. monachus*). And now that there are more data, both from living wild and captive animals and more museum specimens, it is clear the original Spix type is of a large juvenile to subadult male, not an adult. Lönnberg (1938) kept the incorrect location placement, but allowed that *P. inusta* was indeed a true species based on Spix's type and description. Hershkovitz (1987) and others placed it incorrectly with the *P. hirsuta* location as described by Elliot (1913). Likewise, there is no specific location indicated for the Castelnau mounted MNHN No. 449 other than Peru, although from his expedition notes it is clear he was never north of the Río Amazonas (Castelnau *et al.*, 1855).

Specimens from the Rio Juruá, Eirunepé (Igarapé do Gordão and Igarapé Grande) in Brazil are included here as part of *P. inusta* (as per Lönnberg 1938), although further investigation needs to be conducted in this region. In the northern reaches of the Rio Juruá is the much browner, distinctly colored *P. monachus*. But in the southern reaches of the upper river are these provisional *inusta* with the older adult males exhibiting heavy skulls, flares on their zygomatic arches, and large sagittal crests, which are closer to *monachus* than *inusta* skulls except for the heaviness. The older upper Juruá adult males tend to have faces that are intermediate between *P. inusta* and *P. monachus*. The juvenile females tend to be browner than *P. inusta* juveniles of roughly the same age class, but the adult females are most similar to *P. inusta* females, not *P. monachus*. The animals in this region may prove to be subspecies of *P. inusta* or *P. monachus*, a distinct species, or color morphs of either.

Sakis in the Río Pachitea region, particularly in the upper reaches (Puerto Victoria and south to Nevati/Mission) are different from the type, where adult males have a softer "medium brown" (intermediate between *monachus* and *inusta*) face with white below, and females have blacker faces in general. These are possibly different species, subspecies or color variations, but as there are also animals in the region that are very similar to the type (for example, AMNH 239853), thus they are provisionally included in *inusta*.

An additional specimen worth mentioning is also provisionally included in *P. inusta*: SEN No. 16605, skull only, with the compelling label information of "*Pithecia monacha* Geoffr. M *hirsuta* Spix, F *inusta* Spix, location W. Brasilien. Get. 1826 München Mus. gegen Rüppell's Dubl." Is this

Table 15. *Pithecia inusta* post-cranial measurements for Peru and Brazil, Rio Juruá‡ sakis.

Post-crania (mm)	BMNH 28.5.2.42 Adult Male	AMNH 239853 Subadult Male	BMNH 28.5.2.43 Subadult Female	NHRM 2219‡ Adult Male	NHRM 2375‡ Subadult Male	NHRM 2472‡ Adult Female	NHRM 2328‡ Subadult Female
Head-body	425	401	396	410	370	420	375
Tail	488	305	375	500	465	545	470
Hind foot	121	135/137	121	130	117	132	125
Ear	29	37	33	–	–	–	–

‡ Measurements reported by Lönnberg (1938).

the skull belonging to Spix's type in ZSM? Is it one of the Rio Juruá sakis? And it is interesting especially with Rüppell's name associated with it as he was apparently ill and laying low in Africa in 1826, returning to Europe in 1827 (http://en.wikipedia.org/wiki/Eduard_R%C3%BCppell). It could also easily be *monachus* or something else entirely. The skull appears to be subadult and likely female.

The sakis in the lowermost Ucayali, in particular in the area of the ríos Tahuayo and Tapiche, are included in *monachus* for now, although it is unclear if these animals, photographed by tourists in the region, are subadult *monachus* males or are adult *inusta* males. If *inusta* occurs primarily in the Ucayali drainage and *monachus* in the Yavarí/Javarí, there could be a "mixing point" somewhere in the north as well as somewhere around Sarayacu/Serra do Divisor in the south. Regardless, the designations of *P. inusta* and *P. monachus* as distinct in this publication represent an understanding that there are differences in the sakis of that region, that we need to be careful about creating a new "dumping ground" of species such as *monachus* was historically, and that "something is going on" in these populations that is worthy of further research.

Figure 34. *Pithecia inusta* holotype, Plate X from Spix (1823).

Figure 35. Key specimens of *Pithecia inusta*: (a–b) MNHN No. 449, subadult male, full mount and detail, and (c–d) UNMSM No. 54E, adult female, full mount and detail. Photos by L.K. Marsh.

Figure 36. Key specimen, UNMSM No. 29, adult male skin only, full body and detail, from the Río Llullapichis, Peru. Photos by L.K. Marsh.

Figure 37. Key specimen, *Pithecia inusta*. BMNH No. 28.5.2.42, adult male, skin and skull. Photos by L.K. Marsh.

Figure 38. Captive (a) adult male and (b) female *Pithecia inusta* at Leyendas Zoo, Lima, Peru. Photos (a) L.K. Marsh and (b) R.A. Mittermeier.

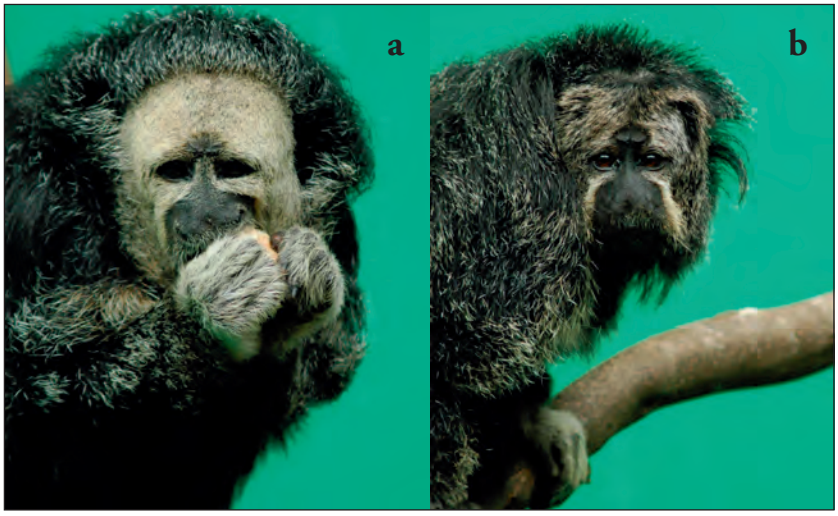


Figure 39. Captive (a) juvenile male and (b) juvenile female *Pithecia inusta* at Leyendas Zoo, Lima, Peru. Photos by J. Vermeer.

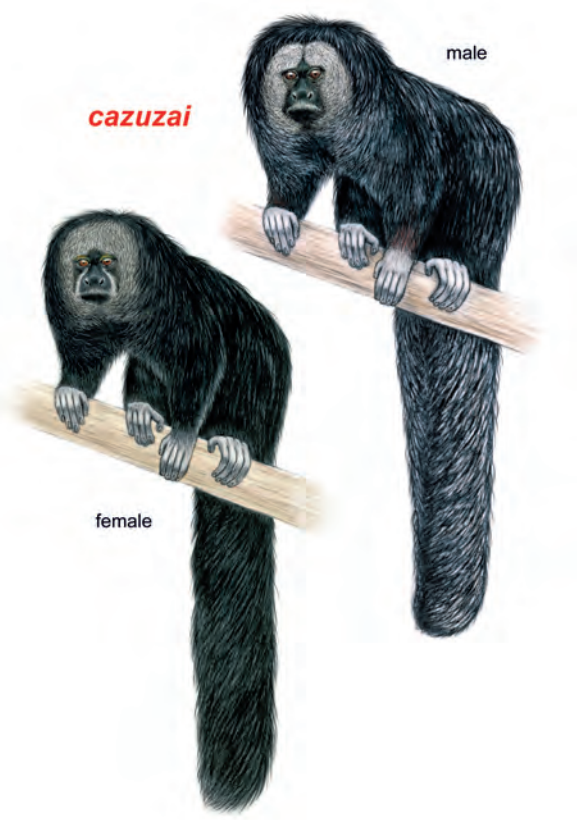
Map 6. Geographic distribution of *Pithecia inusta*, including populations in the Río Pachitea, Peru and Rio Juruá, Brazil.

Brazil
1. Rio Juruá, Igarapé do Gordão
2. Rio Juruá, Igarapé Grande
3. Rio Juruá, formerly João Pessoa (presumed; Olalla 1936 Expedition)
4. Porto Saids, Acre
5. Porongaba, Acre

Peru
6. Tabalosos
7. Sarayacu, Olalla camp May-June 1927
8. Sarayacu, Olalla Camp Mar-5 May 1927
9. Sarayacu, Olalla camp Aug 1927
10. Bomba/Rio Bomba
11. Cerro Azul?
12. Contamana
13. Río Pisqui
14. Pucallpa
15. Maisisa
16. Tushemo
17. Boca Río Pachitea
18. Montealegre (approx.)
19. Río Llullapichis
20. Río Llullapichis, Est. Biol. Panguana
21. Río Utiquinea
22. Puerto Victoria
23. Pto. Pachitea
24. Cumeria
25. Río Pichis (right bank), Nevati Mission approx.
26. Chicosa
27. Lagarto (approx.)
28. Boca Río Urubamba
29. Río Inuya

CAZUZA'S SAKI

Pithecia cazuzai sp. nov.



Synonymy

1987 *Pithecia irrorata* Hershkovitz, P. *Am. J. Primatol.* 12: 42426, in part.

Etymology. The name was selected for a respected, world-renowned Brazilian primatologist, Dr. José de Sousa e Silva-Júnior ("Cazuza"), who has worked many long years at the Museu Paraense Emílio Goeldi in Belém, now as the Curator of Mammals, where he continues to contribute significantly to South American mammalogy and taxonomy.

Holotype. Subadult male, Museu Paraense Emílio Goeldi No. 37127, skin and skull. Collected by J. Urbechi in *várzea*, 30 June 2004. Prepared by Arlindo Jr., J. Muniz, and R. R. Silva.

Paratypes. Adult female MNRJ 21055 skin and skull, 28 July 1948, no collector information, but was part of a yellow fever study, "MES Serviço de Estudos e Pesquisas sobre a Febre Amarela." Large juvenile female MNRJ 3312, skin only, collected by C. Lako, 20 Sept1927.

Type locality. Holotype. Uarini, "margem esquerda médio rio Solimões, comunidade Barroso – Reserva de Desenvolvimento Sustentável Mamirauá." Paratypes. Fonte Boa, Rio Solimões, Amazonas.

Specimens examined. Three (holotype and paratypes), and a photo of a living captive adult male taken in Brazil by www.tatamazonstock.com and wild adult male by Filipe Ennis.

Description. Both males and females are very plain in their overall pelage with very short, light to absent white grizzling on the tips of their dorsal hairs.

Males. Dorsal hairs black with just the tips dotted in white. Slightly more grizzling over the shoulders and arms, with the white being slightly longer and more extensive. The chest is bare with sparse black hairs, including a minimal black ruff under the bare throat patch. Belly appears to be without pigmentation in the prepared specimen (subadult). The arms have brown cuffs at the wrists extending in a brownish 'V' down the backs of the hands. On the ankles, there is also a brown cuff ring on top with a less extensive brown 'V' down the feet. The hands and feet are off white, largely because they are grizzled with brown/black hairs. The skin on the face of the adult male is black; in the subadult it is black over the nose and muzzle under the chin with a black diamond in the center, otherwise the skin is unpigmented or possibly pinkish. White hairs form a loose arch over the forehead and down the sides of the face. It does not appear adpressed (based on the live photo), but nonetheless is still sparsely haired and the skin (black or unpigmented) shows through it. In both subadults and adults, there is a distinct line through the centerline of the forehead, in adults it is black skin and in subadults it is unpigmented or pinkish. White malar lines are likewise sparse and thin, but the hair continues up under the eyes. The hair on the lips is white, stiff, and quite thick.

Females. The dorsal pelage is similar to that of the males in that it is black with only sparse white grizzling throughout and only on the very tips of the hairs. Older females may be slightly more grizzled, in particular on the forearms and upper shoulders. The hands and feet are white with only very slightly brownish cuffs on the wrists, without a 'V' onto the backs of the hands, but with a slight 'V' on the feet. The undersides are barely covered in fine black hairs, with a short dark brown ruff with tannish tips. The hair on the head is in a white arch, and while slightly denser and longer than in males, it is still sparse enough to see the facial skin beneath it. The white band dips a bit above the eyes making a diamond in the forehead showing off the

bare skin in the middle. The arch peters out below the ears where it is black and white along the sides of the face. The facial skin is black, except for the area just above the eyes where either eyelids or the skin is unpigmented or pinkish. Malar lines are thick, white, and obvious. Lips are lined in white hairs like the males, but are not as dense. Subadult/juvenile females are slightly transitional in that they are more grizzled dorsally, have a lighter tan/brown ruff, have a whiter facial arch that covers most of the face to the chin, obvious malar lines as in adults, but pinker or less pigmented facial skin overall.

Diagnosis. These distinct sakis differ from *P. pithecia* in that the males are not silky black, they are coarsely black with very light tips of white throughout, a short, dark black ruff, and faces with such a diffuse white ring that they are easily distinguished not only from *P. pithecia*, but from all others with white facial hairs, especially *P. aequatorialis* which is very grizzled and with a bright orange ruff. They share thick lip hairs with *P. hirsuta* and *P. chrysocephala* to the north and northeast of the Rio Amazonas, but differ significantly from both of those species in that they lack the agouti faces of *P. hirsuta* males and the orange/ochre faces of *P. chrysocephala*. The females of this new species are unlike any others in the region, including *P. monachus* and *P. albicans,* where *P. monachus* females have brown-white shaggy faces and *P. albicans* have distinct orange pelage and very short white adpressed hairs covering their faces.

Measurements. See Table 16.

Distribution. Map 7. Appendix I. Not well known, more information is needed. Only in Brazil, and so far only in very northern sections south of the Rio Solimões on either side of the Rio Juruá at Fonte Boa and Uarini.

Discussion. It is never an easy decision to add a new species based on so few specimens. However, upon discovering what is evidently a living representative, I was compelled to call out these unusual animals as distinct.

Table 16. Measurements of the holotype and paratypes: skin and skulls.

Measurement	Male MPEG 37127	Female MNRJ 21055	Large juv. female MNRJ 3312
Skull (mm)			
Length of brain case	83.5	82.3	–
Width of brain case	43.6	43.2	–
Zygomatic arch width	60.9	52.6	–
Orbits – outer	45.7	43.0	–
Nose bridge	6.7	6.7	–
L-orbit inner width	18.6	15.2	–
L-orbit inner height	18.3	16.4	–
Muzzle width	26.5	23.3	–
L-mandible length	52.0	50.6	–
L-mandible height	36.3	37.8	–
Post-crania (mm)			
Head-body	600	350	480
Tail	300	430	490
Hind foot	115	–	–
Ear	34	–	–
Weight (g)	3200	2750	–

Map 7. Geographic distribution of *Pithecia cazuzai*.

Brazil
1. Fonte Boa
2. Uarini
3. Mamirauá Reserve

Figure 40. *Pithecia cazuzai*, holotype subadult male MPEG 37127.

Figure 41. *Pithecia cazuzai* skull of holotype MPEG 37127.

Figure 42. *Pithecia cazuzai*. Photo of a living male (www.tatamazonstock.com).

Figure 43. *Pithecia cazuzai* adult female MNRJ 21055 full body and detail.

Figure 44. *Pithecia cazuzai*. Adult female MNRJ 21055 skull.

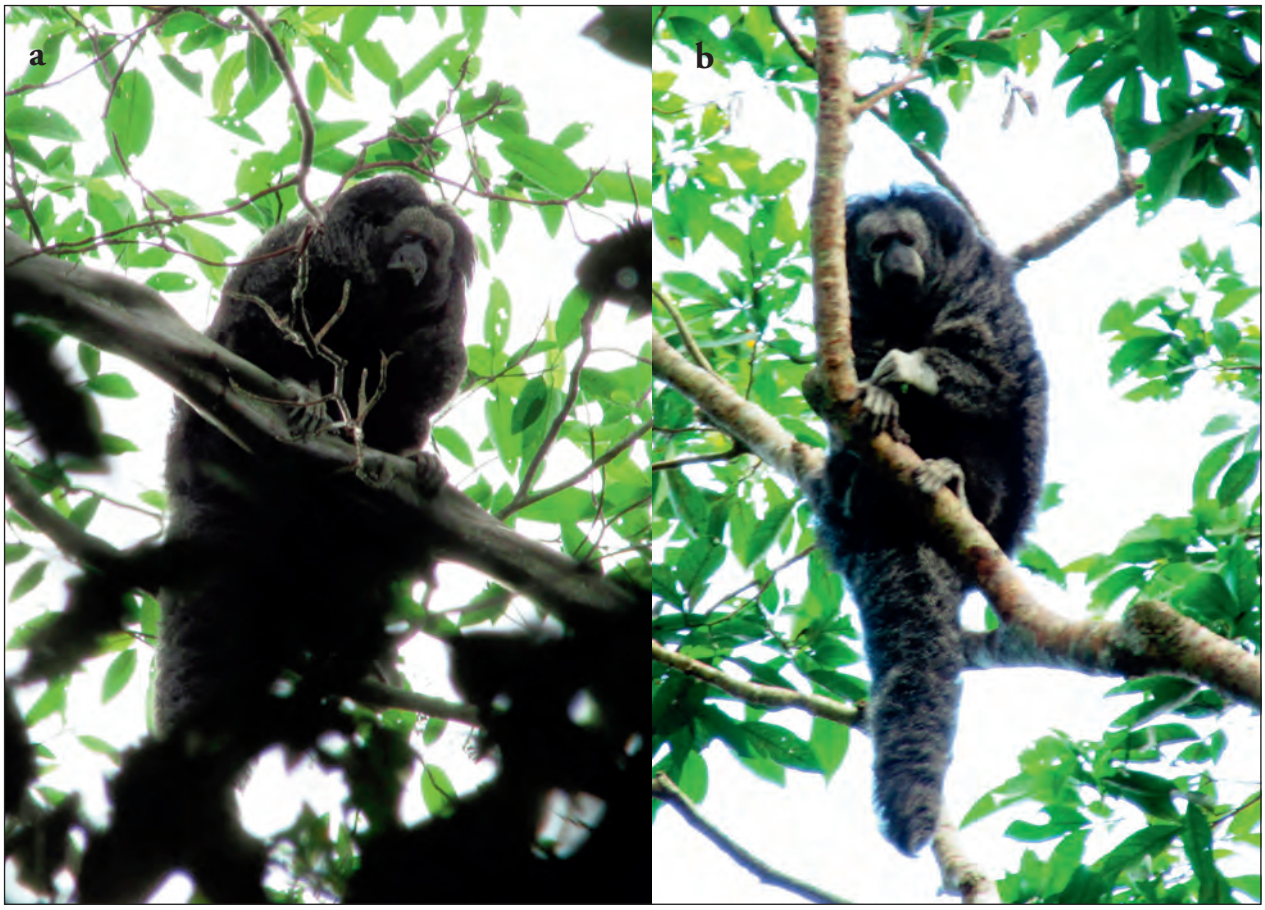


Figure 45. Wild (a) male and (b) female *P. cazuzai* in the Mamirauá Reserve for Sustainable Development, north of the Rio Solimões, Brazil. Photo by Felipe Ennes.

EQUATORIAL SAKI

Pithecia aequatorialis (Hershkovitz, 1987)

Synonymy

1987 *Pithecia aequatorialis* Hershkovitz, P. *Am. J. Primatol.* 12: 429.

Holotype. FMNH No. 86992, adult male, skin and skull, collected by C. Kalinowski, 3 October 1956.

Topotype. FMNH No. 86994, adult female, skin and skull, C. Kalinowski,

9 October 1956.

Paratypes. Three males: adult FMNH No. 86991, adult FMNH No. 86993, and subadult FMNH No. 86996, skins and skulls, all collected by C. Kalinowski in October 1956.

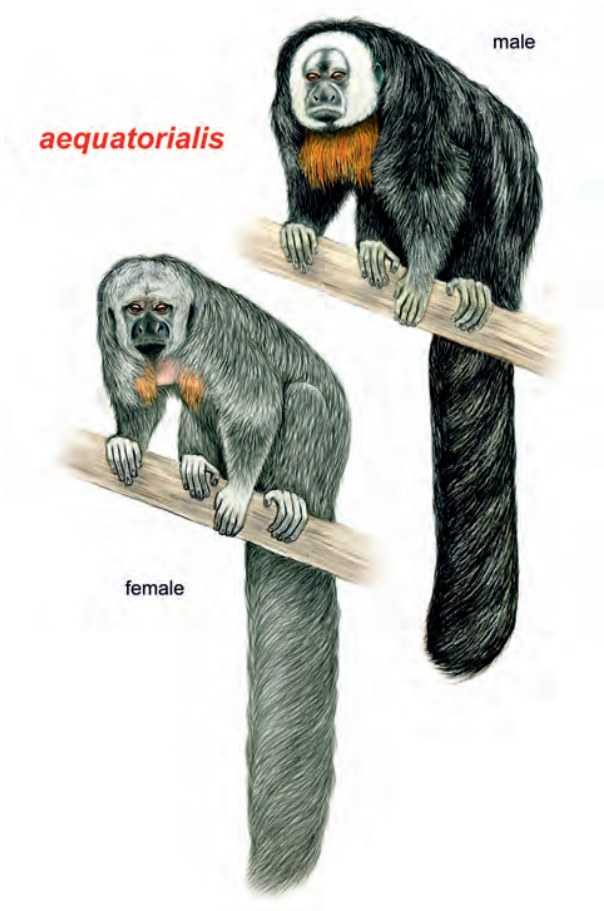
Type locality. Peru, Loreto District, Río Nanay, Santa Luisa, 160 m; for holotypes and paratypes.

Specimens examined. Twenty skins and skulls; captive photo references from M. Bowler and R.A. Mittermeier; wild photo references from R. Aquino, F. Cornejo, and tourist photos online; and observations in the wild by L.K. Marsh (Monkey Island and Pilpintuwasi, Iquitos, Peru).

Description. Males and females are dichromatic (cf. details in Hershkovitz, 1987).

Males. Have a black pelage overall with long grizzled white tips to the hairs, and chest hair bright orange to ochraceous extending below the armpits and along the sides in a ruff. The hands and feet are white. The faces of the males are black with a dense white horseshoe band of hair around face. The band is adpressed in the holotype, but appears much thicker on living animals. There are two often distinct, white patches above each eye that connect to the white band around the face. They have white malar lines around the muzzle and white lip hairs. Juvenile and infant males have very distinctly white heads with the adult coloration apparent even when very young.

Females. Overall pelage grizzled grayish over black producing an overall grey look. They have an orange ruff that can be as distinct as males, even in juveniles, but not as extensive. Forearms have short brown hairs amongst the black and white. Hair around the face is in a loose grayish white band, shaggier and less formed than in males, with distinct white muzzle lines. The skin of the nose and muzzle is black. Hands and feet are white.



Diagnosis. *Pithecia aequatorialis* males are distinct from *P. napensis* and *P. isabela* sp. nov. in the retention of a dense, fully white arch around the face and a very bright, extensive orange ruff on the chest in addition to the grizzled general body pelage. In *P. napensis*, the white of the face is only as eyespots above the eyes and as a "headband" between the ears over the crown. In *P. isabela* sp. nov. the white is focused primarily on the eyespots alone. While both *napensis* and *isabela* have varying degrees of orange ruffs, in neither is it quite as extensive as that of *P. aequatorialis*. Females of *aequatorialis* are distinct from females of both *napensis* and *isabela* in that they are far more white in the ring about the face and much greyer overall than either of the other two species. Juvenile males of all three are quite distinct from each other, with *P. aequatorialis* being the most obvious at a young age (Figure 51).

Measurements. See Table 17.

Table 17. Measurements for *P. aequatorialis* paratypes and topotype with body measurements for holotype.

Measurement	Male FMNH 86991	Male FMNH 86993	Male FMNH 86996	Female FMNH 86994
Skull (mm)				
Length of brain case	82.9	86.0	78.1	81.2
Width of brain case	46.9	47.9	45.0	45.8
Zygomatic arch width	57.5	57.7	51.7	54.7
Orbits – outer	41.9	42.7	42.6	42.1
Nose bridge	6.5	6.8	8.0	7.6
L-orbit inner width	16.9	18.5	16.8	15.8
L-orbit inner height	18.4	18.1	15.8	18.1
Muzzle width	24.0	24.2	22.1	23.1
L-mandible length	51.7	56.8	47.2	53.2
L-mandible height	33.23	37.6	32.3	36.8
L-canine length	13.3	11.0	10.9	10.8
Post-cranial (mm)				
Head-body	888	900	844	853
Tail	474	460	450	448
Hind foot	131	124	121	122
Ear	30	32	28	31
Holotype Male* FMNH 86992				
Head-body	870			
Tail	405			
Hind foot	121			
Ear	30			

* Skull measurements not available, cf. Hershkovitz (1987), Tables V, VIII, and XI.

Distribution. Map 8. *Pithecia aequatorialis* is found only in Peru, south of the Río Napo and south (left side) of the Río Curaray to the Río Tigre in the west (right bank). The northernmost border with *P. napensis* in this region is unknown. It occurs on both sides of the Río Amazonas at Iquitos, but those on the east side (right bank) are primarily rescues, pets, or escapees at or near Monkey Island Tourist Site or Pilpintuwasi Rescue Center. Additional living photo references are needed to confirm the location in Curaca Corriente in the Reserva Nacional Allpahuayo-Mishana, as the only reference photo to date is of a pelt made into a hat.

Specific Locations. Appendix I. PERU. *Loreto*: Puerto Indiana; Iquitos; Maynas – Río Nanay – Santa Luisa; north of Rio Tacshacurary – boca Río Machete; Río Napo – Río Tutapisco; Curaca Stream; Reservado Allpahuayo Mishana.

Discussion. All of the *P. aequatorialis* specimens referenced by Hershkovitz (1987) in Ecuador are *P. napensis*, except for AMNH No. 98468 from Bassler that Hershkovitz incorrectly assigned to the Río Coca, a northern tributary of the Río Napo in Ecuador. The original label says northern Peru and with further investigation this proved correct. Bassler's expedition was in northern Peru, January–December 1924, and this specimen was obtained between "Guamathra and ["S. Q."] Tutapischea", now Tutapisco. This information was obtained from the original expedition records transcribed by Schwartzer at AMNH (unpubl. data).

Aquino *et al.* (2009) studied *P. aequatorialis* in north-eastern Peru in the Río Itaya basin (Yanayacu, Seis Unidos, Nauta, Blanquillo), Río Tigre basin (Patria Nueva, Posayo, Coconilla), and the Río Curaray basin (Quebrada Arabela, Sector Curaray). Their observations extend the range of *P. aequatorialis* in Peru further south-west to between the ríos Tigre and Corrientes, and correctly exclude the area to the north between the ríos Curaray and Napo. I do not dispute their findings; however, they did not take any photographs or samples of the animals throughout their study making it difficult to corroborate this definitively—*Pithecia isabela* sp. nov. occurs west of the Río Tigre and south of the Río Marañón, and *Pithecia napensis* extends all the way south from Ecuador to north of the Río Marañón, and likely occurs also west of the Río Tigre watershed (cf. *P. isabela* sp. nov. and *P. napensis*).

The phenotypes of *P. aequatorialis* have seemingly changed over time as well. If one examines the specimens collected

by Kalinowski in the 1950s (and there are no other specimens that quite resemble these) with animals alive today, the types are more gracile with closely pressed facial hair; whereas, the present day animals appear to be heavier bodied, bulkier like *P. napensis*, with the white facial ring not closely adpressed as in the original specimens, but dense and thick and up off of the face—much more like the facial rings on *P. napensis*, only their white coloration is diffuse and only distinct on the crown (cf. *P. napensis*). At least per this study, it appears that those animals referred to *P. napensis* cover a very large territory; this of course may prove to be an artifact of needing more data on where to draw the lines between potential subspecies or color morphs, but *P. napensis* and *P. aequatorialis* probably have a hybrid zone somewhere that likely includes the region north of Iquitos/Puerto Indiana. Perhaps this is where we now get the bulkier, thicker white faces of *P. aequatorialis* today, or the more gracile, adpressed-faced animals of Kalinowski are distinct and will prove to be a separate population if they still exist.

Map 8. Geographic distribution of *Pithecia aequatorialis*.

1. Puerto Indiana
2. Mazan
3. Río Tutapisco
4. Río Tacshacurary/Rio Machete boca (approx.).
5. Río Nanay
6. Reserva Nacional Allpahuayo-Mishana
7. Nauta (approx. collection site near Nauta)
8. Santa Luisa (exact location unknown. Lower Rio Nanay near Rio Marañon; Stephens & Traylor 1983).

Figure 46. Vintage plate XXXII, 236 × 186 mm, of *Simia pithecia* Linnaeus (*Pithecia aequatorialis*) by Jacques de Seve in Schreber (1775), and (b) *Pithecia aequatorialis* original painting by Zorica Dabich and Philip Hershkovitz, through the courtesy of Field Museum of Natural History.

Figure 47. Skin, whole body and detail, of adult male holotype *Pithecia aequatorialis*, FMNH 86992.

Figure 48. Skull of adult male holotype *Pithecia aequatorialis,* FMNH 86992.

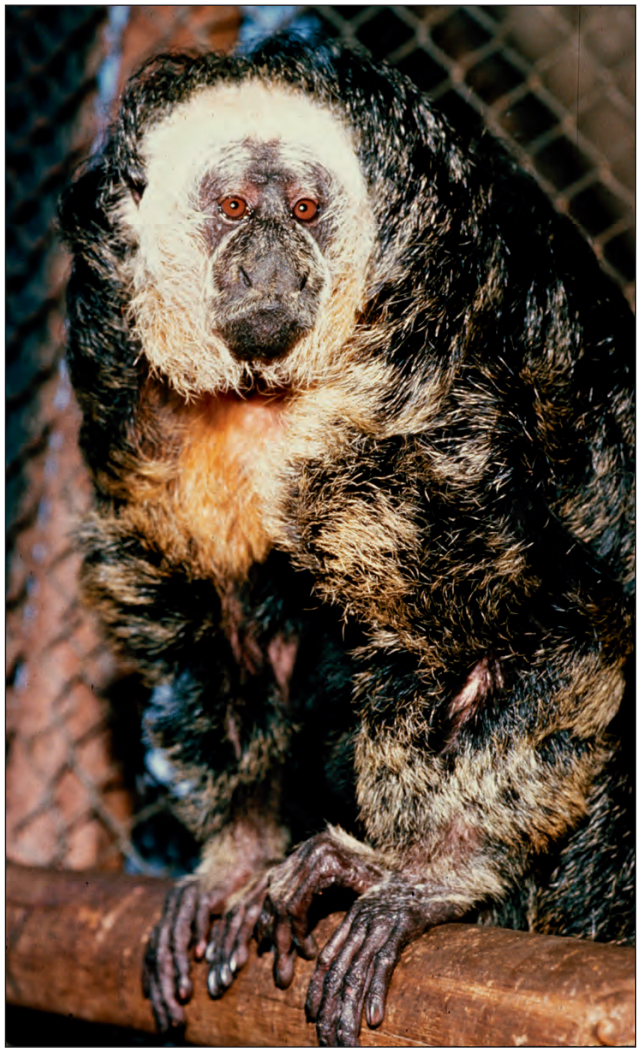


Figure 49. Captive male *P. aequatorialis*. Photo by R.A. Mittermeier.

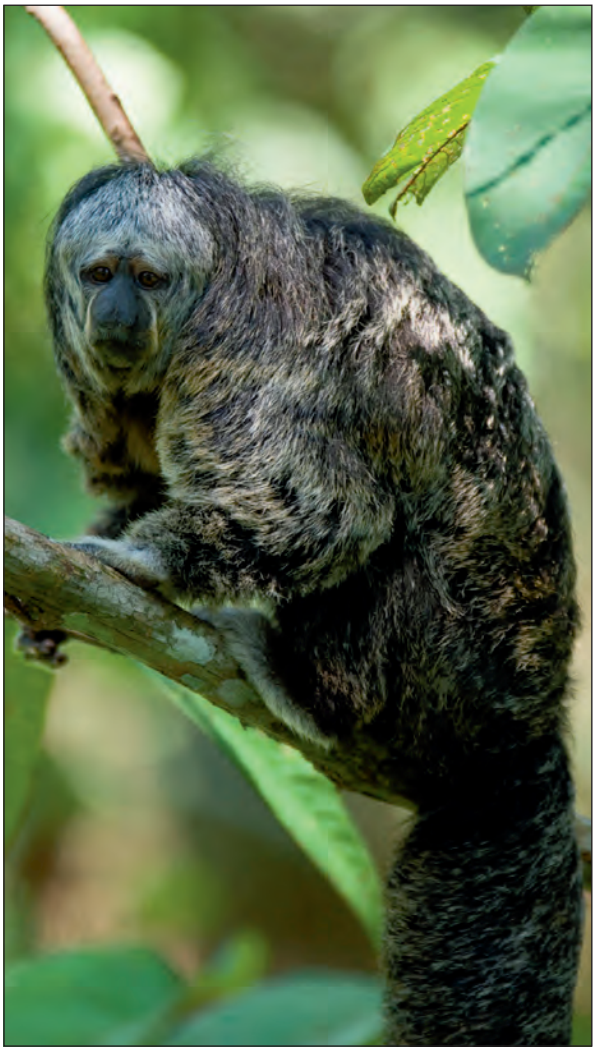


Figure 50. Captive female *Pithecia aequatorialis*. Photo by M. Bowler.

Figure 51. Captive (a) juvenile female and (b) infant/juvenile male *Pithecia aequatorialis*. Photos by M. Bowler.

NAPO SAKI

Pithecia napensis (Lönnberg, 1938)

Synonymy

1938 *P. monachus napensis* Lönnberg, E. *Arkiv f. Zoologi* 30A(18): 9.

1987 *P. monachus monachus* Hershkovitz, P. *Am. J. Primatol.* 12: 423-424. In part.

Holotype. Royal Natural History Museum, Stockholm (RNHM), No. A60-1921, subadult male, skin and skull, collected 13 January 1921 by L. Soderstrom.

Type locality. According to Lönnberg (1938), the type was collected in "Ecuador at Napo river at an altitude of 2000 feet [810 m a.s.l.]" which concurs with Hershkovitz's (1987) information (p. 424). However, the current label reads, "near Napo River and Curaray rivers, west below Macas, approx. 2000 ft, eastern Ecuador" which does not make sense as Macas is in the eastern foothills and the ríos Napo and Curaray are in the north-west. Male key specimen AMNH No. 36468, however, is reported from Baeza, Ecuador. at 3000 feet (914 m), which is not far from the upper reaches of the Río Napo (Allen, 1916), and perhaps is more like the original type.

Key specimens. Adult male, AMNH No. 36468, skin only, collected by W. B. Richardson 1912–1913, purchased from a native collector. Adult male, FMNH No. 41500, skin and skull, collected on 11 February 1922 by R. Olalla from Ecuador, Pastaza, Río Bobanaza, near Montalvo (250 m). BMNH No. 80.5.6.4 adult male, skin and skull, and BMNH No. 80.5.6.5 adult female, skin and skull. Other members of the same group and/or others from the same locale in Ecuador, Río Copataza, 80 miles south-east of Sarayacu: BMNH No. 80.5.6.6 small juvenile male; BMNH No. 80.5.6.7 small juvenile female; BMNH No. 80.5.6.8, large infant male; and BMNH No. 80.5.6.9 small infant male. All BMNH specimens were collected by C. Buckley between December 1877 and February 1878.

Specimens examined. Fifty-eight specimens, including skins and skulls, photographs of living animals from Ecuador and Peru, and observed in the wild in Ecuador by L. K. Marsh.

Description. *Males.* The most striking feature in the males is that the crown of the head is densely covered with short white hair. The facial disk of dense hair forms a partial disk of white that extends no further than the ears. The disk "fades" into white and gray-black stippling at the bottom. The males have white eyebrow patches leading into the crown that may be more or less distinct and typically blend into the solid white crown on older adults. The skin of the face is unpigmented except for the black nose and muzzle,

and appears it could be pinkish in some specimens, but is darker in living animals. Male *P. napensis* are large and "bulky" with white stippled pelage. They have an enlarged scent gland under the chin that is ringed on the upper chest to the armpits with noticeably bright orange to rusty hair. This coloration of the ruff is conspicuous even at a distance (pers. obs). Male dorsal body hair is black and grizzled with white tips. The amount and length of grizzling varies, but in general is longer on the tail than on the back or arms. Hair on the arms and legs is softer and shorter, and is grizzled on the arms, but not the legs. The hands and feet are white to off-white with hands typically whiter than the feet. The ventrum is mostly naked with sparse grayish-black hair that is light and wispy as it is in most saki species. Subadult males can appear at a distance to only have the white eyespots, but the haloing of the white headband between the ears is present.

Females. The dorsum of the females is black and stippled as in males, but appears grayish overall. The hands and feet are whitish to off-white as in males. The ruff on the females is dark brown with light tan to buffy tips. The facial hair is not short and dense forming a ring as it is in males, but is fine and covers the face, growing mostly downward. The

amount of white on and around the face varies with the age of the female, but is never as distinctly organized in a ring as it is in *P. aequatorialis* females. The facial skin is darker in general than in males, with areas of unpigmented, lighter skin. As in the males, there are distinct white malar lines from under the eyes that follow the curve of the muzzle and continue under the chin to form a half circle.

Diagnosis. Hershkovitz assigned this species to *P. hirsuta* in 1979 and *P. monachus* in 1987. Here, I elevate it to species rank. It was correctly described by Lönnberg (1938), although, because of the tenor of the times, he assigned it as a subspecies of *monachus* as *P. m. napensis*. However, it is nothing like *P. monachus* where the adult male faces are brown and not white. And while it is distinct from *P. aequatorialis*—which is not as bulky in the body, has a far more extensive orange ruff, has a clearly fully white, dense horseshoe ring around the face, and whose juvenile males and females are distinctly different than *P. napensis*—were *napensis* to be allied with another species, it would be this one. *Pithecia napensis* is most similar to *P. isabela* sp. nov., and sometimes the subadult males of *P. napensis* can look similar to adult males of *P. isabela*. But as in the differences in the juveniles of *P. aequatorialis* and *napensis*, the *isabela* juvenile males appear distinct from the others as well (cf. *P. isabela* sp. nov.). See also "Discussion" below.

Measurements. See Table 18.

Distribution. Map 9. In Ecuador, they are found south of the Río Napo from Coca in the west into Yasuní National Park to the east. The distribution along the Napo further east is not known although likely as populations have been sampled north of the Río Curaray as far south as the mouth where it meets the Río Napo. In the west, specimens have been collected in the foothills west of the Río Coca and west of the Río Napo in Baeza at 914 m and Estribaciones at 1500 m, south to the ríos Bobanaza, Copataza, Pastaza, and Macas in the Pastaza and Morona Santiago provinces.

In Peru, specimens are from the north bank of the mouth of the Río Curaray at the Río Napo. One was photographed by R. Aquino near the Ecuador border on the north bank of the Río Curaray and the left bank of the Río Nashiño. If a specimen from Parinari Caño is from Peru near present day Parinari, north of the Río Marañón (SEN No. 5305, collected on the Bluntschili and Peyer Expedition 24 September 1913, locally called "hirapu"), then *P. napensis* may extend all the way south to that river. And until there is further data to clarify, animals collected north of the Río Marañón and west of the Río Tigre will be classified as *P. napensis*, while those to the south will be grouped with *P. isabela* sp. nov. However, there are samples collected along the Marañón labeled with villages just north that may actually be *P. isabela* (cf. *P. isabela* sp. nov.). Sakis collected at the mouth of Río Santiago (right bank, along with

Table 18. Measurements for *Pithecia napensis* holotype and key specimens.

Measurement	RNHM 1921 Male	RNHM 1921‡ Male	FMNH 41500 Male	MHN 1932-2817 SA Female
Skull (mm)				
Length of brain case	80.0	84	85.3	82.1
Width of brain case	44.2	45	48.4	43.5
Occipito-nasal length	–	75	–	–
Condylobasal length	–	65	–	–
Zygomatic arch width	52.0	52	58.4	57.0
Orbits – outer	42.5	43	45.3	43.4
Nose bridge	5.7	–	7.2	--
L-orbit inner width	16.0	–	16.5	16.5
L-orbit inner height	17.7	–	18.5	17.2
Muzzle width	21.6	23	25.1	23.9
Maxillary row of cheek teeth length	–	21	–	–
L-mandible length	48.9	–	43.0	54.5
L-mandible height	35.5	–	35.1	36.7
Canine length	–	–	12.5	–
Post-crania (mm)				
Head-body	–	–	870	840
Tail	–	–	440	478
Hind foot	–	–	122	128
Ear	–	–	37	38

‡ Measurements reported by Lönnberg (1938).

Puerto Melendez) will be likewise listed as *P. napensis* until further data are obtained.

Specific locations. ECUADOR. *Napo*: Baeza; Río Pastaza. *Orellana*: Estribaciones; Río Napo; Río Curaray; Macas; Río Cononaco; Yarina; Pamiwa Cocha – Estirão do Equador south Villa Yuca; Río Shiripuno; Yasuní National Park; Napo Wildlife Center; Tiputini Biodiversity Station; Río Maccas. *Pastaza*: Sarayacu; Río Bobanaza; Montalvo; Río Copataza. *Morona Santiago.* PERU. *Loreto*: Boca Río Curaray; Puerto Melendez; Río Tigrillo; Río Marañón. *Amazonas*: Río Santiago; Río Caterpiza – Villa Huambisa.

Discussion. Heymann *et al.* (2002) report on their survey results from the Río Curaray: "We saw […] *Pithecia monachus* only north of the Curaray […] and *P. aequatorialis* only south of the Curaray. The two species of *Pithecia* differ in the distribution of white hair in adult males. In *Pithecia aequatorialis*, the forehead and lateral parts of the face are completely white; in *P. monachus*, white hair is restricted to irregularly formed patches on the forehead, more similar to the individual in Fig. 16 of Hershkovitz (1987), than to the holotype in his Figs. 22 and 23." (p.195). This confusion from Hershkovitz is now corrected with this publication (also see "Introduction, Table 2"), where north of the Curaray we have *P. napensis*, and south *P. aequatorialis*; *P. monachus* is far to the east (cf. *P. monachus*).

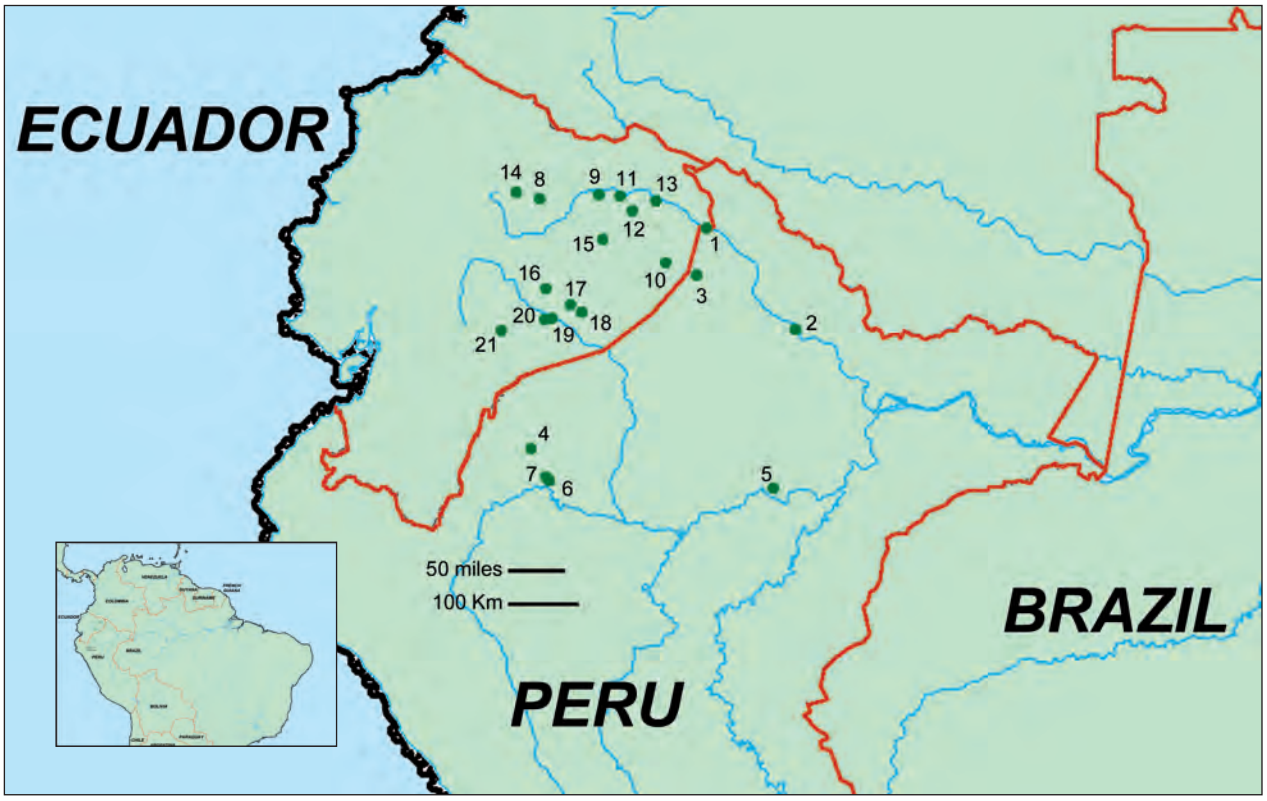
There is a mounted specimen in the Museo Amazónico, Quito, Ecuador, that appears intermediate between *P. aequatorialis* and *P. napensis.* It was collected by Shur/Achuar Indians, reported to be from Ecuador, southern Morona Santiago Province. This male has a diffuse white facial ring and less defined eyebrow spots, and is large and bulky, more like *P. napensis*. As there are few similar specimens, it is unclear if this race is a variation of either *P. napensis* or *P. aequatorialis*, is a subspecies, true species, or simply a color variation of *P. napensis* as the males age where the white becomes more extensive (as it is here presumed). More research on animals in this region is needed.

Subadult male *P. napensis* can appear very similar to adult males of *P. isabela* sp. nov. It will be particularly important to sort out animals in the northern Río Marañón, the lower Río Tigre (left bank), and west to Río Santiago to determine where *P. napensis* and *P. isabela* sp. nov. share a border, if they do, north of the Río Marañón. Animals from the Río Santiago region, including those from the Río Caterpiza (MVZ Nos. 157794, 1557795) appear to be closer to *P. isabela* sp. nov. than *P. napensis*, in particular in the females. They may prove to be different species or subspecies, or included in either *P. isabela* sp. nov. or *P. napensis* as color variations.

Hershkovitz (1987) included a specimen (AMNH No. 71817) collected by "Olalla y hijos, 19 January 1926, from Ecuador, Boca Lagarto Cocha" (labeled Peru, but it is right on the border so could be either) in *P. aequatorialis*, but it is a specimen of *P. napensis*. What is curious about this specimen is exactly where the Olallas may have collected it. Credited with the same location, AMNH No. 71816, is a juvenile male *P. milleri*, (cf. *P. milleri*, "Discussion"). North of the Napo and certainly north of the Río Aguarico is *P. milleri* territory, and no other *P. napensis* specimens have been cited there (per this study). As the Olallas were coming up from the Boca Curaray collection site around that time (Wiley 2010) and had another *P. milleri* in tow (AMNH No. 71802), it is possible they collected it en route on the southern side of the Napo, or it is possible there are *P. napensis* at the confluence of the ríos Napo and Aguarico near the Peru border. More data needs to be gathered in this region.

There is a Bassler Collection specimen: AMNH No. 98472, an adult male *P. napensis* without location data on the label. However, per his collection records and the number, it is likely to be an animal he collected near the mouth of the Río Santiago (unpubl. Bassler Collection records, AMNH). But that location is another "collector's catch-all" of species making it unclear where the specimen was actually from.

Figure 52. *Pithecia napensis* holotype skin, whole and detail, RNHM (Stockholm) No. A60·1921, subadult male.



Map 9. Geographic distribution of *Pithecia napensis*.

Peru
1. Near Nashiño (R. Aquino sighting)
2. Río Curaray, Boca Curaray
3. Between ríos Curaray and Nashiño (R. Aquino sighting)
4. Río Caterpiza
5. Parinari (unknown if correct location for "Parinari Cano," Bluntsali-Peyer Expedition 1913)
6. Puerto Melendez
7. Bazea

Ecuador
8. Estribaciones
9. Yarina Eco Lodge
10. Río Cononaco, Yasuní National Park
11. Napo Wildlife Center
12. Tiputini Biodiversity Station, Yasuní National Park
13. Yuturi Tourist Lodge
14. Río Santiago, Boca Río Santiago
15. Shiripuno Lodge
16. Sarayaku
17. Río Bobanaza
18. Montalvo
19. Río Copataza
20. Río Pastaza
21. Macas

Figure 53. *Pithecia napensis* holotype skull, RNHM (Stockholm) No. A60·1921, subadult male.

Figure 54. Key specimens: (a) AMNH No. 36468, adult male, and (b) adult female (top) No. BMNH 80.5.6.4 and adult male (bottom) No. BMNH 80.5.6.5.

Figure 55. *Pithecia napensis* males: (a) wild in the Napo Wildlife Center, Yasuní National Park, Ecuador, photo by Carol Foil; and (b) captive in Ecuador, photo by R.A. Mittermeier.

Figure 56. (a) Subadult female *Pithecia napensis* pet at the Añangu Community village near the Napo Wildlife Center, Ecuador. Photo by Max Feingold and (b) wild large juvenile male *Pithecia napensis* at Tiputini Biodiversity Station, Ecuador. Photo by L.K. Marsh.

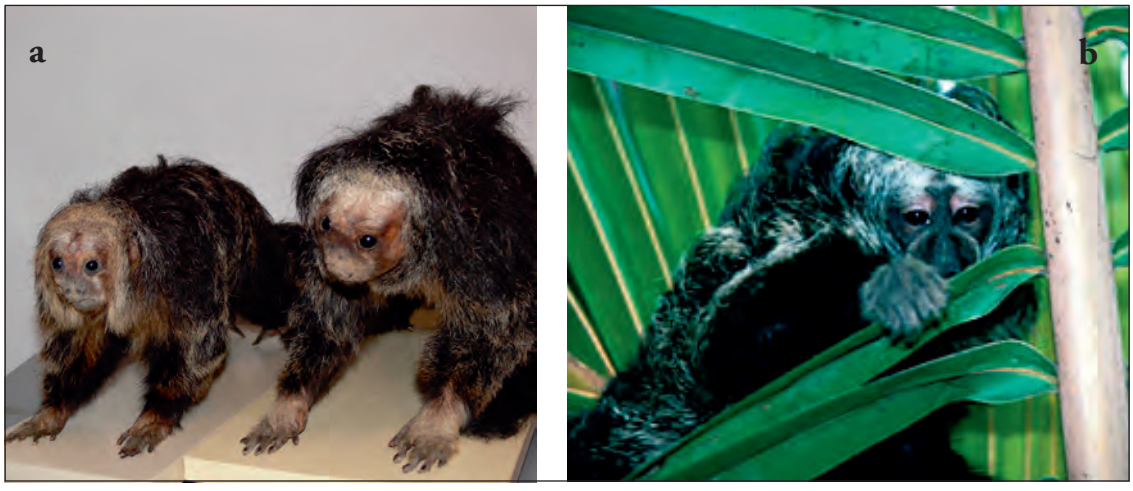


Figure 57. Juvenile male *Pithecia napensis*: (a) mounted specimens, NNNM, Leiden collected by C. Buckley, 1880, Río Copataza, Ecuador, photo by L.K. Marsh, and (b) living rescued juvenile male, photo by B. Junek.

ISABEL'S SAKI

Pithecia isabela sp. nov.

Synonymy

1987 *P. monachus monachus* in Hershkovitz, P. *Am. J. Primatol.* 12: 422–424. In part.

Holotype. FMNH No. 87001, adult male, skin and skull, collected by C. Kalinowski on 25 November 1956.

Paratypes. Subadult male, skin and skull, FMNH No.122796, collected by P. Hershkovitz, 24 November 1980. Adult male, skin and skull, SEN No. 5304, "Uapu", collected by Bluntschili and Peyer, 27 August 1912. Adult female, skin only, FMNH No. 86999, collected by C. Kalinowski, 24 November 1956. Subadult female, FMNH 122797, collected by P. Hershkovitz, 30 November 1980.

Etymology. The species is named for an aristocratic colonial Peruvian (*recte* Ecuadorian) woman named Isabel Grameson Godin des Odonais (Isabel Godin). In 1768, after a 20-year separation from her husband Jean Godin, a cartographer on Charles Marie La Condamine's historic expedition to measure the equator, she mounted an expedition to French Guiana to rejoin him. Her Indian porters, personal African slaves, young Quichua handmaidens, two brothers, a seven-year old nephew, and other travelers amounting to a total of 41 people struck out to cross the Amazon starting from the Río Bamba in the Andes. In less than a month, all of the members of her party either abandoned her or died leaving Isabel alone to struggle in the rainforest for 28 days. She was eventually found by Quichua Indians, who nursed her to health and took her downstream to Andoas, where the priests sent her through the mission system via the ríos Marañon and Amazon. She eventually reached her husband in French Guiana, where they had a happy reunion. Isabel's story of courage and strength is an amazing piece of South American history that absolutely needed proper recognition.

Type locality. The holotype is from Peru, Loreto, along the Río Samiria at Santa Elena (130 m above sea level). The paratypes are all from the region of the Río Samiria with FMNH Nos. 122798 and 122797 in the Reserva Nacional de Pacaya-Samiria (Base Atun and Biological Station "Pithecia") and FMNH No. 86999 from Santa Elena.

Specimens examined. Ten skins and skulls, photos of live sakis from M. Bowler, and photos by tourists along the Río Samiria and in the Reserva Nacional de Pacaya-Samiria.

Description of male holotype. Overall the pelage is black with very light, short white stippling. The "hood" that forms in all sakis with the whirl of hair at the base of the neck is black with little or no stipples. The hands and feet are white with a distinct black "V" extending from the wrists and ankles down the backs of the hands/feet. The forearms have scant to light stippling, but more than on the hind limbs, which are nearly without stippling. The tail is lightly stippled in the manner of the dorsum. The facial disk is dense and dark agouti black to dark brown, with scant white throughout. The eyespots are long, more like stripes, and diffuse with a distinct line between them extending to the dark facial disk. There are white malar lines with some white hairs covering the nose. The skin of the face is black. The ruff is short, orange-ochre, and directly under the throat gland, which is not as distinctly colored as it is in other saki species.

General characteristics. *Males*. The pelts of some specimens appear coppery almost shiny. The dorsal hairs are black with light, diffuse, short stippling on the back and forearms, very little on the hind legs. The ventrum is sparsely covered with black hairs, the short ruff is on the upper chest right under the throat scent gland and is a dark rusty orange, often very dark, and not appearing more than brown. The hands and feet are white to off-white. White malar lines trace either side of the muzzle. The skin of the face is black, in both, dried specimens and living animals.

The facial ring is dark black in adult males and agouti brown in young males, with some light white sprinkled throughout in older animals, but the grizzling varies in intensity or is absent and is mostly sparsely restricted to the forehead if it occurs at all. The facial disk as a whole is dark at the base with light grizzling of whitish or grayish throughout, but lacks a distinct band of white as is seen in *P. napensis* or *P. aequatorialis* (cf. "Diagnosis"). The facial hair is short, dense, and straight, and is clearly separate from the hair on the head, with white eyebrow spots over each eye that vary from simple "dots" directly above the eyes (as seen in wild animals at present) to longer stripes up to the darker facial band (as in the holotype), to very diffuse, nearly patternless whitish patches above the eyes.

Females. Overall pelage is similar to males in that it is black, coppery almost in some specimens, with short, light grizzling throughout. There is slightly more grizzling in females than males, but distinctly less than in neighboring *P. napensis* or *P. aequatorialis*. The ruff is black with dark brown tips, also right under the throat, but females have a less distinct scent gland. The muzzle lines are thick and distinct and the facial skin is black. The facial disk is black and silky in young females, tighter and black-agouti brown in older females. Adults can have white possible in the facial disk, and with tiny white eyebrows and a small white star just above the eyes. The face is less white than in *P. aequatorialis* and *P. napensis* females.

Diagnosis. *Pithecia isabela* is most similar to *P. napensis*, with which it shares white patches above the eyes, but differs consistently in the amount of white on the forehead—where *napensis* is clearly dense and white on the crown and grizzled white throughout the facial disk, *P. isabela* is vastly more diffuse, with spots smaller and closer to the eyes, and little to no white grizzling around the rest of the face. *Pithecia napensis* is bulkier, larger, and has a brighter and more extensive orange ruff, whereas *P. isabela* has a shorter, darker brown-orange ruff that is occasionally a brighter shade. The males in particular are far less grizzled overall in *P. isabela*, and, in some cases, the grizzling appears nearly absent. *Pithecia isabela* obviously differs from *P. aequatorialis* to the north of the Río Marañón in that males have dense, fully white half-circles around their faces with extensive orange ruffs on their chests. Juvenile and subadult males are distinctly different from either *P. napensis* or *P. aequatorialis* of the same age. In *P. isabela*, the faces are plain except for the small white eyespots above the eyes and some diffuse white haloing along the crown. There is no obvious ruff color in the young animals and the grizzling across the back is nearly absent.

Measurements. See Table 19.

Distribution. Map 19. The species occurs only in Peru. The paratypes and most other specimens are from the Pacaya-Samiria region. The paratype was collected along the Río Samiria at Santa Elena. Additional specimens were collected similarly along the Río Samiria at the Base Atun and Estación Biológica "Pithecia." Mark Bowler reported the species along the Río Yanayacu. Tourist photos show them

Table 19. Measurements for *P. Isabela*, including holotype and paratypes.

Measurement	FMNH 87001 Male	FMNH 122796 Male	SEN 5304 Male	FMNH 86997 SAM	FMNH 86998 SAM	FMNH 86999 Female	FMNH 87000 SAM
Skull (mm)							
Length of brain case	79.7	79.0	83.7	84.1	79.2	80.3	78.8
Width of brain case	44.1	45.1	43.1	47.6	46.1	44.0	42.8
Zygomatic arch width	57.1	57.9	54.3	59.1	38.6	54.6	50.0
Orbits – outer	37.8	42.4	45.5	42.1	49.8	42.7	38.3
Nose bridge	6.5	7.3	0.72	7.5	5.9	6.8	5.9
L-orbit inner width	16.9	17.1	16.4	18.1	17.8	16.7	17.7
L-orbit inner height	17.8	17.4	17.3	19.4	17.8	17.6	16.9
Muzzle width	23.4	24.5	23.8	24.4	21.4	24.4	21.5
L-mandible length	50.9	49.9	52.0	53.3	44.9	50.8	49.8
L-mandible height	37.1	34.2	37.5	34.4	31.2	34.8	33.4
L-Canine Length	12.4	11.6	–	9.9	10.6	11.3	9.4
Post crania (mm)							
Total body	920	765	–	862	796	853	867
Tail	486	400	–	450	433	445	448
Hind foot	131	121	–	122	122	124	124
Ear	30	33	–	31	30	30	30

at Quebrada Sapote near the Ucayali, and collections by R. Olalla suggest they are near Sarayacu on the west side.

Specific distribution. Appendix I. PERU. *Loreto*: Río Samiria – Santa Elena, Biological Station "Pithecia", Base Atun; Pacaya-Samiria National Park; Río Yanayacu; Río Ucayali – Sarayacu.

Discussion. This species was originally recognized as distinct and suggested as a new species in 2002 at the Tiputini Biodiversity Station, Ecuador (Marsh, 2004), prior to research for taxonomic revision. In the course of time, the discovery of this new species led to a revision of the genus, and later to placing those in Ecuador with *P. napensis* upon review of the type specimen in Stockholm.

The Pacaya-Samira National Reserve has become a popular destination for tourists, particularly on riverboats out of Iquitos (for example, Dawn of the Amazon: http://www.dawnontheamazon.com or La Amatista, a boat run by International Expeditions: http://www.ietravel.com/central-south-america/amazon-river-cruises). As a result, numerous lodges have sprouted up, some with sakis as free-ranging pets. There is some photographic evidence per tourist photos in the region, particularly in the upper reaches of the Pacaya-Samiria near the south side of Nauta, that *P. aequatorialis* and perhaps *P. napensis* have been brought from the north side of the Río Marañón. It is unclear if these animals ever leave the facilities they were captured for, but if they do, there may be some interesting ramifications for the *P. isabela* in the area as time goes on.

In some photos by M. Bowler, females seem to be more similar to *P. napensis*, where overall pelage appears greyish with more stippling than males. Forearms and chest appear tan, mixed in with the greyish-black, and the hands and feet are white. Faces appear more gray, or at least, with more white mixed into the hair surrounding the face. It is possible it is the lighting or the way in which they were photographed that makes them look closer to *P. napensis* females as compared to the specimens. Bowler's photos were along the Río Yanayacu, very near to the Rio Marañón. It will be important to study animals throughout the Pacaya-Samiria to determine whether or not *P. napensis* has in fact established on both sides of the Río Marañon, and where the border with *P. isabela* lies.

Figure 58. *Pithecia isabela*. Holotype adult male, skin, FMNH 8700 I.

Map 10. Geographic distribution of *Pithecia isabela*.

Peru

1. Río Samiria, Santa Elena
2. Yanayacu
3. Nauta -- right bank
4. Río Samiria, Biological Station "Pithecia"
5. Río Samiria, Base Atun
6. Reserva Nacional Pacaya - Samiria
7. Quebrada Sapote
8. Sarayacu – left bank

Figure 59. *Pithecia isabela*. Holotype adult male, skull, FMNH 87001.

Figure 60. *Pithecia isabela*. Adult female, skin, FMNH No. 86999.

Figure 61. Wild adult male *Pithecia isabela* in the Reserva Nacional Pacaya-Samiria: (a) photo by J. Vermeer, (b) photo by Wilderness Classroom.com.

Figure 62. Juvenile male *Pithecia isabela*, Reserva Nacional Pacaya-Samiria, Peru. Photo by Rick Thomas.

Figure 63. Adult female *Pithecia isabela*: (a) Río Yanayacu, photo by M. Bowler, and (b) Reserva Nacional Pacaya-Samiria, photo compilation by TrekNature.