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# The Taxonomic Status of Wied's Black-tufted-ear Marmoset, *Callithrix kuhlii* (Callitrichidae, Primates)

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**Abstract:** In this paper we provide a description of Wied's black tufted-ear marmoset, or the Southern Bahian marmoset, *Callithrix kuhlii* Coimbra-Filho, 1985, from the Atlantic forest of southern Bahia in Brazil. It was first recorded by Prinz Maximilian zu Wied-Neuwied during his travels in 1815–1816. Its validity was questioned by Hershkovitz (1977, *Living New World Monkeys [Platyrrhini]*, Chicago University Press, Chicago), who considered it a hybrid of two closely related marmosets, *C. penicillata* and *C. geoffroyi*. Vivo (1991, *Taxonomia de Callithrix Erxleben 1777 [Callitrichidae, Primates]*, Fundação Biodiversitas, Belo Horizonte), on the other hand, while demonstrating it was not a hybrid, argued that it was merely a dark variant of *C. penicillata*. We discuss a number of aspects concerning the taxonomic history of the forms *penicillata*, *jordani*, and *kuhlii* and the validity of the form *kuhlii*, examining the supposition that it may be a hybrid, besides the evidence concerning vocalizations, morphology, pelage, and ecology. We also discuss the use of the taxonomic category of subspecies to classify the different forms of the Atlantic forest marmosets, and the circumstances prevailing for the correct assignment of the authorship of the name *kuhlii*. We conclude that *Callithrix kuhlii* is a distinct and valid taxon, today restricted to the Atlantic forest between the Rio de Contas and Rio Jequitinhonha in southern Bahia, Brazil.

**Key Words:** Primates, Callitrichidae, *Callithrix kuhlii*, marmoset, Atlantic forest, Brazil

## Introduction

The marmosets—small, gum-eating, frugivore-insectivores of the family Callitrichidae—comprise a remarkable radiation of (currently) 14 “Amazonian” species, genus *Mico*, which range south of the Rio Amazonas and east of the Rio Madeira, south through eastern Bolivia to the north-eastern chaco in Paraguay, and six “eastern Brazilian” species, genus *Callithrix*, occurring through a large part of the Atlantic forest and central savanna (Cerrado) in Brazil, north from the basin of the Rio Paraíba do Sul in the state of São Paulo to the interfluvium of the Rios Mearim and Itapecurú in the state of Maranhão (Rylands *et al.* 1993, 2000, in press; Silva Jr. 1999).

In his major revision of 1977, Hershkovitz recognized just one species of marmoset in the Atlantic forest, *Callithrix*

*jacchus*, with five subspecies: *jacchus*, *penicillata*, *geoffroyi*, *flaviceps*, and *aurita*. These he referred to as the “Jacchus” group, or tufted-ear marmosets; as opposed to the “Argentata” group, which consists of the bare-ear marmosets, *C. argentata* (with three subspecies), and the tassel-ear marmosets, *C. humeralifer* (also with three subspecies). Seven more Amazonian marmosets have been discovered since then (Ferrari and Lopes 1992; Alperin 1993; Silva Jr. and Noronha 1998; Van Roosmalen *et al.* 1998, 2000), and taxonomic treatments subsequent to Hershkovitz (1977) have opted for the classification of all forms as distinct species (Mittermeier and Coimbra-Filho 1981; Mittermeier *et al.* 1988; Vivo, 1991; Groves 1993, 2001, 2005; Rylands *et al.* 1993, 2000, in press).

Coimbra-Filho (1971) considered that the Atlantic forest marmosets recognized by Hershkovitz (1977) should be treated as full species and not subspecies of *C. jacchus*. He

also pointed out that there were two distinct subspecies of the black tufted-ear marmoset, *C. penicillata* (see also Coimbra-Filho and Mittermeier 1973). The nominate subspecies (*penicillata* [Humboldt, 1812]) Coimbra-Filho and Mittermeier (1973) ascribed to the coastal forest of southern Bahia, and the other (*jordani* Thomas, 1904) to the marmosets occurring inland in central and south-east Brazil. Hershkovitz (1975, 1977) discussed the arguments of Coimbra-Filho (1971) and Coimbra-Filho and Mittermeier (1973) at length, and concluded that the form in southern Bahia was first described by Prinz Maximilian zu Wied-Neuweid (1826), as *Hapale penicillatus Kuhlii* [sic], but was in fact nothing more than a hybrid between *penicillata* and the white-faced marmoset, *C. j. geoffroyi*, to the south. Mittermeier and Coimbra-Filho (1981) insisted that what they then referred to as *C. penicillata kuhlui* was in fact a valid form and possibly even a valid species. Mittermeier *et al.* (1988) maintained that the marmoset in southern Bahia was distinct, and a “good” species, *C. kuhlui*. Vivo (1991) reviewed the systematics of the marmosets and concluded that they should all be considered species, but that the form *kuhlui*, though not a hybrid, was a junior synonym of *C. penicillata*.

In this paper, we discuss a number of aspects concerning the taxonomic history of the forms *penicillata*, *jordani*, and *kuhlui* and the validity of the form *kuhlui*, examining the supposition that it may be a hybrid, besides the evidence concerning vocalizations, morphology, pelage, and ecology. We also discuss the use of the taxonomic category of subspecies to classify the different forms of the Atlantic forest marmosets, and the circumstances prevailing for the correct assignment of the authorship of the name *kuhlui*.

### ***Simia penicillata* Humboldt, 1812 and *Hapale penicillata jordani* Thomas, 1904**

Humboldt (1812) described *Simia penicillata*, attributing authorship of the specific name to É. Geoffroy St. Hilaire. Geoffroy St. Hilaire (1812) described *Jacchus penicillata*, but published his monograph a few months after that of Humboldt, who placed it as a junior synonym. The author of the name *penicillata* for this species is, therefore, given to Humboldt, but its source should be sought in É. Geoffroy St. Hilaire (1812) (Hershkovitz and Rode 1947). The type, from “le Brésil,” was collected by Alexandre Rodrigues Ferreira between 1783 and 1792, and taken from the Museu Real d’Ajuda, Lisbon, by É. Geoffroy Saint Hilaire in 1808 following Napoleon Bonaparte’s conquest of Portugal (Carvalho 1965; Hershkovitz 1977). Although the type no longer exists (Elliot 1913), the possibility that *Simia penicillata* Humboldt was the form from southeast Bahia is denied in the original description by St. Hilaire (taken from Carvalho 1965):

“2. Pinceau (noir). *Jacchus penicillatus* Geoff., 1812: 119. (Pelage cendré: croupe et queue annelées de brun et de cendré: une tache blanche au front: un pinceau de poils noirs et très-longs devant les oreilles: la tête et le haut-col noirs.)”

The key features are the black head and neck (collar) and the ash color of the general pelage, not features of the marmosets from southeast Bahia. According to Vivo (1991), Spix (1823) was the first to provide a more precise locality for *Simia penicillata*—forest of low altitude in Minas Gerais. Wied-Neuwied (1826) subsequently reported *Hapale penicillatus* from southeast Bahia, giving the localities of Belmonte, Rio Pardo, and Ilhéus. Ávila-Pires (1969) pointed out that Schlegel (1876) had noted that forms from the coast (eastern Bahia) were different from those inland, but made no further inferences or comments. Hershkovitz (1977) and Vivo (1991) relate the subsequent taxonomic history of *penicillata* during the 19th century, including proposals by some authors for its synonymy, variously with *C. geoffroyi* or *C. jacchus*.

In 1901, Thomas reported on a series of skins, collected from May to July in the same year by Alphonse Robert, from the Rio Jordão, Minas Gerais. Thomas (1901) identified them as *Hapale penicillata*. Based on this material, however, Thomas (1904) subsequently described *Callithrix penicillata jordani*: type locality Araguari, Rio Jordão, Minas Gerais, 700–900 m [Ribeirão Jordão is a left bank (south) affluent of the upper Rio Paranaíba, in its upper reaches, near to the town of Araguari, 18°30’S, 48°08’W]. The holotype, an adult female (1901.11.3.9), and six paratypes, are in the British Museum (Natural History), London (Napier 1976). Thomas (1904) also described *C. p. penicillata* from “Lamarão, near Bahia,” based on a series of nine specimens in the British Museum collected by Alphonse Robert in May and June 1903 (see Napier 1976; accession numbers: 9.5.8–15 and 9.5.160). Rode and Hershkovitz (1945) interpreted this as a restriction of the type locality, and this was maintained by recent authors (Cabrera 1958; Hill 1957; Ávila-Pires 1969; Hershkovitz 1975, 1977).

Rode and Hershkovitz (1945) designated as a lectotype for *Jacchus penicillata* a specimen from Goiás in the Paris Museum. They retracted this two years later, however, because the individual selected was not one of the original series examined by É. Geoffroy St Hilaire, and was referable in fact to *C. penicillata jordani* Thomas, and therefore not even available as a neotype (Hershkovitz and Rode 1947).

The exact locality of “Lamarão, near Bahia” is uncertain. In the distribution map of Hershkovitz (1968, p.567), Lamarão is placed in the north-central region of the state of Bahia on the uppermost reaches of the Rio Itapicurú (locality 292 in Hershkovitz [1968, p.567], and listed as locality 292d, “Lamarão, upper Rio Itapicurú, 10°46’S, 40°21’W, 490 meters, *Callithrix penicillata penicillata*, A. Robert, May–June, 1903, at 300 meters” by Hershkovitz [1975, p.168; 1977, p.937]). Napier (1976, p.8) gave the coordinates for the type locality as “10°45’S, 40°20’W, 300 meters”, probably read from the map of Hershkovitz (1968). Kinzey (1982) gives the same coordinates as those of Hershkovitz (1977), which place this locality about 320 km northwest as the crow flies from Bahia, today the city of Salvador, capital of the state of Bahia. Vivo (1991) made no reference to the location of Lamarão.

We have been unable to identify, however, any reference to a “Lamarão” on the upper Rio Itapicurú (for example,

Brazil, IBGE 1972). A town called Lamarão, however, does exist on the railway line midway between the towns of Água Fria (south) and Serrinha (north), 11°45'S, 38°53'W, northwest of Salvador, about 140 km as the crow flies (Vanzolini and Papávero 1968; Brazil, IBGE 1972). Paynter and Traylor (1991) also give this as the locality that Alphonse Robert visited in 1903: "Lamarão, Bahia, 291 m, on railroad 140 km NW of Salvador, eastern Bahia." An atlas in the British Museum (*Stieler's Hand-Atlas*, Gotha: Justus Perthes, 1905) was used by Oldfield Thomas, and contains numerous annotations in his own hand. He underlined this town of Lamarão, indicating the probability that this is the correct locality where Alphonse Robert collected the series of *C. penicillata* that he studied, although it will be necessary to check whether any field notes or publications of Robert himself might clarify the exact locality and the origin of that designated by Hershkovitz (1968, 1977).

The region immediately north of Salvador is referred to as the Recôncavo da Bahia, and contains populations of *C. jacchus* as well as hybrids between *C. jacchus* and *C. penicillata* along a narrow zone about 50 km wide (see Hershkovitz 1977; Alonso *et al.* 1987). The forests of the entire region north of Salvador well into the state of Sergipe and along the Rio São Francisco suffered widespread destruction even in the early 1500s (Coimbra-Filho and Câmara 1996). The presence of *C. jacchus* south of the Rio São Francisco along the coast as far south as Salvador (south of the Rio São Francisco) was registered even by Wied-Neuwied (1826). This may be part of their original distribution (with the hybrid zone resulting from forest destruction; see Alonso *et al.* 1987), but may also be the result of numerous, repeated introductions of *C. jacchus*. Under any circumstances, the town of Lamarão lies west of the hybrid zone identified by Alonso *et al.* (1987), and within what is considered to be the natural range of *C. penicillata*.

The general appearances of *C. p. penicillata* and *C. p. jordani* are very similar, explaining the fact that Thomas (1901) initially regarded the series of specimens collected by Alphonse Robert from the Rio Jordão as typical *C. penicillata*. Thomas (1904, pp.188–189) provides an excellent, meticulous, and clear description of the differences between the two forms, from "Lamarão, near Bahia," and from the "Rio Jordão, Province Araguay, Minas Geraes," when describing the latter. The differences are easily seen when examining the skins carefully, and his description of *C. p. jordani* is, therefore, quoted verbatim here:

"Size averaging slightly larger than in *penicillata*. General tone of the light colour of the back buffy whitish instead of pure greyish white. Under surface with less black on the throat, this part being grey, only slightly washed with blackish; the black, however, tends to form a black central line over the sternum. Belly and anterior face of thighs strongly suffused with dull yellowish, the hairs of *penicillata* being blackish tipped with white over the whole under surface. Flank-hairs, where overhanging belly, less vividly coloured, their bases dark slaty instead

of black; their next ring dull instead of vivid orange, and their subterminal dark band narrower and less conspicuous. Face less brightly picked out with black and white, the white patches below the eyes almost obsolete, and the centre line between the nostrils pale brownish white instead of pure white. Hands and feet more or less marbled with black and orange instead of clear greyish. Tail-hairs, even near its base, almost or quite without orange rings, the great majority of the hairs being simply black with white tips.

Skull much as in true *penicillata*, but the middle upper incisors show a curious difference in shape; for in *jordani* they are longer, narrower, more parallel-sided, and less strongly convergent towards each other than in *penicillata*, their breadth in the latter about two-thirds their length, while it is about half in the former. [...] The yellowish aspect of the belly and inguinal region, the dulled whiteness of the nasal septum, the general absence of yellow on the tail-hairs, and the long narrow incisors are the most tangible characteristics of this inland race of the well-known *Callithrix penicillata*."

As pointed out by Vivo (1991), Thomas' (1904) arrangement of two *penicillata* subspecies was generally accepted for many years (Elliot 1913; Vieira 1955; Cabrera 1958; Hill 1957; Ávila-Pires 1969; Coimbra-Filho 1971, 1972; Coimbra-Filho and Mittermeier 1973). *Callithrix p. penicillata* was considered to be the form in the north and from the Atlantic forest of southeast and eastern Bahia, and *C. p. jordani* the form inland in the states of Goiás, Minas Gerais, and western Bahia. Auricchio (1995) maintained the division of *C. penicillata* in two subspecies, *jordani* and *penicillata*, but also recognized *C. kuhlii* (well illustrated in Plate 1, following p. 55) from between the Rio de Contas and Rio Jequitinhonha in southeast Bahia and extreme northeast Minas Gerais. *Callithrix p. penicillata*, he indicated, occurred north of the Rio de Contas to the lower and middle Rio San Francisco and along the south (right) bank of the Rio Grande (a western tributary of the Rio São Francisco), and *C. p. jordani* occurred in the states of Goiás, Tocantins, and Minas Gerais.

Hershkovitz (1968, 1975, 1977), however, was discordant in considering *penicillata* (which included the nominate subspecies and *jordani*) to be a subspecies of *Callithrix jacchus*, and the form from southeast Bahia to be merely a hybrid (see below). He regarded the differences between *C. p. penicillata* and *C. p. jordani* as described by Thomas (1904) to be trivial. Emmons and Feer (1990) followed Hershkovitz's classification, and, making no mention of *jordani*, included southeast Bahia and northern Espírito Santo as part of the geographic range of *C. j. penicillata*. Later, Emmons and Feer (1997) recognized *C. jacchus kuhlii*, however, from between the Rio de Contas and the Rio Jequitinhonha, following Rylands *et al.* (1993) in the description of its range, but maintaining Hershkovitz's (1977) classification of all Atlantic forest and central and northeastern Brazilian marmosets as subspecies of



*C. jacchus*. Vivo (1991), likewise, did not recognize Thomas' (1904) arrangement, considering just one species, *C. penicillata*, with no subspecific forms, and wrote that the form *kuhlii*, although not a hybrid as was argued by Hershkovitz (1975, 1977), was not sufficiently distinct to warrant separation from *C. penicillata*.

#### “*Hapale penicillata Kuhlii* Wied, 1826”

Hershkovitz (1975, p.142) was the first to indicate that Wied-Neuwied (1826) had referred to the marmoset of southeast Bahia as “*Hapale penicillata Kuhlii*” [*sic*]. According to Hershkovitz this was on the basis of a male collected at the mouth of the Rio Belmonte (= Rio Jequitinhonha), southern Bahia, distinguishable from the form *penicillata* on the basis of a “weisslich-graubraun” crown and whitish cheeks. Wied-Neuwied noted that specimens from the Rio Pardo and Ilhéus farther north were also characterized by their more buffy cheeks and frontal blaze. However, Hershkovitz (1975, 1977) argued at length that *kuhlii* was not a valid taxon, being merely an intergrade between *C. j. penicillata* and *C. j. geoffroyi*: “Their geographic position, buffy crown, pale cheeks, well-defined white median rostral line and large frontal blaze extending over the crown mark them as intergrades between *geoffroyi* and *penicillata*.” (1975, p.142). Hershkovitz (1977) also gave the opinion that those from Ilhéus are nearer to *penicillata* (to the west) and those from Belmonte nearer to *geoffroyi*, and indicated that marmosets in adjoining regions to the south into Espírito Santo “belong to the same or similarly mixed stock.”

However, Vivo (1991, pp.80–81) argued that Wied-Neuwied (1826) had not intentionally given it this name. According to him: “Wied (1826) systematically placed the name of the author beside the scientific name he used. Unfortunately some of the author’s names (as was the case for *penicillata*) were printed in italics, as were the names of the species. In other cases the names of the authors were printed in the typescript of the text, sometimes separated by a comma, or abbreviated, sometimes not.” Vivo (1991) gives an example of this, where Wied-Neuwied (1826, p.135) refers to “*H. Leucocephalus Kuhlii*” in meaning merely the *H. leucocephalus* of Kuhl, with no intention of designating a subspecies. Elliot (1913, p.227) reported several specimens of *C. penicillata* in the Paris Museum, the earliest dated 1822, and in all the name *penicillatus* is attributed to H. Kuhl from his publication in 1820 (p.47). It is notable that Thomas (1901) also attributed the authorship of *Hapale penicillata* to Kuhl. This might explain Wied-Neuwied’s attachment of “Kuhlii” (rather than É. Geoffroy or Humboldt) to the scientific name. Besides this, Vivo (1991) argued that, contrary to Hershkovitz’s (1975, p.142) affirmation, Wied-Neuwied did not compare his material from southeast Bahia with “true *penicillata*,” but with the previous species he was discussing, *Hapale leucocephalus* (= *C. geoffroyi*), that he had encountered to the south. Vivo (1991) pointed out that the first person who intentionally used the name *kuhlii* to describe the marmosets from southeast Bahia was Hershkovitz, and gave the opinion that he

should, therefore, be attributed authorship if, as we argue here, the form is to be considered a taxon distinct from *penicillata*. However, the fact that Hershkovitz (1975, 1977) argued that the form was not a valid taxonomic entity disqualifies the possibility of him being attributed authorship (see below).

#### “*Callithrix penicillata kuhlii* Wied, 1826”

Coimbra-Filho (1971, 1972), and Coimbra-Filho and Mittermeier (1973) maintained that the southeast Bahian marmoset was distinct from populations inland in Goiás, western Bahia, and Minas Gerais. In the absence of a contemporary study of the taxonomy and geographic distribution, they followed Thomas (1904) in referring to the marmoset of coastal Bahia as *C. p. penicillata*, even though the description of the pelage of the specimens from Lamarão, Bahia (ascribed to the nominate subspecies by Thomas [1904]), was not consistent with that of the specimens from southeast Bahia. In pointing out that (it would seem erroneously, see above) Wied-Neuwied (1826) had given the name *H. penicillata kuhlii* to the marmosets from southeast Bahia as if he was describing a new subspecies, Hershkovitz (1975) provided the name used subsequently by Coimbra-Filho and Mittermeier (1977; Mittermeier and Coimbra-Filho 1981), even though he argued that the form was merely a hybrid between *C. j. penicillata* and *C. j. geoffroyi*. Mittermeier and Coimbra-Filho (1981), following Hershkovitz’s affirmation that Wied-Neuwied had given the subspecific name to this marmoset, suggested that *penicillata* should remain as the subspecific name for all forms inland, subsuming as such the form *jordani* Thomas 1904,

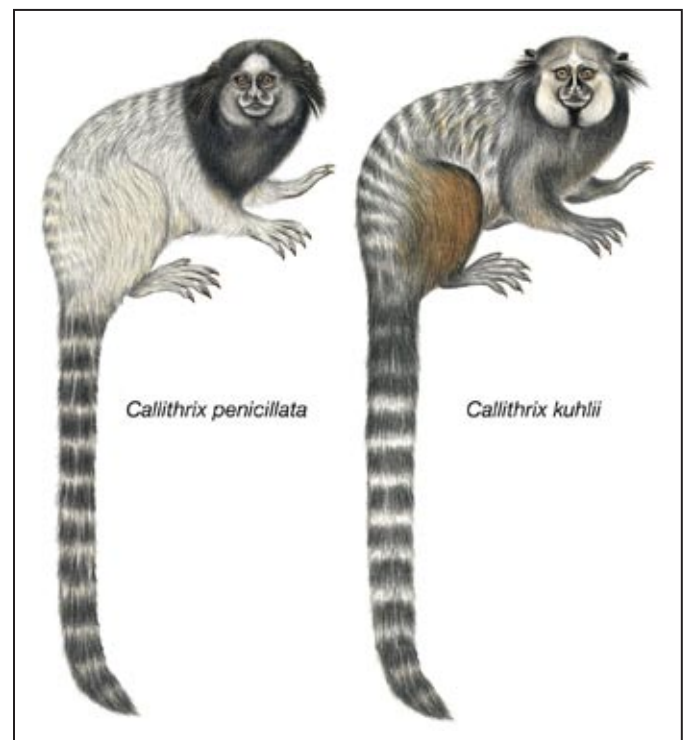


Figure 1. *Callithrix penicillata* and *C. kuhlii*. Illustration by Stephen D. Nash.

while *C. penicillata kuhlii* (Wied-Neuwied, 1826) should be the correct name for the southeast Bahian marmosets (p.35 and footnote). This is reinforced by the fact that the original description of *Jacchus penicillatus* by St. Hilaire does not conform to the southeast Bahian marmosets (see above).

### “Jacchus” Group Marmosets—Species or Subspecies?

Mittermeier and Coimbra-Filho (1981) maintained that the marmosets comprising Hershkovitz’s (1975) “Jacchus” group should be considered good species rather than subspecies of *C. jacchus*. Fertile hybrids had been produced in captivity (Hill 1957; Coimbra-Filho 1970, 1971, 1973, 1974, 1978; Mallinson 1971; Hampton *et al.* 1971; Coimbra-Filho and Mittermeier 1973; see also Coimbra-Filho *et al.* 1993), and Hershkovitz (1975, 1977) had provided evidence of intergradation in the wild. However, Mittermeier and Coimbra-Filho (1981) argued that the issue was controversial and depended on the resolution of three questions: (1) Do the forms naturally overlap in their ranges without interbreeding? (2) What is the correct taxonomic interpretation of the intergrades reported by Hershkovitz (1975, 1977), considering they might be merely individual or ontogenetic variants rather than hybrids? and (3) Presuming natural zones of intergradation do exist, are they regions of broad clinal variation or narrow contact zones? Mittermeier *et al.* (1988, p.21) provided answers to these questions, which reinforced the argument that at least the forms *aurita*, *geoffroyi*, *penicillata*, *jacchus*, and *kuhlii* should be considered valid species (*flaviceps* may be subspecific to *aurita*, see below), even though it would seem that none of the “Jacchus” group marmosets overlap in their geographic distributions without interbreeding. Evidence is now available for a

number of natural hybrid zones either at the distributional limits of the various forms or due to introductions (see Table 1). They are reviewed in Coimbra-Filho *et al.* (1993) and Mendes (1997). Coimbra-Filho *et al.* (1993) classified the hybrid localities into three types: (1) at distributional limits and ecotones of ecologically distinct species (*C. penicillata* × *C. geoffroyi*, *C. penicillata* × *C. kuhlii*, and *C. geoffroyi* × *C. flaviceps*); (2) ecologically similar forms at their distributional limits but not involving ecotones (*C. aurita* × *C. flaviceps*) and; (3) ecologically similar species but involving introductions of one or both in areas that may or may not be ecotones (*C. jacchus* × *C. penicillata*). The similarities between *C. flaviceps* and *C. aurita* (pelage patterns such as the ear tufts and the skull-like facial mask, ecological adaptations, ontogeny, vocalizations and clinal variation in overall pelage color) indicate to us that *flaviceps* might well be best considered a subspecies of *aurita* (Coimbra-Filho 1986a, 1986b; Coimbra-Filho *et al.* 1993, 1997). The important feature is that, in all cases, the documented contact zones are narrow or confined and clinal variation is not evident (Vivo 1991; Coimbra-Filho *et al.* 1993; Mendes 1997). Vivo (1991) classified all the “Jacchus” group marmosets (except for *kuhlii*, which he did not recognize as distinct from *C. penicillata*) as species, arguing that allopatry or parapatry alone cannot be used to determine subspecific or specific status, and that there is no evidence for widespread intergradation or clinal variation, and protesting that the use of subspecific classifications merely on the basis of similarity in pelage between forms is inadequate. Examining pelage color and patterns alone, Rosenberger (1984) also argued that they should be considered species rather than subspecies, but qualified that more information is needed from other systems—genetic and morphological.

**Table 1.** Hybrids born at the Rio de Janeiro Primate Center (CPRJ/FEEMA), Rio de Janeiro.

Registration no. <sup>1</sup>	Birth number	Date of birth	No. of offspring (sex)	Death
<b><i>C. kuhlii</i> (male) × <i>C. jacchus</i> (female)</b>				
- MP 075	First	3 April 1976	2 (0.1.1)	29 June 1976 <sup>2</sup> 29 June 1976
MP 122 MP 123	Second	?	2 (2.0)	29 March 1978 29 March 1978
<b><i>C. kuhlii</i> (male) × <i>C. penicillata</i> (female)</b>				
MP 191 MP 197	First	9 December 1978	2 (1.1)	7 February 1980 25 February 1980
<b><i>C. kuhlii</i> (male) × <i>C. geoffroyi</i> (female)</b>				
MP 106	First	19 June 1973	1 (0.1)	13 November 1975
- MP 033	Second	28 November 1973	2 (0.1.1)	5 December 1973 <sup>1</sup> 5 May 1976
MP 121	Third	2 May 1974	1 (0.1)	20 March 1978
MP 127	Fourth	17 September 1974	1 (0.1)	22 August 1978
MP 221	Fifth	23 May 1975	1 (1.0)	25 July 1980
<b><i>C. geoffroyi</i> (male) × <i>C. penicillata</i> (female)</b>				
MP 145 MP 152	First	16 November 1977	2 (2.0)	19 January 1979 24 May 1979
MP 181 MP 221	Second	14 September 1979	2 (2.0)	16 January 1980 Alive

<sup>1</sup>MP = Museu de Primatologia (CPRJ).

<sup>2</sup>Material lost, no registration number.

The lack of evidence for the classification of the “Jacchus” group marmosets as subspecies of *C. jacchus* led Groves (1993, 2001, 2005) to list them all as species, explicitly following the Phylogenetic Species Concept. Natori (1986, 1990) and Natori and Shigehara (1992) in their studies of the dental morphology, and Natori (1994) in his craniometrical study, also argued for their ranking as species, on the basis of, however, compliance with the separation of *C. argentata* and *C. humeralifera* as distinct species. Natori (1986) examined six dental characters and tooth size in *Callithrix*. On the basis of molar tooth size alone, he found that the differences among the “Jacchus” group marmosets were greater than between the Amazonian *argentata* and *humeralifera*. He argued that if the latter were to be considered separate species, then so should the “Jacchus” group marmosets. The same conclusion was drawn by Natori (1994) in his study of 19 cranial measures. On the basis of Q-mode correlation of these measures, the distances between the “Jacchus” group members were greater than those between *C. argentata* and *C. humeralifera*, and, excepting *C. jacchus* and *C. penicillata*, were greater than between *Cebuella* and *C. argentata* and between *Cebuella* and *C. humeralifera*.

Mendes (1997) argued for their species status on the basis of a reanalysis of their geographical distributions and pelage variation (agreeing with the conclusions of Mittermeier *et al.* [1988] and Rylands *et al.* [1993] regarding hybrid zones), as well as a detailed study of their vocalizations (see below). Most recently, Marroig *et al.* (2004; see also Marroig 1995) reported on a study of the cranial morphology of the “Jacchus” group marmosets. They concluded that they should be classified as separate species rather than subspecies, based on their finding that “morphological distances among marmosets are similar to or higher than distances found among other related taxa usually accepted as good species, like the tamarins (Moore and Cheverud 1992; Ackermann and Cheverud 2000, 2002)” (p.17). They also failed to find evidence for intergradation along contact zones, but instead “a sharp, steep morphological boundary between taxa with no trend of species being more morphologically similar at contact zones than at other parts of their ranges.”

Cytogenetics and molecular genetics have to date been indecisive in their contribution to the debate concerning the taxonomic status of the “Jacchus” group marmosets. Peixoto (1976) and Peixoto and Pedreira (1982) compared the chromosomes of *C. jacchus*, *C. penicillata*, and *C. geoffroyi* and recorded clear differences in G-banding, indicating paracentric inversions not found in later studies by Seuánez *et al.* (1988) and Nagamachi (1995). Nagamachi (1995; Nagamachi *et al.* 1997) carried out a study of the chromosome morphology of *C. kuhlii* and the other “Jacchus” group marmosets except *C. flaviceps*. All of the eastern Brazilian marmosets have a diploid chromosome number of 46, with 30 two-armed and 14 acrocentric autosomes, a conservative submetacentric X chromosome, and a Y chromosome that is highly variable in size and morphology. In *C. kuhlii* the Y chromosome is small and two-armed (metacentric). An analysis of the G-banding

patterns demonstrated a lack of any chromosomal rearrangements to differentiate their karyotypes. C-banding, likewise, demonstrated no differences between the species. Heterochromatin was found to occur in small quantities in the centromeric regions of all the chromosomes, in the telomeric region of the short arm of pair 6, and in the telomeric region of the long arm of chromosome 22. Ag-NOR staining marked secondary constrictions of the small arms of the acrocentric chromosomes. Nagamachi (1995; Nagamachi *et al.* 1997) concluded that the five species they studied were extremely homogeneous in their karyotypes (except for the size and morphology of the Y chromosome, which in the case of *C. jacchus* was variable even between populations) and that nothing can be said as a result concerning the taxonomic status of each.

Tagliaro *et al.* (1997) analyzed mitochondrial DNA control region sequences in all the “Jacchus” group marmosets except for *C. flaviceps*. In reconstructing the phylogeny of these marmosets from their findings, they concluded that “Our trees certainly do not come down in strong support of a monophyletic *C. kuhlii*, although their paraphyly is also only weakly supported (i.e., a monophyletic *C. kuhlii* adds only one substitution to the MP tree)” (p.682), and later (p.683): “our data do not support a clear taxonomic distinction between *C. kuhlii*, *C. penicillata*, and possibly *C. jacchus*, which [...] we regard as a tentative proposal but one that needs to be further explored...”. They found, on the contrary, strong support that both *C. aurita* and *C. geoffroyi* are “distinct evolutionary entities.” Studying electrophoretic patterns in protein systems in four of the “Jacchus” group marmosets (*jacchus*, *penicillata*, *geoffroyi*, and *kuhlii*), Meireles *et al.* (1992, 1998) concluded that Hershkovitz’s (1977) use of subspecies was the most appropriate taxonomy based genetic distance values.

### Evidence for the Validity of *Callithrix kuhlii*

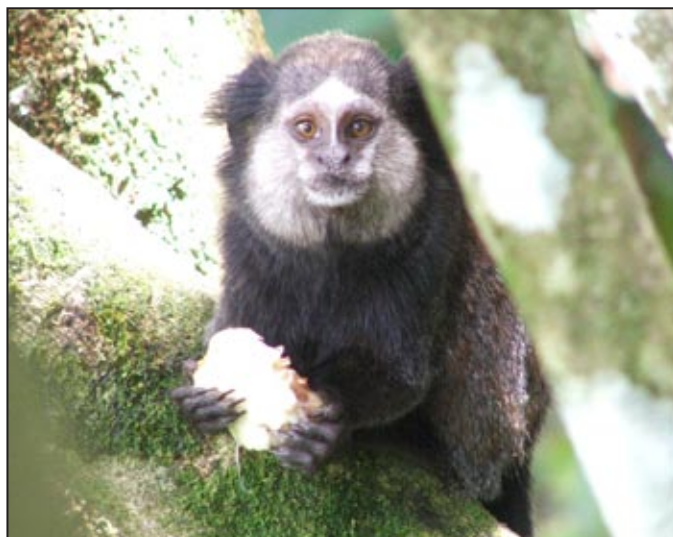
#### *Intergradation and hybrid zones in the wild*

Hershkovitz (1975, 1977) argued that the form *kuhlii* was a natural hybrid of *C. j. penicillata* and *C. j. geoffroyi*. Rylands (1989), however, argued that the consistency of the pelage characteristics of *C. kuhlii* both within social groups and between distant parts of its geographical distribution would militate against them being hybrids. In part, Hershkovitz’s argument was based on the misbelief that *C. j. penicillata* extended into the northern part of the state of Espírito Santo. As pointed out by Hershkovitz (1975), there has been considerable confusion over this. Ruschi (1964, see also 1965) stated that the form *penicillata* occurred along coastal Espírito Santo from Conceição da Barra to Barra do Itapemerim, near the state boundary with Rio de Janeiro. Coimbra-Filho (1971; see also Coimbra-Filho and Mittermeier 1973) pointed out that if this was so, it was a recent range extension, the majority of this region (between the Rios Jucu and Itaunas) being the domain of *C. geoffroyi*. Although emphasizing the lack of concrete evidence, Hershkovitz (1975) argued that “...should *penicillata* and *geoffroyi* meet in Espírito Santo, they would almost certainly merge [...]. Offspring of the predicted inter-





**Figure 2.** Adult *C. kuhlii* in the Una Biological Reserve, southern Bahia. Note the brownish grey crown, which the species develops as an adult (compare with the juvenile in Figure 6. Photograph by Gustavo Canale.



**Figure 3.** Adult *C. kuhlii* in the Una Biological Reserve, southern Bahia. Photograph by Gustavo Canale.

gradation would likely be classified as *geoffroyi* or *penicillata*, depending on the degree of phenetic resemblance to either parent.” (p.142). Hershkovitz (1975) then argued that intergradation between the two species in southeastern Bahia is evidence for the likelihood of this. Despite the affirmation of Ruschi (1964, 1965), there is no evidence that *penicillata* has ever naturally occurred in Espírito Santo, nor of intergradation between *penicillata* and *geoffroyi* in the northeastern part. The localities listed by Ruschi (1964) are uncorroborated (Hershkovitz 1975, 1977).

The only confirmed outlying locality for *C. j. penicillata*, listed by Hershkovitz (1977), Kinzey (1982) and Vivo (1991), is the Rio Jucuruçu, southern Bahia, south of the Rio Jequitinhonha (see Fig. 5). This locality is based on four specimens in the Museum of Zoology, São Paulo (MZSP): Specimens MZSP 3843, 3844, and 3854 (young), collected by Olivério M. O. Pinto in March 1933, are very similar and clearly

referable to *Callithrix kuhlii*. MZSP 3843 has a tail ringed off-white on black, the tip grayish-white. There are rusty red brown hairs on outer thighs (from the base of the hair: black, rusty red, black or whitish tips). On the back, the hairs, from the base, are: black, rusty red, and black with a white tip. The grayish-white transverse banding on the lower back becomes less distinct on the middle. Mantle and shoulders black, hairs with white tips (flecking). Flanks reddish brown. Back of head and nape black. Crown brownish gray-beige. Hands and lower arms brownish black with white speckling (tips of some hairs whitish). Hairs of upper arms: from base, black, rusty red, and black with a whitish tip. Pale yellowish-white star between eyes. Cheeks as in crown but paler buffy brown.

The fourth specimen, MZSP 3842, is labeled “R. Jucuruçu, Bahia,” collected by Camargo (listed by Kinzey 1982, locality 25). It is strikingly paler than the other three, and referable to typical *C. penicillata*, with a black head and nape, off-white cheek patches not extending to the throat, a striated gray/white dorsum, a distinctly striped tail, and a pale orangy-brown showing through on the outer thighs. The back and upper arms are also pale gray whereas in the other three specimens these parts are dark, almost black.

The actual locality of the Rio Jucuruçu is not clearly identified. Vivo (1991, locality 26) listed it as “Rio Jucuruçu (boca [mouth]) 17°32’S, 39°14’W”, which is a little south of the mouth of the Rio Jucuruçu, south of the town of Prado. In the place name index “Localidades da Coleção do Museu de Zoologia de São Paulo,” a compilation by Paulo Emílio Vanzolini, kept in the museum, the following coordinates are given “Rio Jucuruçu (= Cachoeira Grande), Bahia (17°15’S, 39°46’W)”, a location on the middle of the southern arm of the Rio Jucuruçu, near to the village of Torcida, inland. Kinzey (1982) listed the Rio Jucuruçu (locality 25) with the coordinates 17°21’S, 39°13’W. We have been unable to clarify the origin of the name Cachoeira Grande given as a synonym for the Rio Jucuruçu by Vanzolini. Today there is a Rio Cachoeira Grande farther north, a little north of the Rio de Contas, south of the town of Valença, where the phenotypes of the Pinto specimens would be expected (see below). The Rio Jucuruçu is otherwise the domain of *C. geoffroyi*.

The striking difference between the three specimens collected by Pinto on the one hand and that collected by Camargo on the other (not commented upon by Vivo [1991]), the odd sequence of registration numbers of the four specimens in the MZSP, and the lack of certainty regarding the precise locality where these specimens were collected, means that it is very difficult to arrive at any conclusion about the significance and veracity, or otherwise, of this record. Mendes (1997) concluded that it almost certainly results from introduced animals or possibly mistaken provenance. A survey of the Rio Jucuruçu would hopefully resolve the doubts concerning these specimens.

Today, *C. geoffroyi* occurs throughout northern Espírito Santo, extending north as far as the south bank of the Rio Jequitinhonha in southern Bahia and northeastern Minas Gerais, west as far the Rio Araçuai (Santos *et al.* 1987; Rylands *et al.* 1988; Oliver and Santos 1991; Vivo 1991; Mendes 1997).



There is no evidence of intergradation between the form *kuhlii* on the north bank of the lower Rio Jequitinhonha and *geoffroyi* on the opposite bank. Oliver and Santos (1991) obtained reports of both *kuhlii* and *geoffroyi* occurring in two localities on the south of the Rio Jequitinhonha (Itapebi and Belmonte), but they argued that this probably resulted from small, introduced populations of the former. Hybrids possibly occur along the upper Rio Araçuaí, where the geographic distributions of *penicillata* and *geoffroyi* meet. Likewise, an evidently hybrid group of *kuhlii* and *penicillata* was observed at Almenara, north of the Rio Jequitinhonha, at the interface between the caatinga (dry thorn scrub) of the middle reaches of the river and the humid Atlantic forest of the lower reaches (Rylands *et al.* 1988). During extensive surveys in southern Bahia, Oliver and Santos (1991), and L. P. de S. Pinto (unpubl. data) have confirmed that the *kuhlii* phenotype is consistent from the north bank of the lower Rio Jequitinhonha to the north of Rio de Contas, perhaps as far as Valença, midway between the Rio de Contas and Rio Paraguaçu.

Hybrid groups of *C. penicillata* × *C. geoffroyi* have been found to occur along the eastern slopes of the Serra do Espinhaço in Minas Gerais, at the interface between the cerrado (west) and Atlantic forest (east). Hybrid groups containing animals typical of both species as well as a variable mixes have been observed at the Serra da Piedade (I. B. Santos and C. M. C. Valle, pers. comm.), and in the municipality of Santa Bárbara, both near to Belo Horizonte (Rylands and Costa 1988; Coimbra-Filho *et al.* 1993). Although some of the hybrids had off-white face masks, none have been observed with the appearance of the *C. kuhlii* phenotype.

#### *Experimental hybridization*

Besides the lack of evidence for the wide zone of intergradation supposed by Hershkovitz (1975, 1977), experimental hybridization of *geoffroyi* × *penicillata* in captivity has failed to reproduce a phenotype similar to that of *kuhlii* (Coimbra-Filho *et al.* 1993). Hybrids of *C. kuhlii* with other Atlantic forest marmosets have demonstrated that its phenotype is genetically dominant. Hybrids from the following matings *C. kuhlii* × *C. geoffroyi*, *C. kuhlii* × *C. jacchus*, *C. kuhlii* × *C. penicillata*, and *C. geoffroyi* × *C. penicillata* have been obtained at the Rio de Janeiro Primate Center (CPRJ) (Table 1).

As in the wild, the offspring of *C. geoffroyi* × *C. penicillata* are very variable in pelage patterns and color. Newborn *C. geoffroyi* × *C. penicillata* have a phenotype more similar to newborn pure *C. penicillata*, with two pale, oval areas above the eyes. The white mask of *C. geoffroyi* is present to varying degrees and generally dirty white to greyish and extending to the forehead and crown. The whitish hairs on the front of crown can be mixed with dark hairs providing the suggestion only of the typical white interorbital “star” on the forehead of *C. penicillata* and *C. kuhlii*. In general, the mask and head of 30-day-old hybrids are much darker. The dorsum in the hybrid offspring can be quite pale grey, with the well-defined black of the crown, nape, shoulders, and upper chest typical of *C. penicillata* but not of *C. kuhlii*.

In *C. geoffroyi* the hairs of the back, flanks, and outer thighs have a yellowish-ochre bar instead of the intense reddish brown bar of *C. kuhlii*, but in both this chromatic field is much more intense than in *C. jacchus* and *C. penicillata*, in which it is a very pale yellowish or very light reddish. The intense reddish brown field of the hairs of *C. kuhlii* is evidently a dominant feature, transmitted to its hybrids, and even dominant to the corresponding allele in *C. geoffroyi*. This demonstrates that *C. kuhlii* is not simply a natural hybrid of *C. penicillata* and *C. geoffroyi*, nor a variant of *C. penicillata*. The dominance of its phenotype in hybrid forms would indicate a genetic stability acquired during speciation over some considerable time.

#### *Is C. kuhlii a variant of C. penicillata?*

Although concluding that *C. kuhlii* is probably not an intergrade between *C. penicillata* × *C. geoffroyi*, Vivo (1991) argued that the distinct features of the pelage of southeast Bahian marmosets were not sufficient to warrant its separation from *C. penicillata*, most especially the darker forms recorded in central Minas Gerais (upper Rio São Francisco). He analyzed a number of cranial measurements for *C. penicillata*, and examined their geographic distribution. The measurements included skull length and width, condylo-basal length, width of the zygomatic arch, interorbital width, width of M<sup>1</sup>, mandible length, height of the mandibular condyle, length of the lower postcanine tooth row, and width of upper canines. The southeast Bahian marmosets were found to be indistinguishable in these measures from *C. penicillata* from northern and central Minas Gerais. According to Vivo (1991) “The only important difference, although inconsistent, is that the southeast Bahian specimens tend to have a paler face than those of central Minas Gerais” (p.81). He considered, however, that the difference was not sufficient for the recognition of two taxa, and defined *C. penicillata* as the marmoset with black pre-auricular tufts and a brown (*castanho*) to pale gray (*cinza-claro*) face, and corresponding strictly to the *C. jacchus penicillata* of Hershkovitz (1975, 1977). As pointed out by Mendes (1997), Vivo did not take into account two other important and consistent pelage differences—the pale, grayish-beige crown of *C. kuhlii* (black in *C. penicillata* and *C. geoffroyi*), well illustrated in Hershkovitz (1975, p.143–144), and the conspicuous red-brown underlying the otherwise black pelage on the outer thigh and lower back. The reddish-brown bars on the hairs of the back of the lower and outer thigh are much broader than in *C. geoffroyi* and much more evident as a result. Mendes (1997) concluded that this feature and the grayish-beige crown are diagnostic for *C. kuhlii*. Since his publication in 1991, Vivo (pers. comm., December 1997) has come to accept that the distinct pelage coloration of the southeast Bahian marmosets does warrant their classification as separate from *C. penicillata*.

Far from being a variant of *C. penicillata*, a number of studies have indicated that it is in fact phylogenetically closer to *C. geoffroyi*. Rosenberger (1984) pointed this out in considering pelage color patterns. In broad ecological terms,

*C. kuhlii* and *C. geoffroyi* are more similar in occupying lowland evergreen forests in eastern Brazil, whereas *C. penicillata* occupies the more intensely seasonal gallery forests and semideciduous forest patches of the *cerrado* and *caatinga* in the interior of Brazil to the west. Natori, examining the morphology of the postcanine dentition (1990) and cranial morphology (1994), and Natori and Shigehara (1992) the lower anterior dentition, concluded in all cases that *C. kuhlii* was distinct and more similar to *C. geoffroyi* than to *C. penicillata*. Marroig *et al.* (2004), on the other hand, also studying cranial morphology, found that *C. penicillata* and *C. geoffroyi* are more similar to each other than either is to *C. kuhlii*. They specifically tested, and refuted, the hypothesis of Vivo (1991) that *C. kuhlii* does not differ to any significant extent from the *C. penicillata* populations in the region of the upper Rio São Francisco in the state of Minas Gerais.

#### Habitat

Whereas *C. penicillata* is the marmoset typical of seasonal semi-deciduous forest, *cerradão*, and gallery forests of the central savanna (*Cerrado*) of Central Brazil, *C. kuhlii* is restricted to the coastal evergreen humid lowland and mesophytic (farther inland) forests along the Atlantic coast (Mori and Silva 1979; Fonseca and Lacher 1984; Rylands and Faria 1993). The two species meet in the strip of liana forest along the leeward side of the coastal mountain range that extends farther west into *caatinga*. The type locality of *C. penicillata* (“Lamarão, near Bahia” Thomas, 1904) is to the west of the Atlantic forest domain, whether it is considered to be the upper Rio Itapicurú (Hershkovitz 1968, 1975, 1977; Napier, 1976; Kinzey 1982) or the town of Lamarão, northwest of Salvador (see above).

#### Dental anatomy

Although Vivo (1991) did not find any difference between *C. penicillata* and *C. kuhlii* in the width of M<sup>1</sup>, the length of the lower post-canine tooth row, and the width of the upper canines, a detailed study of the crown shape of the post-canine dentition of *C. kuhlii*, *C. penicillata*, and *C. geoffroyi* by Natori (1990) discriminated *C. kuhlii* clearly from the other two species. Natori also concluded that there was no evidence for intermediacy in *C. kuhlii* in the characters he studied, arguing against them being hybrids of *C. penicillata* and *C. geoffroyi*, and reinforcing their taxonomic position as a distinct species. Natori and Shigehara (1992) came to a similar conclusion when comparing the lower anterior dentition of all the “Jacchus” group marmosets, with *C. jacchus* and *C. penicillata* clearly separated from the remainder in having distinctly larger lower incisors and canines, which they associated with the higher degree of tree-gouging characteristic of the two species.

#### Cranial anatomy

A detailed study of the craniometry of the “Jacchus” group marmosets was carried out by Natori (1994). On the basis of 19 measures, Natori found “quite large morphologi-

cal differences between the six forms of the *C. jacchus* group” (p.174)—differences that were greater than those observed between *C. argentata* and *C. humeralifera*, and between each of the two Amazonian species and *Cebuella* (except in the case of *C. jacchus* and *C. penicillata*). *Callithrix kuhlii* was clearly recognized as a separate species in this study. Marroig *et al.* (2004) also studied cranial morphology in five of the six “Jacchus” group marmosets (all but *C. flaviceps*) and concluded that *C. kuhlii* was a good species.

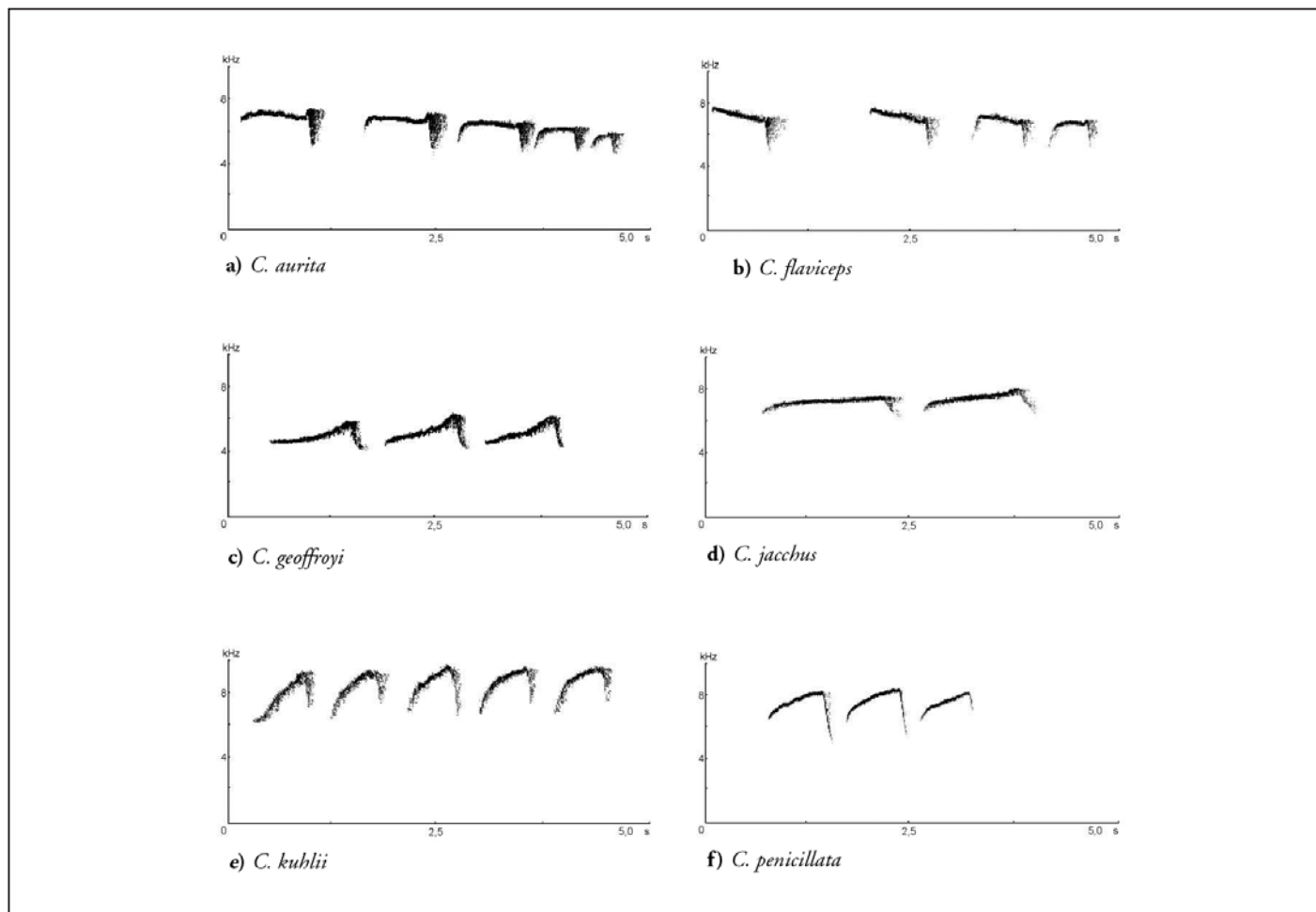
#### Genetics

As mentioned above, genetic studies have not contributed decisively in the debate concerning the taxonomic status of any of the “Jacchus” group marmosets, and have provided no evidence that would argue for *kuhlii* being anything more than a junior synonym of *penicillata*. Nagamachi *et al.* (1997) found the karyotypes in five of the six species (*C. flaviceps* not studied) except for the Y chromosome, to be extremely homogeneous. Tagliaro *et al.* (1997) analyzed mitochondrial DNA control region sequences in all the “Jacchus” group marmosets except for *C. flaviceps*. Although they found that *C. geoffroyi* and *C. aurita* were distinct, they failed to find a clear distinction of *C. kuhlii*, *C. jacchus*, and *C. penicillata*. While inconclusive, Tagliaro *et al.* (1997) interpreted their results as not providing any convincing indication that *C. kuhlii* should be regarded as a distinct taxon. Canavez *et al.* (1999) found few differences in nucleotide sequences between species in the each of the *Callithrix* groups (“Argentata” and “Jacchus”), and their phylogenetic resolution was weak. *Callithrix kuhlii* and *C. penicillata* were associated due to a single synapomorphy. Canavez *et al.* (1999) pointed out that the polytomic phylogeny for the “Jacchus” group differed from the paryphyly observed by Tagliaro *et al.* (1997) probably because they shared an ancestral polymorphism.

Meireles *et al.* (1998) also concluded that their results examining electrophoretic polymorphism in blood proteins militated against the validity of *kuhlii* as separate from *penicillata*; “A comparison of the distance values recorded among *geoffroyi*, *kuhlii*, and *penicillata* populations [...] and the existence of a genetic marker (*LDHA*\*3) shared only by *penicillata* (60%) and *kuhlii* (47%) also support De Vivo’s (1991) view on the status of the latter, based on morphological evidence, i.e., that the *kuhlii* form should be synonymized with *penicillata*.” (p.238).

#### Vocalizations

Mendes *et al.* (in press) carried out an analysis of the long calls of the “Jacchus” group marmosets. They measured note (syllable) duration, the interval between notes, minimum and maximum frequencies, and the initial and final frequencies. Recordings of *C. kuhlii* were obtained both from the wild (between the towns of Camacã and Mascote, Bahia [15°32’S, 39°20’W] and the Lemos Maia Experimental Station of the Regional Cocoa Growing Authority – CEPLAC, Una, Bahia [15°15’S, 39°05’W]) and from captive animals at the Rio de Janeiro Primate Center (CPRJ/FEEMA), Rio de Janeiro, and



**Figure 4.** Sonograms of representative long calls of *Callithrix*. a) *C. aurita*, b) *C. flaviceps*, c) *C. geoffroyi*, d) *C. jacchus*, e) *C. kuhlii*, and f) *C. penicillata*.

the Museu de Biologia Mello Leitão, Santa Teresa, Espírito Santo. The distinctive call (Fig. 4) was found to be consistent between the captive and wild populations, and clear and consistent differences were found between *C. kuhlii* and the remaining “Jacchus” group marmosets. The structure of the long call of *C. kuhlii* was not intermediate between that of *C. penicillata* and *C. geoffroyi*, as might be expected if it were a hybrid. In fact, Mendes *et al.* (in press) found that *C. kuhlii* had the most distinctive call of the species they studied, the notes showed little variation in terms of duration and the interval between them, and were shorter, higher pitched, and more modulated than in all other Atlantic forest species (see Table 2). Mendes *et al.* (in press) concluded that evidence from the study of the long call in the “Jacchus” group marmosets argues clearly for the species’ status of the southeast Bahian *C. kuhlii*.

#### ***Callithrix kuhlii* Coimbra-Filho, 1985**

Vivo (1991) pointed out that Wied-Neuwied (1826) did not use the name “Kuhlii” in the sense of a latin name for the species, and he suggested that the name of the southeast Bahian marmoset should be attributed to Hershkovitz (1977), the first person to consciously use the trinomial for the sub-

species. In fact, the first time that Hershkovitz discussed this form was in a paper in *Folia Primatologica* in 1975. However, because Hershkovitz (1975, 1977) argued that it was not valid, merely a hybrid of *C. j. penicillata* × *C. j. geoffroyi*, this disqualifies him as the author, despite the fact that he described and illustrated features of its pelage, and the differences from the “parent forms.” Other references to *C. p. kuhlii* were made by Coimbra-Filho and Mittermeier in 1977 (in *Biology and Conservation of the Callitrichidae*, ed. D. G. Kleiman, p.107, Smithsonian Institution Press, Washington, DC), and by the same authors in the first volume of *Ecology and Behavior of Neotropical Primates* in 1981 (pp.34–35, 36, Academia Brasileira de Ciências, Rio de Janeiro). Coimbra-Filho (1982, p.93) also mentioned *C. penicillata kuhlii*. In none of these cases, however, was the form described or details given of the characteristics that distinguish it from *C. penicillata* (or *C. p. penicillata*) and *C. geoffroyi*. These publications cannot, therefore, be considered for the purposes of attributing authorship. Likewise, Coimbra-Filho (1984, p.23) discussed the conservation status of *C. kuhlii*, but no description was given. The first publication that gives a description of this marmoset, along with its geographic distribution and some observations on its behavior and conservation status, is that of Coimbra-Filho (1985, *FBCN/Inf.*, Rio de Janeiro 9[4], p.5, out./dez.).



**Table 2.** Parameters of the first note and the first three-note sequence of the long call of *C. kuhlii* (from Mendes *et al.* in press).

Parameter	<i>C. kuhlii</i>	Other “Jacchus” group marmosets
Note duration	Consistent in the first three notes	Notes progressively shorter after the first note, except in <i>C. jacchus</i> (subsequent notes variable).
Duration of 1st note	Short (653 ms)	The shortest of any of the “Jacchus” group marmosets.
Interval between notes	Consistent in first three notes	Interval progressively shorter in <i>C. aurita</i> and <i>C. flaviceps</i> ), but no difference in other species.
Interval between 1st and 2nd notes	Short (253 ms)	The shortest of any of the “Jacchus” group marmosets, but not significantly different from <i>C. penicillata</i> , <i>C. geoffroyi</i> , and <i>C. jacchus</i> .
Initial frequency	No change along the call sequence	Same, except for <i>C. flaviceps</i> and <i>C. aurita</i> in which 2nd and 3rd notes are lower in frequency.
Initial frequency of 1st note	High (7.19 kHz)	No different to <i>C. aurita</i> and <i>C. jacchus</i> , but higher than in <i>C. geoffroyi</i> and <i>C. penicillata</i> , and lower than in <i>C. flaviceps</i> .
Mean frequency	Variable but tendency to increase from 1st to 3rd note	Same, except in <i>C. flaviceps</i> and <i>C. aurita</i> (mean frequency falls from 1st to 3rd note).
Mean frequency of 1st note	High (7.69 kHz)	Higher than in <i>C. geoffroyi</i> , <i>C. penicillata</i> , and <i>C. aurita</i> , but similar to <i>C. jacchus</i> and <i>C. flaviceps</i> .
Frequency modulation	No significant difference between 1st and 3rd notes	Same in <i>C. aurita</i> . In <i>C. flaviceps</i> modulation progressively less, in others 3rd note tends to be more modulated.
Frequency modulation of 1st note	Ascending (1.53 kHz/ms)	Significantly higher modulation than in any of the other “Jacchus” group marmosets. Descending in <i>C. flaviceps</i> and <i>C. aurita</i> ascending in remaining species.

Adelmar F. Coimbra-Filho (1985) is, therefore, considered to be the author of *Callithrix kuhlii*.

It is evident that Wied-Neuwied (1826) latinized the name of Heinrich Kuhl to Kuhlius prior to using the genitive, hence Kuhlii, with a double “i”. Article 33(d) of the Zoological Code of Nomenclature determines that “The use of a termination *-i* in a subsequent spelling of a species group name that is a genitive based upon a personal name in which the correct original spelling terminates with *-ii*, or vice-versa, constitutes an incorrect subsequent spelling, even if the change in spelling is deliberate...” The use of the specific name “kuhli” with one “i” would, therefore, be incorrect. Coimbra-Filho (1985) referred to the species as *Callithrix kuhlii*.

**Type.** Of *H[apale] penicillatus Kuhlii* Wied-Neuwied, 1826, designated by Hershkovitz (1975) as a male collected by Prince Maximilian zu Wied-Neuwied near the mouth of the Rio Belmonte, Bahia (1975, p.142; 1977, p.502). According to Hershkovitz (1977) it is part of the collection of Prince Maximilian zu Wied-Neuwied.

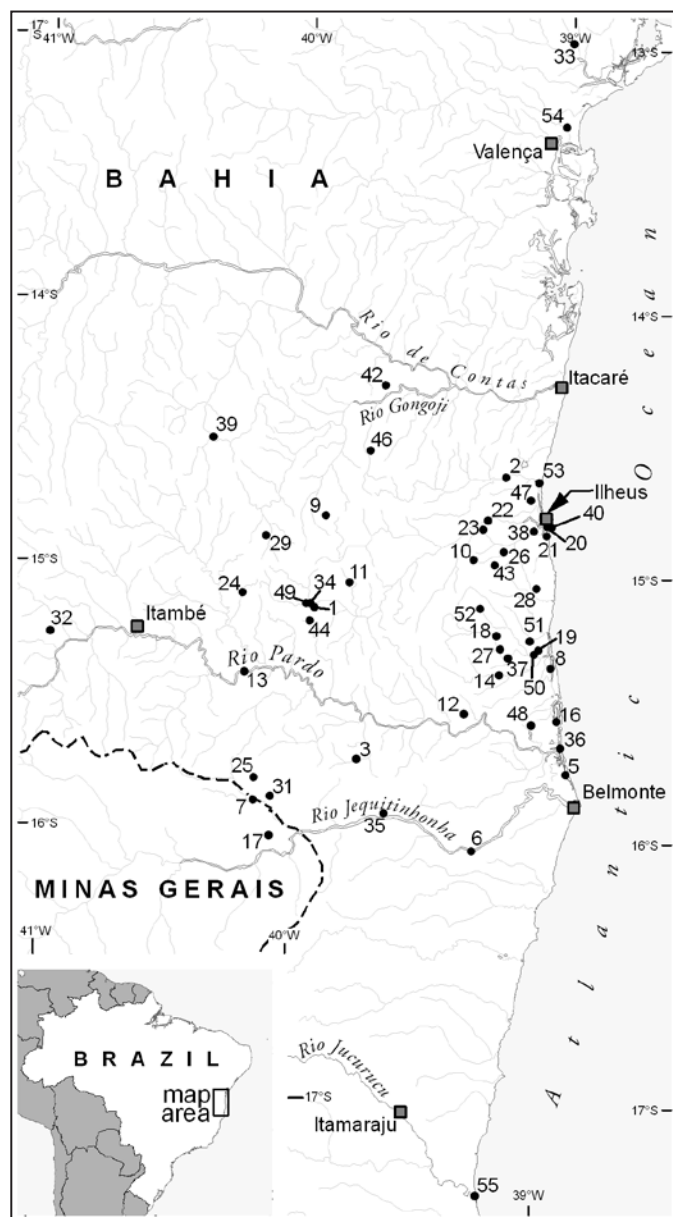
According to Ávila-Pires (1965), this collection was purchased by D. G. Elliot in 1869 to stock the American Museum of Natural History, New York. Ávila-Pires (1965) did not include it in his descriptions of the type specimens collected by Wied, because it was only 10 years later that Hershkovitz argued that Wied had described it (as a subspecies). Robert S. Voss, Division of Vertebrate Zoology, American Museum of Natural History, informed us that the type of *Hapale penicillatus kuhlii* has unfortunately been lost (*in litt.* 10 May 2006). Hershkovitz (1975, 1997) evidently did not see the type he designated, mentioning only that the three specimens from Ilhéus he did examine — two in the Field Museum of Natural History (FMNH), Chicago, and one in the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ) — agreed with Wied’s (1826) description of the male from Belmonte. On

the suggestion of Voss (*in litt.* 10 May 2006) one of the three Ilhéus specimens mentioned by Hershkovitz (1975) could be designated a neotype, but further investigation would be appropriate to determine whether the Belmonte type can still be located. Alternatively, but less satisfactorily, a specimen in the Museu Nacional, Rio de Janeiro “MNRJ 23794. Passuí, Belmonte, Bahia. Male. Col. Unknown. 16 July 1949. Skin M29732(33). SEPSFA, Rockefeller Foundation. Wt. 350 g” could be designated as a topotype.

**Type locality.** Given by Hershkovitz (1975, pp.142 and 168) as near the mouth of the Rio Belmonte, Bahia [cf. Rio Jequitinhonha], 15°45’S, 38°53’W. (Locality 306 on the map, Figure 1, of Hershkovitz [1975]). Hershkovitz (1977, p.502) also lists Serra do Mundo Novo, Rio Pardo, Rio Ilhéus, south-east of the state of Bahia, Brazil.

**Description.** Black pre-auricular tufts, white patch in the middle of the forehead, cheeks and throat pale greyish-beige to pale brown, back striped, hands and feet black, outer thighs reddish brown, tail ringed. The following is a translation from Portuguese of the description given in Coimbra-Filho (1985).

“Species slightly larger than the common marmoset (*C. jacchus*). Its most evident characteristics are the small, white, frontal mark (*estrela*) [\*] and the generally dark coloration, noting in certain zones of the hairs, a beautiful reddish-brown coloration, principally on the external parts of the thighs. The hands, arms, feet and legs are very dark, almost black. The head shows a distinct chromogeny, where the grayish-beige tone appears on the sides of the face and the front part of the head. The auricular pencil-like tufts are black, long, and the tufts are less dense than those of *C. penicillata*. The young differ visibly from those of *C. penicillata*,



**Figure 5.** Locality records for *C. kuhlii*. Note that the known distribution is between the Rio de Contas and the Rio Jequitinhonha, extending inland about 200 km, delimited by the transition from forest formations (dry forest and liana forest) to the caatinga and scrub of the interior of the state of Bahia (see Mori 1989; Pinto and Rylands 1997). Localities 33 and 54 are both records of sightings of marmosets attributed to *C. kuhlii* by Oliver and Santos (1991). Locality 55 at the mouth of the Rio Jucuruçu is an anomaly and is very probably erroneous. See gazetteer, Appendix 1. Map kindly drawn by Mark Denil, Center for Applied Biodiversity Science, Conservation International, Washington, DC.

being much darker, and only people who have never seen them could confuse them.” [\**estrela* = star].

**Cranial dimensions.** Natori (1994) carried out a detailed craniometrical study of *C. kuhlii*, involving 19 measures of the skull and mandible. Four of the principal measures are as follows: Mean skull length (nasion to lambda)  $40.71 \pm 1.01$  mm,  $n = 43$ ; mean cranial width (euryon to euryon)  $22.92 \pm 0.80$  mm,  $n = 44$ ; mean mandible width (bicondylar breadth)  $25.6 \pm 0.76$  mm,  $n = 43$ ; mean length of upper post-incisor tooth



**Figure 6.** A juvenile *C. kuhlii* in Una, Bahia. Note the typical reddish-brown showing through on the flanks and outer thighs. The black crown becomes brownish grey when adult (see Figs. 2 and 3). Photograph by Russell A. Mittermeier, 1980.

row (mesial surface of left  $C^1$  to distal surface of left  $M^2$ )  $11.89 \pm 0.37$  mm,  $n = 33$ .

**Distribution.** The known distribution is in the humid lowland forests and higher elevation mesophytic forests between the Rio Jequitinhonha (in the south) and the Rio de Contas (in the north), in the south of the state of Bahia, Brasil (Coimbra-Filho 1985, 1990) (Fig. 5). It is possible that its range extended north along the coast to the Rio Paraguaçu, or even the Rio São Francisco, in the past, but the degradation and destruction of the region’s forests (Coimbra-Filho *et al.* 1991, 1991/1992; Coimbra-Filho and Câmara, 1996) and the widespread mixing of populations with *C. jacchus* and *C. penicillata* through introductions makes this difficult or impossible to ascertain today. Likewise, it is possible that in the recent past the range extended south of the Rio Jequitinhonha to the Rio Jucuruçu, Bahia, but again this is now difficult to establish. Today, *C. geoffroyi* occurs along the south bank of the Rio Jequitinhonha, west as far as the right bank of the Rio Araçuaí (Rylands *et al.* 1988).

**Comparisons with other species.** Differs from *C. jacchus* in being darker overall, with conspicuous reddish brown showing through the blackish (variously white-flecked) pelage of the thighs and flanks. The ear tufts are black and pencil-like as in *C. penicillata* and *C. geoffroyi*; those of *Callithrix*

*jacchus* are white and fan-like. *C. jacchus* has a dark crown; adult *C. kuhlii* have pale grey/brown crown. The dark neck and nape of *C. jacchus* contrast with the paler grey dorsum and flanks. Differs from *C. penicillata* in having thinner ear-tufts and is also much darker, with the characteristic red-brown showing through the ruffled pelage of the thighs and, to a lesser extent, the flanks. *C. penicillata* has a black crown, but adult *C. kuhlii* have a pale grey/brown crown. Infant *C. kuhlii* differ from infant *C. penicillata* in being much darker. The cheek fur of *C. kuhlii* is a distinct pale grey/brown, that of *C. penicillata* is darker grey. *C. geoffroyi* has a distinctly white and more expansive face-mask overall. The forehead and throat of *C. geoffroyi* are white, whereas *C. kuhlii* has the white patch forming a small fan above and between the eyes as in *C. penicillata*. The dark back and flanks (flecked with white) of *C. geoffroyi* are more strongly suffused with reddish brown, the thighs less so.

**Vocalizations.** Mendes (1997; Mendes *et al.* in press) analyzed the long call in a comparative study of the “Jacchus” group marmosets. He found that the long calls of *C. kuhlii* are characterized by a variable number of notes or syllables, but about 70% of its long calls include three or four notes, differing, for example, from *C. geoffroyi* and *C. penicillata*, whose long calls tend to have a smaller number of notes. The notes are high pitched, with a minimal frequency around 6 kHz or more. Although in most marmosets the first note of the long call is the longest, with the other notes getting progressively shorter, in *C. kuhlii* the notes did not differ significantly in duration. The note duration is about 650 ms, shorter than in other marmosets. Mendes *et al.* (in press) concluded that *C. kuhlii* has the most distinctive call of the six species, that the long calls show little variation in terms of duration and frequency parameters, and that the notes are more modulated than in all other Atlantic forest species (Fig. 4).

**Chromosome morphology.** Nagamachi (1995; Nagamachi *et al.*, 1997) carried out a study of the chromosome morphology of *C. kuhlii* and the other “Jacchus” group marmosets, except *C. flaviceps*. All of the eastern Brazilian marmosets have a diploid chromosome number of 46, with 30 two-armed and 14 acrocentric autosomes, a conservative submetacentric X chromosome, and a Y chromosome that is highly variable in size and morphology. In *C. kuhlii* the Y chromosome is small and two-armed (metacentric).

**Vernacular name.** Wied’s black tufted-ear marmoset or Wied’s marmoset, Southern Bahian marmoset, sagüi-de-Wied (Portuguese).

**Specimens examined:** Museu de Zoologia, Universidade de São Paulo (MZSP); Departamento de Zoologia, Secretaria de Agricultura do Estado de São Paulo (DZ); Museu Nacional, Rio de Janeiro (MNRJ); British Museum (Natural History) (BM).

#### *Callithrix penicillata*

MZSP 2155. Ponte do Ipê, Arcado, Goiás. 7 May 1904. Female. Coll. Otto Dreher. [Labeled *C. p. jordani*]

- MZSP 2588. Vila Nova, Bahia. [= Senhor do Bonfim]. 1908. Coll. E. Garbe.  
 MZSP 3842. Rio Jucuruçu, Bahia. Coll. Camargo.  
 MZSP 4137. Jaraguá, 29 August 1934. Male. Coll. José Lima.  
 MZSP 10638-39. Goiânia, Goiás. 27 August 1963. Male. Coll. J. Hidasí.  
 MZSP 11283-85. Cabeceiras, Lagoa Formosa, Minas Gerais. 25 October 1964. Coll. Exp. DZ.  
 MZSP 11286, 11288-89. Rio Urucuia, Cachoeira, municipality of Buritis, Minas Gerais. 3 November 1964. Coll. Exp. DZ.  
 MZSP 28534. Itabirito, Minas Gerais. Male. 21 February 1988. Coll. C. J. M. Araújo.  
 BM 1903.9.5.8-15, 1903.9.5.160. Lamarão, near Bahia. May–June 1903. Alt. 300 m. Coll. Alphonse Robert. [See Thomas (1904), Napier (1976), type locality of *C. j. penicillata*, restricted by Hershkovitz (1977)].  
 BM 1901. 11.3.6-8. Rio Jordão, near Araguary, Minas Gerais. May/June 1901. Coll. Alphonse Robert. [See Thomas (1904), Napier (1976), paratypes of *C. p. jordani*.]  
 BM 1901. 11.3.9. Rio Jordão, near Araguary, Minas Gerais. May/June 1901. Coll. Alphonse Robert. [See Thomas (1904), Napier (1976), holotype of *C. p. jordani*.]  
 BM 1901. 11.3.10-12. Rio Jordão, near Araguary, Minas Gerais. May–July 1901. Coll. Alphonse Robert. [See Thomas (1904), Napier (1976), paratypes of *C. p. jordani*.]

#### *Callithrix kuhlii* [See Laemmert *et al.* 1946; Vaz 2005]

- MZSP 3498. Fazenda Pontal, Ilhéus, Bahia. August 1919. Male. Coll. E. Garbe.  
 MZSP 3500. Itabuna, Bahia. 1919. Male. Coll. E. Garbe 16.  
 MZSP 3843. Rio Jucuruçu, Bahia. March 1993, Coll. Pinto.  
 MZSP 3844. Rio Jucuruçu, Bahia. March 1993, Coll. Pinto.  
 MZSP 3854. Rio Jucuruçu, Bahia. March 1993, Coll. Pinto.  
 MZSP 7048. Rio do Braço, Ilhéus, Bahia. 24 February 1944. Female. Coll. Serviço de Estudos e Pesquisas sôbre a Febre Amarela (SEPSFA), J. Moojen. Ex. MNRJ 17403.  
 MNRJ 7898. Fazenda Ribeirao da Fortuna, municipality of Ilhéus. Cacao plantation. 10 January 1944. Adult female. HBL 230 mm, tail 315 mm. Labeled *Callithrix penicillata*. Coll. Galdino Pereira.  
 MNRJ 8524. Fazenda Retiro, Aritaguá, municipality of Ilhéus. 1 November 1944. Adult female. HBL 230 mm, tail 305 mm, weight 370 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.  
 MNRJ 8525. Sambaituba, Aritagua, municipality of Ilhéus. Secondary growth scrub. 21 October 1944. Adult male. HBL 210 mm, tail 315 mm, weight 300 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.  
 MNRJ 8526. Fazenda Provisão, Rio do Braço, municipality of Ilhéus. Cacao plantation. 6 February 1945. Adult male. HBL 210 mm, tail 330 mm, weight 360 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.



- MNRJ 8527. Fazenda Provisão, Rio do Braço, municipality of Ilhéus. Cacao plantation. 6 February 1945. Adult male. HBL 210 mm, tail 325 mm, weight 320 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8528. Fazenda Itinga, Pontal, municipality of Ilhéus. Secondary growth scrub. 16 December 1944. Adult male. HBL 215 mm, tail 340 mm, weight 340 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8529. Fazenda Bonfim, Rio do Braço, municipality of Ilhéus. Cacao plantation. 4 February 1945. Adult female. HBL 220 mm, tail 240 mm, weight 400 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8530. Fazenda Almada, Rio do Braço, municipality of Ilhéus. Cacao plantation. 7 November 1944. Adult female. HBL 210 mm, tail 315 mm, weight 370 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8531. Urucutuba, Aritagua, municipality of Ilhéus. Secondary growth scrub. 2 October 1944. Adult. HBL 250 mm, tail 305 mm, weight 400 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8532. Fazenda Bonfim, Rio do Braço, municipality of Ilhéus. Cacao plantation. 23 October 1944. Adult female. HBL 230 mm, tail 320 mm, weight 310 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8533. Fazenda Bonfim, Rio do Braço, municipality of Ilhéus. Cacao plantation. 27 September 1944. Adult male. HBL 190 mm, tail 310 mm, weight 250 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8534. Fazenda Santa Luzia, Rio do Braço, municipality of Ilhéus. Secondary growth scrub. 19 October 1944. Adult male. HBL 200 mm, tail 330 mm, weight 280 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8535. Fazenda Bonfim, Rio do Braço, municipality of Ilhéus. Secondary growth scrub. 29 September 1944. Subadult male. HBL 190 mm, tail 300 mm, weight 250 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8536. Fazenda Quixada, Rio do Braço, municipality of Ilhéus. Cacao plantation. 9 October 1944. Adult female. HBL 215 mm, tail 330 mm, weight 380 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8537. Fazenda Bonfim, municipality of Ilhéus. 23 October 1944. Adult male. Labeled *Callithrix penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8538. Fazenda Bonfim, Rio do Braço, municipality of Ilhéus. Cacao plantation. 11 October 1944. Adult female. HBL 200 mm, tail 312 mm, weight 350 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8539. Fazenda Bonsucesso, Castelo Novo, municipality of Ilhéus. Secondary growth scrub. 19 December 1944. Adult male. HBL 215 mm, tail 325 mm, weight 270 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8540. Sambaituba, Aritagua, municipality of Ilhéus. Forest. 11 November 1944. Adult male. HBL 220 mm, tail 315 mm, weight 450 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8541. Sambaituba, Aritagua, municipality of Ilhéus. Banana plantation. 1 November 1944. Adult female. HBL 220 mm, tail 305 mm, weight 340 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8542. Fazenda Santa Luiza, Rio do Braço, municipality of Ilhéus. Secondary growth scrub. 22 October 1944. Adult female. HBL 225 mm, tail 320 mm, weight 400 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8543. Fazenda Corumba, Rio do Braço, municipality of Ilhéus. Cacao plantation. 29 October 1944. Adult female. HBL 225 mm, tail 325 mm, weight 320 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8544. Sambaituba, Aritagua, municipality of Ilhéus. Banana plantation. 7 November 1944. Adult male. HBL 223 mm, tail 336 mm, weight 320 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8545. Fazenda Novo Horizonte, Castelo Novo, municipality of Ilhéus. Cacao plantation. 27 October 1944. Adult female (old). HBL 210 mm, tail 270 mm, weight 380 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8546. Fazenda Viçosa, Castelo Novo, municipality of Ilhéus. Cacao plantation. 11 November 1944. Adult male. HBL 205 mm, tail 310 mm, weight 380 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8547. Fazenda Baleia, Rio do Braço, municipality of Ilhéus. Cacao plantation. 14 October 1944. Adult male. HBL 225 mm, tail 330 mm, weight 400 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8548. Fazenda Almada, Rio do Braço, municipality of Ilhéus. Secondary growth scrub. 16 December 1944. Adult male. HBL 220 mm, tail 310 mm, weight 400 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8549. Fazenda Almada, Rio do Braço, municipality of Ilhéus. Cacao plantation. 7 November 1944. Adult male. HBL 215 mm, tail 300 mm, weight 370 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8550. Fazenda Provisão, Rio do Braço, municipality of Ilhéus. Cacao plantation. 6 February 1945. Adult female. HBL 220 mm, tail 350 mm, weight 310 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8558. Repartimento, Pontal, municipality of Ilhéus. Forest. 19 October 1944. Adult male. HBL 245 mm, tail 390 mm, weight 400 g. Labeled *Callithrix p. penicillata*. Coll. Galdino Pereira.
- MNRJ 8559. Japu, Repartimento, municipality of Ilhéus. Forest. 24 December 1944. Adult female. HBL 526 mm, tail 300 mm. Labeled *Callithrix penicillata*. Coll. Pedro M. Britto.
- MNRJ 8562. Banco da Vitória, Banco da Vitória, municipality of Ilhéus. Secondary growth scrub. 19 October 1944. Adult male. HBL 215 mm, tail 340 mm, weight 350 g. Labeled *Callithrix penicillata*. Coll. Hugo W. Laemmert.

- MNRJ 8565. Fazenda Promissão, Banco da Vitória, municipality of Ilhéus. Cacao plantation. 9 March 1945. Adult female. HBL 185 mm, tail 320 mm, weight 260 g. Labeled *Callithrix penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8569. Ribeirão da Fortuna, Buerarema, municipality of Ilhéus. Forest. 10 January 1944. Adult male. HBL 210 mm, tail 320 mm. Labeled *Callithrix penicillata*. Coll. GIP.
- MNRJ 8571. Fazenda Ipiranga, Rio do Braço, municipality of Ilhéus. Cacao plantation. 14 March 1945. Juvenile female. HBL 95 mm, tail 140 mm, weight 40 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8574. Fazenda Primavera, Banco da Vitória, municipality of Ilhéus. Secondary growth scrub. 24 January 1945. Adult male. HBL 210 mm, tail 310 mm, weight 330 g. Labeled *Callithrix p. penicillata*. Coll. Hugo W. Laemmert.
- MNRJ 8577. Ribeirão da Fortuna, Buerarema, municipality of Ilhéus. Closed forest. 15 March 1945. Adult female. HBL 205 mm, tail 298 mm, weight 335 g. Labeled *Callithrix p. penicillata*. Coll. GIP.
- MNRJ 23790. Ilhéus. Maintained in a zoo. 26 April 1945. Adult female. HBL 534 mm, tail 300 mm, weight 335 g. Labeled *Callithrix p. penicillata*. Coll. Pedro M. Britto.
- MNRJ 23794. Passui, Belmonte. 16 August 1949. Adult male. HBL 195 mm, tail 340 mm, weight 350 g. Labeled *Callithrix p. penicillata*.
- MNRJ 43933. A sul da Boca do Corrego, Bahia. Juvenile. Labeled *Callithrix kuhlii*. Coll. Lucia Lorini.

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## Appendix 1

Gazetteer — Localities for *Callithrix kuhlii* (Fig. 5)

- MNRJ = Museu Nacional do Rio de Janeiro, Brazil  
 MZUSP = Museu de Zoologia, Universidade de São Paulo, Brazil  
 USNM = National Museum of Natural History, Washington, DC  
 DZ = Departamento de Zoologia, Secretaria de Agricultura do Estado de São Paulo
1. Alegre (Fazenda), região do Barro Branco, sudeste de Rio do Meio, Itororó, Bahia, 15°09'S, 39°56'W. Observation by Pinto (1994).
  2. Almada (Fazenda), Rio Almada, 14°38'S, 39°12'W. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA). Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.938, locality 299). Vaz (2005) lists a series of collecting localities under the general name of “Almada, municipality of Ilhéus, district of Rio do Braço (14°39'S, 39°11'W)”. Attributed to *C. j. geoffroyi* by Ávila-Pires (1969).
  3. Angelim and Salinada, streams in the region of, 19 km to the southeast of Potiraguá, Potiraguá, Bahia, 15°43'S, 39°45'W. Observation by Pinto (1994).
  4. Banco da Vitória, Ilhéus, Bahia. Attributed to *C. penicillata* by Vivo (1991; locality 21), who listed eight skins and eight skulls in the MNRJ. Cited by Mendes (1997; locality K7) and attributed to *C. kuhlii*. Not mapped.
  5. Belmonte, Rio (c.f. Rio Jequitinhonha) 15°45'S, 38°55'W. Wied-Neuwied 1815–1817. Attributed to *C. jacchus penicillata* (= *C. j. penicillata* × *C. j. geoffroyi*) by Hershkovitz (1975, p.142; 1977, p.938, locality 306). Also cited by Kinzey (1982; locality 24). Vivo (1991; locality 25) lists a specimen (skin) from Belmonte, Passui in the MNRJ. Type locality of *C. kuhlii*.
  6. Boa Vista (Fazenda), Belmonte, right bank of lower Rio Jequitinhonha, Bahia, 16°03'S, 39°17'W. Lima (1990, locality 80), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K17), attributed to *C. kuhlii*.
  7. Boa Vista (Fazenda), Itarantim, Bahia, 15°53'S, 40°09'W. Rylands *et al.* (1988, locality 41), attributed to *C. kuhlii*.
  8. Bolandreira (Fazenda), 10 km to the south of Una, BA-001 (Ilhéus-Canavieiras road), Una, Bahia, 15°21'S, 39°00'W. Observation by Pinto (1994).
  9. Buenos Aires (Fazenda), Ribeirão dos Índios, between Ibicuí and Água Doce, Ibicuí, Bahia, 14°48'S, 39°54'W. Observation by Pinto (1994).
  10. Buerarema, Ribeirão da Fortuna. Estação da Mata do Cacau, 14°57'S, 39°19'W. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA). 17 October 1949. Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.938, locality 299). Also cited by Kinzey (1982; locality 18). Vivo (1991) lists three skins and two skulls in the MNRJ. Cited by Mendes (1997; locality K2) and attributed to *C. kuhlii*. See Vaz (2005).
  11. Café sem Troco (Fazenda), km 11, Santa Cruz da Vitória-Itajú do Colônia road, Santa Cruz da Vitória, Bahia, 15°03'S, 39°48'W. Observation by Pinto (1994).
  12. Camacá and Mascote (between), Bahia, 15°32'S, 39°20'W. Mendes (1997, locality K18), attributed to *C. kuhlii*.
  13. Camponesa (Fazenda), Rio Pardo ferry road to the south of Itapetinga, Itapetinga, Bahia, 15°24'S, 40°12'W. Observation by Pinto (1994).
  14. Canavieiras, Estação Experimental (CEPLAC), 16 km to the southwest of Una, Rio São Pedro, Canavieiras, Bahia, 15°23'S, 39°12'W. Observation by Pinto (1994).



15. Castelo Novo, Ilhéus, Bahia. Attributed by Vivo (1991) to *C. penicillata*, listing one skin in the USNM, and six skins and skulls in the MNRJ. Not mapped.
16. Cotovelo (Fazenda), 14 km to the north of Canavieiras, Bahia, 15°33'S, 38°58'W. Observation by Pinto (1994).
17. Cristal (Fazenda), Jacinto and Jordania, Minas Gerais, 16°01'S, 40°05'W. Rylands *et al.* (1988, locality 40), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K14), attributed to *C. kuhlii*.
18. Dendhevea, Fazenda 20 km to the east of Una, Una-Arataka road, Una, Bahia, 15°14'S, 39°13'W. Observation by Pinto (1994).
19. Djalma Bahia, Estação Experimental (CEPLAC), Una, Bahia, 15°17'S, 39°03'W. Observation by Pinto (1994).
20. Ilhéus, 14°49'S, 39°02'W, sea level. Wied-Neuwied 1815–1817. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA). September 1944. E. Garbe, August 1919. Attributed to *C. jacchus penicillata* (*C. j. penicillata* × *C. j. geoffroyi*) by Hershkovitz (1977, p.938, locality 299). Attributed to *C. j. penicillata* by Ávila-Pires (1969). Also cited by Kinzey (1982; locality 18), Vivo (1991; locality 22) lists two specimens (1 skin and 1 skull) in the USNM, 2 skulls in the MZUSP, and one skin in the MNRJ. See Vaz (2005).
21. Ilhéus, 7 km south of, Bahia, 14°51'S, 39°02'W. Oliver and Santos (1991, locality 61), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K12), attributed to *C. kuhlii*.
22. Itabuna, Rio Ilhéus, 14°48'S, 39°16'W. Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.938, locality 300). Also cited by Vivo (1991; locality 23), who listed one skin and one skull in the MUZSP, attributed to *C. penicillata*.
23. Itabuna, vicinity of, Bahia, 14°50'S, 39°17'W. Oliver and Santos (1991, locality 60), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K11), attributed to *C. kuhlii*.
24. Itajubá (Fazenda), Rio Piabanha, 16 km to the north of Itapetinga, Itambé, Bahia, 15°06'S, 40°13'W. Observation by Pinto (1994).
25. Itapetinga (Fazenda), Serra do Felícimo, south of Itarantim, Bahia, 15°48'S, 40°09'W. Observation by Pinto (1994).
26. Japu, Repartimento, Ilhéus, Bahia, 14°55'S, 39°12'W. One specimen in the MNRJ, listed by Mendes (1997) and attributed to *C. kuhlii*. Listed under the general heading of Fortuna (Vaz, 2005).
27. José Deodato Araújo (Fazenda de), 14 km west of Una Una-Arataka road, Una, Bahia, 15°17'S, 39°12'W.
28. Limeira (Fazenda), Sapucaieira, region of the Rio Aguipe, Ilhéus, Bahia, 15°03'S, 39°04'W.
29. Limoeiro, Fazenda, 10 km from the Nova Canaã-Itajai road, Nova Canaã, Bahia, 14°53'S, 40°08'W. Observation by Pinto (1994).
30. Morro das Pedras (Fazenda), Ilhéus, 14°49'S, 39°02'W. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA). September 1944. Attributed to *C. jacchus penicillata* (*C. j. penicillata* × *C. j. geoffroyi*) by Hershkovitz (1977, p.938, locality 299). See location 20 (Fig. 5).
31. Morro Grande (Fazenda do), Salto de Divisa, Minas Gerais, 15°52'S, 40°05'W. Rylands *et al.* (1988, locality 40), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K15), attributed to *C. kuhlii*.
32. Mundo Novo, Rio Pardo, 15°16'S, 40°58'W. Wied-Neuwied 1815–1817. Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.938, locality 298). Also cited by Kinzey (1982; locality 21).
33. Nazaré, vicinity of, Bahia, 12°59'S, 39°00'W; Oliver and Santos (1991, locality 24), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K9), attributed to *C. kuhlii*.
34. Nova Guaiquil (Fazenda), vicinity of Rio do Meio, Itororó, Bahia, 15°08'S, 39°57'W. Observation by Pinto (1994).
35. Palmeira (Fazenda), Palmeira, Serra das Guaribas, left bank of the Rio Jequitinhonha, Itapebi, Bahia, 15°55'S, 39°37'W. Observation by Pinto (1994).
36. Pardo, Rio, 15°39'S, 38°57'W. Wied-Neuwied 1815–1817. Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.938, locality 304). Also cited by Kinzey (1982; locality 23).
37. Pindorama (Fazenda), 10 km to the southwest of Una, right bank of the Rio Aliança, Una, Bahia, 15°19'S, 39°10'W. Observation by Pinto (1994).
38. Pirataquise (Fazenda), 14°50'S, 39°05'W. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA). Attributed to *C. jacchus penicillata* (*C. j. penicillata* × *C. j. geoffroyi*) by Hershkovitz (1977, p.938, locality 299). Also cited by Kinzey (1982; locality 18). Vivo (1991) lists one skull and one skin in the USNM, and 25 skins, 21 skulls in the MNRJ. Cited by Mendes (1997; locality K4) and attributed to *C. kuhlii*. Attributed to *C. j. penicillata* by Ávila-Pires (1969). Vaz (2005) lists a number of localities under the general heading of “Pirataquissé, municipality of Ilhéus. District of Banco da Vitória (14°48'S, 39°07'W).
39. Poções, 14°31'S, 40°21'W. Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.490, locality 301).
40. Pontal dos Ilhéus, 14°49'S, 39°01'W. Attributed to *C. jacchus penicillata* by Kinzey (1982; locality 18). Vivo (1991) listed Fazenda Pontal, Repartimento, Ilhéus, with one skin and one skull in the MZUSP, seven skins and five skulls in the MNRJ, attributed to *C. penicillata*. Cited by Mendes (1997; locality K8) and attributed to *C. kuhlii*.
41. Retiro (Fazenda), Aritaguá, Ilhéus, Bahia. Attributed to *C. penicillata* by Vivo (1991; locality 21), who listed six skins and six skulls in the MNRJ. MNRJ 8524, female. See Vaz (2005). Not mapped.
42. Riacho Filó (Fazenda), region of Piancó, left bank of the Rio Gongoji, Gongoji, Bahia, 14°18'S, 39°41' W. Observation by Pinto (1994).
43. Ribeirão da Fortuna (Fazenda), Ilhéus, Bahia, MN7898, Skin and skull. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA), The Rockefeller Foundation. Collector Galdino Pereira, 10 January 1944. Vaz (2005) lists “Fazenda Ribeirão da Fortuna (mata D, G, P., mata da lagoa, est da mata do cacau); Repartimento; Santa Rita, Japu, rodovia Buerarema km 5” under the general heading of “Fortuna, municipality of Buerarema (14°58'S, 39°14'W)”.
44. Ribeirão das Minhocas, Rio Ilhéus 15°12'S, 39°57'W. Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.490, locality 302).
45. Rio do Braço, Ilhéus, Bahia. Attributed to *C. penicillata* by Vivo (1991; locality 24), who listed one skin in the MZUSP, three skins and three skulls in the USNM, and 43 skins and 40 skulls in the MNRJ. Cited by Mendes (1997; locality K1) and attributed to *C. kuhlii*. See Vaz (2005). Not mapped.
46. Rio do Ouro, headwaters of, southeast of Ibitupã, Ibicuí, Bahia, 14°33'S, 39°44'W. Observation by Pinto (1994).
47. Sambaituba, Aritaguá, Ilhéus, Bahia, 14°43'S, 39°06'W. Attributed to *C. penicillata* by Vivo (1991; locality 21) who listed 11 skins and 10 skulls in the MNRJ. Cited by Mendes (1997; locality K6) and attributed to *C. kuhlii*. See Vaz (2005).
48. Santa Clara (Fazenda), km 9 km of BA-270 (Canavieiras-Santa Luzia road), Canavieiras, Bahia, 15°34'S, 39°04'W. Observation by Pinto (1994).
49. Santa Terezinha (Fazenda), region of Barro Branco, southeast of the Rio do Meio, Itororó, Bahia, 15°08'S, 39°58'W. Observation by Pinto (1994).
50. Una, 15°18'S, 39°04'W. Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.490, locality 303). *C. kuhlii* has also been

- recorded from Una by Rylands (1982, 1989), Santos *et al.* (1987), Mittermeier *et al.* (1981, 1982), Pinto (1994), Raboy (1998).
51. Una, Estação Experimental de Lemos Maia (CEPLAC/CEPEC), Bahia, 15°15'S, 39°05'W. Rylands (1982, 1984, 1989), Stevenson and Rylands (1988), Rylands *et al.* (1991/1992) attributed to *C. kuhlii*. Also Oliver and Santos (1991, locality 67), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K13), attributed to *C. kuhlii*.
  52. Unacau (Fazenda), Bahia, 15°08'S, 39°17'W. Lima (1990, locality 36), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K16), attributed to *C. kuhlii*.
  53. Urucutuca, Aritaguá, Ilhéus, Bahia, 14°39'S, 39°04'W. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA). Attributed to *C. jacchus penicillata* by Hershkovitz (1977, p.938, locality 299). Attributed to *C. penicillata* by Vivo (1991; locality 21). Cited by Mendes (1997; locality K3) and attributed to *C. kuhlii*. Vaz (2005) includes the localities of Fazenda Retiro, Sambaituba, and Cajucatinga under the general heading of "Urucutuca, municipality of Ilhéus, district of Aritaguá (14°39'S, 39°07'W)".
  54. Valença, vicinity of, Bahia, 13°18'S, 39°01'W. Oliver and Santos (1991, locality 36), attributed to *C. kuhlii*. Cited by Mendes (1997, locality K10), attributed to *C. kuhlii*.
  55. [Fazenda Jucuruçu, Rio 17°21'S, 39°13'W. Attributed *C. jacchus penicillata* by Hershkovitz (1977, p.938 and p.490, locality 307a). Ávila-Pires (1969) listed a specimen from Rio Jucuruçu [sic] in the DZ, attributed to *C. p. penicillata*. Also cited by Kinzey (1982, locality 25). Vivo (1991; locality 26) cites four specimens (skins) in the MZUSP. This is outside the recognized geographic distribution of *C. kuhlii* and *C. penicillata*, and may well refer to an introduced specimen of the latter.]

## Appendix 2

Specimens of *Callithrix kuhlii* in the Museu Nacional, Rio de Janeiro, Brazil. List compiled by Sérgio Maia Vaz, Secção de Mamíferos, Museu Nacional, Rio de Janeiro. See Vaz (2005).

MNRJ = Museu Nacional, Rio de Janeiro

SEPSFA = *Serviço de Estudos e Pesquisa sobre a Febre Amarela*, a program in collaboration with the International Health Division of the Rockefeller Foundation, in the municipalities of Ilhéus and Buerarema, state of Bahia, Brazil, December 1943–April 1945 (Laemmert *et al.* 1946).

H.W.L. = H. W. Laemmert, collector.

- MNRJ 7898. Fazenda Ribeirão da Fortuna, Buerarema, Bahia, Female. Col. Galdino Pereira, 10 January, 1944. Skin and skull. M17068, SEPSFA, Rockefeller Foundation.
- MNRJ 8524. Fazenda Retiro, Aritaguá, Ilhéus, Bahia, Female. Col. H. W.L., 1 November, 1944. Skin and skull M22107, SEPSFA, Rockefeller Foundation. Wt. 370 g.
- MNRJ 8525. Sambaituba, Aritaguá, Ilhéus, Bahia, Male. Col. H. W. L., 21 October, 1944. In *capoeira*. Skin and skull M21941, SEPSFA, Rockefeller Foundation. Wt. 300 g.
- MNRJ 8526. Fazenda Provisão, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 6 February 1945. In a cocoa plantation. Skin and skull M22807. SEPSFA, Rockefeller Foundation. Wt. 360 g.
- MNRJ 8527. Fazenda Provisão, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 6 February 1945. In a cocoa plantation. Skin and skull M22808. SEPSFA, Rockefeller Foundation. Wt. 320 g.
- MNRJ 8528. Fazenda Itinga, Pontal, Ilhéus, Bahia, Female. Col. H.W.L., 16 December 1944. In *capoeira*. Skin and skull M22670. SEPSFA, Rockefeller Foundation. Wt. 320 g.
- MNRJ 8529. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 4 February 1945. In a cocoa plantation. Skin and skull M22799. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8530. Fazenda Almada, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 7 November 1944. In a cocoa plantation. Skin and skull M22196. SEPSFA, Rockefeller Foundation. Wt. 370 g.
- MNRJ 8531. Urucutuca, Aritaguá, Ilhéus, Bahia, Unsexed. Col. H.W.L., 2 October 1944. In *capoeira*. Skin and skull M19776. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8532. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 23 October 1944. In a cocoa plantation. Skin and skull M21955. SEPSFA, Rockefeller Foundation. Wt. 310 g.
- MNRJ 8533. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 27 September 1944. In a cocoa plantation. Skin and skull M19744. SEPSFA, Rockefeller Foundation. Wt. 250 g.
- MNRJ 8534. Fazenda Santa Luzia, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 19 October 1944. In *capoeira*. Skin and skull M21918. SEPSFA, Rockefeller Foundation. Wt. 280 g.
- MNRJ 8535. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 29 September 1944. In a cocoa plantation. Skin and skull M19752. SEPSFA, Rockefeller Foundation. Wt. 250 g.
- MNRJ 8536. Fazenda Quixadá, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 9 October 1944. In a cocoa plantation. Skin and skull M21887. SEPSFA, Rockefeller Foundation. Wt. 380 g.
- MNRJ 8537. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 23 October 1944. In a cocoa plantation. Skin and skull M21956. SEPSFA, Rockefeller Foundation. Wt. 300 g.
- MNRJ 8538. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 11 October 1944. In a cocoa plantation. Skin and skull M21860. SEPSFA, Rockefeller Foundation. Wt. 350 g.
- MNRJ 8539. Fazenda Bom Sucesso, Castelo Novo, Ilhéus, Bahia, Male. Col. H.W.L., 19 December 1944. In *capoeira*. Skin and skull M22682. SEPSFA, Rockefeller Foundation. Wt. 270 g.
- MNRJ 8540. Sambaituba, Aritaguá, Ilhéus, Bahia, Male. Col. H.W.L., Col. 11 November 1944. In tall forest. Skin and skull M22230. SEPSFA, Rockefeller Foundation. Wt. 450 g.
- MNRJ 8541. Sambaituba, Aritaguá, Ilhéus, Bahia, Female. Col. H.W.L., 1 November 1944. In banana plantation. Skin and skull M22123. SEPSFA, Rockefeller Foundation. Wt. 340 g.
- MNRJ 8542. Fazenda Santa Luzia, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 22 October 1944. In *capoeira*. Skin and skull M21948. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8543. Fazenda Corumbá, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 29 October 1944. In cocoa plantation. Skin and skull M22082. SEPSFA, Rockefeller Foundation. Wt. 320 g.
- MNRJ 8544. Sambaituba, Aritaguá, Ilhéus, Bahia, Male. Col. H.W.L., 7 November 1944. In banana plantation. Skin and skull M22205. SEPSFA, Rockefeller Foundation. Wt. 320 g.
- MNRJ 8545. Fazenda Novo Horizonte, Castelo Novo, Ilhéus, Bahia, Female. Col. H.W.L., 27 October 1944. In cocoa plantation. Skin and skull M22049. SEPSFA, Rockefeller Foundation. Wt. 380 g.
- MNRJ 8546. Fazenda Viçosa, Castelo Novo, Ilhéus, Bahia, Male. H.W.L. Col. 11 November 1944. In cocoa plantation. Skin and skull M22226. SEPSFA, Rockefeller Foundation. Wt. 380 g.
- MNRJ 8547. Fazenda Baleia, Rio do Braço, Ilhéus, Bahia, Male. H.W.L. Col. 14 October 1944. In a cocoa plantation. Skin and skull M21876. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8548. Fazenda Almada, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 16 December 1944. In *capoeira*. Skin and skull M22671. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8549. Fazenda Almada, Rio do Braço, Ilhéus, Bahia, Male. Col. H.W.L., 7 November 1944. In a cocoa plantation. Skin and skull M22195. SEPSFA, Rockefeller Foundation. Wt. 370 g.
- MNRJ 8550. Fazenda Provisão, Rio do Braço, Ilhéus, Bahia, Female. Col. H.W.L., 6 February 1945. In a cocoa plantation. Skin and skull M22806. SEPSFA, Rockefeller Foundation. Wt. 310 g.

- MNRJ 8551. Fazenda Pedra Branca, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 15 October 1944. In a cocoa plantation. Skin and skull M21888. SEPSFA, Rockefeller Foundation. Wt. 280 g.
- MNRJ 8552. Fazenda Novo Horizonte, Castelo Novo, Ilhéus, Bahia. Female. Col. H.W.L., 8 November 1944. In a cocoa plantation. Skin and skull M22203. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8553. Fazenda Quixadá, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 9 October 1944. In a cocoa plantation. Skin and skull M21884. SEPSFA, Rockefeller Foundation. Wt. 290 g.
- MNRJ 8554. Fazenda Novo Horizonte, Castelo Novo, Ilhéus, Bahia. Female. Col. H.W.L., 8 November 1944. In a cocoa plantation. Skin and skull M22201. SEPSFA, Rockefeller Foundation. Wt. 420 g.
- MNRJ 8555. Fazenda Santa Rita, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 15 December 1944. In a cocoa plantation. Skin and skull M22673. SEPSFA, Rockefeller Foundation. Wt. 280 g.
- MNRJ 8556. Fazenda Almada, Mirante, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 19 September 1944. In a cocoa plantation. Skin and skull M19686. SEPSFA, Rockefeller Foundation. Wt. 380 g.
- MNRJ 8557. Fazenda Progresso, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 30 March 1944. In a cocoa plantation. Skin and skull M17716. SEPSFA, Rockefeller Foundation. Wt. 350 g.
- MNRJ 8558. Repartimento, Pontal, Ilhéus, Bahia. Male. Col. Galdino Pereira, 19 October 1944. In forest. Skin and skull M21967. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8559. Repartimento, Mata do Japú, Ilhéus, Bahia. Female. Col. Pedro M. Britto, 24 December 1943. In forest. Skin and skull. M170003. SEPSFA, Rockefeller Foundation.
- MNRJ 8560. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 14 December 1944. In a cocoa plantation. Skin and skull M22667. SEPSFA, Rockefeller Foundation. Wt. 370 g.
- MNRJ 8561. Sambaituba, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 8 November 1944. In *capoeira*. Skin and skull M22215, SEPSFA, Rockefeller Foundation. Wt. 370 g.
- MNRJ 8562. Banco da Vitória, Banco da Vitória, Ilhéus, Bahia. Male. Col. H.W.L., 19 October 1944. In *capoeira*. Skin and skull M21930, SEPSFA, Rockefeller Foundation. Wt. 350 g.
- MNRJ 8563. Sambaituba, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 8 November 1944. In *capoeira*. Skin and skull M22214. SEPSFA, Rockefeller Foundation. Wt. 390 g.
- MNRJ 8564. Urucutuca, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 13 December 1944. In *capoeira*. Skin and skull M22666. SEPSFA, Rockefeller Foundation. Wt. 250 g.
- MNRJ 8565. Fazenda Promissão, Banco da Vitória, Ilhéus, Bahia. Female. Col. H.W.L., 9 March 1945. In a cocoa plantation. Skin and skull M22884. SEPSFA, Rockefeller Foundation. Wt. 260 g.
- MNRJ 8566. Sambaituba, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 11 November 1944. In forest. Skin and skull M22231. SEPSFA, Rockefeller Foundation. Wt. 350 g.
- MNRJ 8567. Sambaituba, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 6 November 1944. In *capoeira*. Skin and skull M22190. SEPSFA, Rockefeller Foundation. Wt. 280 g.
- MNRJ 8568. Fazenda Provisão, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 10 February 1945. In a cocoa plantation. Skin and skull M22817. SEPSFA, Rockefeller Foundation. Wt. 450 g.
- MNRJ 8569. Ribeirão da Fortuna, Buerarema, Bahia. Male. Col. G.I.D., 10 January 1944. In forest. Skin and skull M17067. SEPSFA, Rockefeller Foundation.
- MNRJ 8570. Sambaituba, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 7 November 1944. In a coffee plantation. Skin and skull M22209. SEPSFA, Rockefeller Foundation. Wt. 360 g.
- MNRJ 8571. Fazenda Ipiranga, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 14 March 1945. In a cocoa plantation. Skin and skull M22895. SEPSFA, Rockefeller Foundation. Wt. 40 g.
- MNRJ 8572. Sambaituba, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 7 November 1944. In a coffee plantation. Skin and skull M22208. SEPSFA, Rockefeller Foundation. Wt. 320 g.
- MNRJ 8573. Fazenda Baleia, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 28 September 1944. In a cocoa plantation. Skin and skull M19746. SEPSFA, Rockefeller Foundation. Wt. 340 g.
- MNRJ 8574. Fazenda Primavera, Banco da Vitória, Ilhéus, Bahia. Female. Col. H.W.L., 24 January 1945. In *capoeira*. Skin and skull M22768, SEPSFA, Rockefeller Foundation. Wt. 330 g.
- MNRJ 8575. Urucutuca, Aritaguá, Ilhéus, Bahia. Male. Col. G.I.P., 10 October 1944. In *capoeira*. Skin and skull M21600. SEPSFA, Rockefeller Foundation.
- MNRJ 8576. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 14 December 1944. In a cocoa plantation. Skin and skull M22668. SEPSFA, Rockefeller Foundation. Wt. 330 g.
- MNRJ 8577. Ribeirão da Fortuna, Buerarema, Bahia. Female. Col. G.I.P., 15 March 1945. In forest. Skin and skull M23756. SEPSFA, Rockefeller Foundation. Wt. 335 g.
- MNRJ 8578. Fazenda Almada, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 11 November 1944. In a cocoa plantation. Skin and skull M22299. SEPSFA, Rockefeller Foundation. Wt. 350 g.
- MNRJ 8579. Fazenda Tamburi, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 11 November 1944. In a cocoa plantation. Skin and skull M22228. SEPSFA, Rockefeller Foundation. Wt. 310 g.
- MNRJ 8580. Sambaituba, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 21 October 1944. In *capoeira*. Skin and skull M21940. SEPSFA, Rockefeller Foundation. Wt. 320 g. (Missing).
- MNRJ 8581. Fazenda Bonfim, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 24 September 1944. In a cocoa plantation. Skin and skull M19728. SEPSFA, Rockefeller Foundation. Wt. 310 g.
- MNRJ 8582. Fazenda Triunfo, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 6 March 1945. In forest. Skin and skull M22874. SEPSFA, Rockefeller Foundation. Wt. 500 g. (Pregnant, gave birth to twins on 8 March 1945).
- MNRJ 8583. Urucutuca, Aritaguá, Ilhéus, Bahia. Male. Col. H.W.L., 13 December 1944. In *capoeira*. Skin and skull M22665. SEPSFA, Rockefeller Foundation. Wt. 370 g.
- MNRJ 8584. Fazenda Lavapés, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 15 October 1944. In *capoeira*. Skin and skull M21903. SEPSFA, Rockefeller Foundation. Wt. 390 g.
- MNRJ 8585. Ponto da Baleia, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 10 October 1944. In a cocoa plantation. Skin and skull M21859. SEPSFA, Rockefeller Foundation. Wt. 360 g.
- MNRJ 8586. Sambaituba, Aritaguá, Ilhéus, Bahia. Female. Col. H.W.L., 23 October 1944. In *capoeira*. Skin and skull M21997. SEPSFA, Rockefeller Foundation. Wt. 370 g.
- MNRJ 8587. Fazenda Santa Luzia, Banco da Vitória, Ilhéus, Bahia. Male. Col. H.W.L., 4 February 1945. In a cocoa plantation. Skin and skull M22801. SEPSFA, Rockefeller Foundation. Wt. 365 g.
- MNRJ 8588. Fazenda Santo Antônio, Pontal, Ilhéus, Bahia. Female. Col. H.W.L., 9 March 1945. In a banana plantation. Skin and skull M22887. SEPSFA, Rockefeller Foundation. Wt. 270 g.
- MNRJ 8589. Urucutuca, Aritaguá, Ilhéus, Bahia. Female. Col. H.W.L., 13 December 1944. In *capoeira*. Skin and skull M22664. SEPSFA, Rockefeller Foundation. Wt. 390 g.
- MNRJ 8590. Fazenda Saudade, Banco da Vitória, Ilhéus, Bahia. Male. Col. H.W.L., 1 February 1945. In a cocoa plantation. Skin and skull M22786. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8591. Fazenda Santa Luzia, Banco da Vitória, Ilhéus, Bahia. Male. Col. H.W.L., 7 February 1945. In a cocoa plantation. Skin and skull M22812. SEPSFA, Rockefeller Foundation. Wt. 430 g.



- MNRJ 8592. Fazenda São Francisco, Castelo Novo, Ilhéus, Bahia. Female. Col. H.W.L., 27 February 1945. In *capoeira*. Skin and skull M22864. SEPSFA, Rockefeller Foundation. Wt. 360 g.
- MNRJ 8593. Fazenda Saudade, Banco da Vitória, Ilhéus, Bahia. Female. Col. H.W.L., 11 February 1945. In *capoeira*. Skin and skull M22819. SEPSFA, Rockefeller Foundation. Wt. 310 g.
- MNRJ 8594. Repartimento, Pontal, Ilhéus, Bahia. Male. Col. G.D., 19 October 1944. In forest. Skin and skull M21971. SEPSFA, Rockefeller Foundation. Wt. 400 g.
- MNRJ 8595. Repartimento, Pontal, Ilhéus, Bahia. Male. Col. G.D., 19 October 1944. In forest. Skin and skull M21968. SEPSFA, Rockefeller Foundation. Wt. 275 g.
- MNRJ 8596. Fazenda Almada, Rio do Braço, Ilhéus, Bahia. Female. Col. G.I.P., 15 November 1944. In *capoeirão*. Skin and skull M22393. SEPSFA, Rockefeller Foundation. Wt. 333 g.
- MNRJ 8597. Fazenda Pirataquissé, Primavera, Ilhéus, Bahia. Male. Col. G.I.P., 29 January 1944. In *capoeirão*. Skin and skull M17188. SEPSFA, Rockefeller Foundation.
- MNRJ 8598. Fazenda Santa Rita, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 28 September 1944. In a cocoa plantation. Skin and skull M19742. SEPSFA, Rockefeller Foundation. Wt. 260 g.
- MNRJ 10998. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Pedro M. Britto, 19 January 1944. Skin M17219. SEPSFA, Rockefeller Foundation.
- MNRJ 10999. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 6 February 1944. Skin M17108. SEPSFA, Rockefeller Foundation.
- MNRJ 11001. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 4 February 1944. Skin and skull M17208. SEPSFA, Rockefeller Foundation.
- MNRJ 11002. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 11 February 1944. Skin and skull M17242. SEPSFA, Rockefeller Foundation.
- MNRJ 11003. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 24 January 1944. Skin and skull M17141. SEPSFA, Rockefeller Foundation.
- MNRJ 11004. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 2 February 1944. Skin and skull M17200. SEPSFA, Rockefeller Foundation.
- MNRJ 11005. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 27 January 1944. Skin and skull M17165. SEPSFA, Rockefeller Foundation.
- MNRJ 11006. Repartimento, Ilhéus, Bahia. Female. Col. Pedro de M. Britto, 24 December 1943. Skin M17004. SEPSFA, Rockefeller Foundation.
- MNRJ 11007. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 14 January 1944. Skin and skull M17143. SEPSFA, Rockefeller Foundation.
- MNRJ 11008. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 24 January 1944. Skin and skull M17142. SEPSFA, Rockefeller Foundation.
- MNRJ 11009. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 28 January 1944. Skin and skull M17176. SEPSFA, Rockefeller Foundation.
- MNRJ 11010. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 9 February 1944. Skin and skull M17233. SEPSFA, Rockefeller Foundation.
- MNRJ 11011. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 4 February 1944. Skin and skull M17207. SEPSFA, Rockefeller Foundation. (Missing).
- MNRJ 11013. Rio do Braço, Ilhéus, Bahia. Female. Col. Pedro M. Britto, 24 February 1944. Skin and skull M17401. SEPSFA, Rockefeller Foundation. (Missing).
- MNRJ 11014. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Pedro M. Britto, 19 January 1944. Skin M17107. SEPSFA, Rockefeller Foundation.
- MNRJ 11015. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 28 January 1944. Skin and skull M17177. SEPSFA, Rockefeller Foundation.
- MNRJ 11016. Rio do Braço, Ilhéus, Bahia. Female. Col. J. Moojen, 24 February 1944. Skin and skull M17402. SEPSFA, Rockefeller Foundation.
- MNRJ 11018. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 3 February 1944. Skin and skull M17202. SEPSFA, Rockefeller Foundation.
- MNRJ 11019. Rio do Braço, Ilhéus, Bahia. Male. Col. J. Moojen, 24 February 1944. Skin and skull M17427. SEPSFA, Rockefeller Foundation.
- MNRJ 11020. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 28 January 1944. Skin and skull M17175. SEPSFA, Rockefeller Foundation.
- MNRJ 11021. Rio do Braço, Ilhéus, Bahia. Male. Col. J. Moojen, 26 February 1944. Skin and skull M17410. SEPSFA, Rockefeller Foundation.
- MNRJ 11023. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 23 January 1944. Skin and skull M17139. SEPSFA, Rockefeller Foundation.
- MNRJ 11024. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 6 February 1944. Skin and skull M17220. SEPSFA, Rockefeller Foundation.
- MNRJ 11025. Rio do Braço, Ilhéus, Bahia. Male. Col. Pedro M. Britto, 26 February 1944. Skin and skull M17407. SEPSFA, Rockefeller Foundation.
- MNRJ 11026. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 23 January 1944. Skin and skull M17138. SEPSFA, Rockefeller Foundation.
- MNRJ 11027. Rio do Braço, Ilhéus, Bahia. Female. Col. J. Moojen, 26 February 1944. Skin and skull M17409. SEPSFA, Rockefeller Foundation.
- MNRJ 11028. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 9 February 1944. Skin and skull M17231. SEPSFA, Rockefeller Foundation.
- MNRJ 11030. Rio do Braço, Ilhéus, Bahia. Female. Col. Pedro M. Britto, 26 February 1944. Skin and skull M17411. SEPSFA, Rockefeller Foundation.
- MNRJ 11031. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 8 February 1944. Skin and skull M17229. SEPSFA, Rockefeller Foundation.
- MNRJ 11032. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 6 February 1944. Skin and skull M17218. SEPSFA, Rockefeller Foundation.
- MNRJ 11034. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 3 February 1944. Skin and skull M17204. SEPSFA, Rockefeller Foundation. (Missing).
- MNRJ 11035. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 23 January 1944. Skin and skull M17137. SEPSFA, Rockefeller Foundation.
- MNRJ 11036. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 9 February 1944. Skin and skull M17232. SEPSFA, Rockefeller Foundation.
- MNRJ 11038. Ilhéus, Bahia. Unsexed. Col. Galdino Pereira. Skin and skull M17151. SEPSFA, Rockefeller Foundation.
- MNRJ 11039. Fazenda Pirataquissé, Ilhéus, Bahia. Female. Col. Galdino Pereira, 29 January 1944. Skin and skull M17187. SEPSFA, Rockefeller Foundation.
- MNRJ 11040. Ilhéus, Bahia. Male. Col. Galdino Pereira. Skin and skull M17602. SEPSFA, Rockefeller Foundation.

- MNRJ 11041. Ilhéus, Bahia. Female. Col. Galdino Pereira. Skin and skull M17604. SEPSFA, Rockefeller Foundation.
- MNRJ 11042. Ilhéus, Bahia. Unsexed. Col. Galdino Pereira. Skin and skull M17585. SEPSFA, Rockefeller Foundation.
- MNRJ 11043. Ilhéus, Bahia. Male. Col. Galdino Pereira. Skin. SEPSFA, Rockefeller Foundation.
- MNRJ 11044. Ilhéus, Bahia. Unsexed. Col. Galdino Pereira. Skin and skull M17136. SEPSFA, Rockefeller Foundation.
- MNRJ 11045. Ilhéus, Bahia. Unsexed. Col. Galdino Pereira. Skin and skull M171584 SEPSFA, Rockefeller Foundation.
- MNRJ 11046. Ilhéus, Bahia. Female. Col. Galdino Pereira. Skin and skull M17654. SEPSFA, Rockefeller Foundation.
- MNRJ 11047. Ilhéus, Bahia. Female. Col. Galdino Pereira. Skin and skull M11834. SEPSFA, Rockefeller Foundation.
- MNRJ 11048. Ilhéus, Bahia. Female. Col. Galdino Pereira. Skin and skull M17158. SEPSFA, Rockefeller Foundation.
- MNRJ 23787. Rio do Braço, Ilhéus, Bahia. Female. Col. J. Moojen, 26 February 1944. Skin and skull M17412. SEPSFA, Rockefeller Foundation.
- MNRJ 23788. Ribeira das Pedras, Rio do Braço, Ilhéus, Bahia. Male. Col. H.W.L., 13 October 1944. In *capoeira*. Skin and skull M21871. SEPSFA, Rockefeller Foundation. Wt. 300 g.
- MNRJ 23789. Fazenda Quixadá, Rio do Braço, Ilhéus, Bahia. Female. Col. H.W.L., 9 October 1944. In a cocoa plantation. Skin and skull M21885. SEPSFA, Rockefeller Foundation. Wt. 390 g.
- MNRJ 23790. Ilhéus, Bahia. Female. Col. Pedro M. Britto, 26 April 1945. Skin M5136. Jardim Zoológico, Rio de Janeiro.
- MNRJ 23791. Rio do Braço, Ilhéus, Bahia. Female. Col. J. Moojen, 26 February 1944. Skin M17408. SEPSFA, Rockefeller Foundation.
- MNRJ 23792. Ilhéus, Bahia. Male. Col. H.W.L., 8 November 1944. In *capoeira*. Skin M22214. SEPSFA, Rockefeller Foundation. Wt. 310 g. (Missing).
- MNRJ 23793. Fazenda Pirataquissé, Ilhéus, Bahia. Male. Col. Galdino Pereira, 6 February 1944. Skin M17221. SEPSFA, Rockefeller Foundation.
- MNRJ 23794. Passuí, Belmonte, Bahia. Male. Col. Unknown, 16 July 1949. Skin M29732(33). SEPSFA, Rockefeller Foundation. Wt. 350 g.
- MNRJ 24775. Ilhéus, Bahia. Unsexed. Col. Galdino Pereira. Skin M17890. SEPSFA, Rockefeller Foundation.
- MNRJ 33519. Ilhéus, Bahia. Male. Col. Galdino Pereira. Skin and skull M5138(7). Jardim Zoológico, Rio de Janeiro.
- MNRJ 33520. Ilhéus, Bahia. Female. Col. Galdino Pereira. Skin and skull M5139(84). Jardim Zoológico, Rio de Janeiro.
- MNRJ 33521. Ilhéus, Bahia. Female. Col. Pedro M. Britto, Skin and skull M5137 Jar.dim Zoológico, Rio de Janeiro.
- MNRJ 33522. Ilhéus, Bahia. Male. Col. Pedro M. Britto. Skin M17858. SEPSFA, Rockefeller Foundation.
- MNRJ 43933. S de Boca do Córrego, Bahia. Unsexed. Col. L. Lorini. Skin, skull and skeleton.
- + 814 skulls.