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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, 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 proposition 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 assignation 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; Alpern 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 (1977) 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-Neuwied (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 kuhlii* 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. kuhlii*. Vivo (1991) reviewed the systematics of the marmosets and concluded that they should all be considered species, but that the form *kuhlii*, 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 *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 assignation of the authorship of the name *kuhlii*.

**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 (Eliott 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):


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, variably 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 Paraíba, 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 “Lamarãö, 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).


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, north-west 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, Prov-ince 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 *penicil-
lata*. 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 *penicil-
lata* 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 major-
ity 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 yel-
low 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; Avila-Pires 1969; Coimbra-Filho 1971, 1972; Coim-
bra-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. *Cal-
lichritis 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
"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.
Table 1. Hybrids born at the Rio de Janeiro Primate Center (CPRJ/FEEMA), Rio de Janeiro.

<table>
<thead>
<tr>
<th>Registration no.¹</th>
<th>Birth number</th>
<th>Date of birth</th>
<th>No. of offspring (sex)</th>
<th>Death</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C. kuhlii (male) × C. jacchus (female)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>First</td>
<td>3 April 1976</td>
<td>2 (0.1.1)</td>
<td>29 June 1976², 29 June 1976</td>
</tr>
<tr>
<td>MP 075</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MP 122</td>
<td>Second</td>
<td>?</td>
<td>2 (2.0)</td>
<td>29 March 1978, 29 March 1978</td>
</tr>
<tr>
<td>MP 123</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>C. kuhlii (male) × C. penicillata (female)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MP 191</td>
<td>First</td>
<td>9 December 1978</td>
<td>2 (1.1)</td>
<td>7 February 1980, 25 February 1980</td>
</tr>
<tr>
<td>MP 197</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>C. kuhlii (male) × C. geoffroyi (female)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>First</td>
<td>19 June 1973</td>
<td>1 (0.1)</td>
<td>13 November 1975</td>
</tr>
<tr>
<td>MP 106</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>Second</td>
<td>28 November 1973</td>
<td>2 (0.1.1)</td>
<td>5 December 1973, 5 May 1976</td>
</tr>
<tr>
<td>MP 033</td>
<td>Third</td>
<td>2 May 1974</td>
<td>1 (0.1)</td>
<td>20 March 1978</td>
</tr>
<tr>
<td>MP 121</td>
<td>Fourth</td>
<td>17 September 1974</td>
<td>1 (0.1)</td>
<td>22 August 1978</td>
</tr>
<tr>
<td>MP 127</td>
<td>Fifth</td>
<td>23 May 1975</td>
<td>1 (1.0)</td>
<td>25 July 1980</td>
</tr>
<tr>
<td>MP 221</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>C. geoffroyi (male) × C. penicillata (female)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MP 145</td>
<td>First</td>
<td>16 November 1977</td>
<td>2 (2.0)</td>
<td>19 January 1979, 24 May 1979</td>
</tr>
<tr>
<td>MP 152</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MP 181</td>
<td>Second</td>
<td>14 September 1979</td>
<td>2 (2.0)</td>
<td>16 January 1980, Alive</td>
</tr>
<tr>
<td>MP 221</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹MP = Museu de Primatologia (CPRJ).
²Material lost, no registration number.

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. Hilare 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.
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 Shigebara (1992) in their studies of the dental morphology, and Natori (1994) in his cranio-metric 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 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 Seuánz et al. (1988) and Nagamachi (1995). Nagamachi (1995; Nagamachi et al. 1997) carried out a study of the chromosome morphology of *C. kuhl* 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. kuhl* 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. kuhl*, although their paralogy is also only weakly supported (i.e., a monophyletic *C. kuhl* 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. kuhl*, *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 *kuhl*), 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 kuhl**

**Intergradation and hybrid zones in the wild**

Hershkovitz (1975, 1977) argued that the form *kuhl* 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. kuhl* 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 Espirito Santo from Conceição da Barra to Barra do Itapemirim, 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 Espirito Santo, they would almost certainly merge [...]. Offspring of the predicted inter-
Taxonomic status of the *Callithrix kuhlii*

gradation would likely be classified as *geoffroyi* or *penicillata*, depending on the degree of phenetic resemblance to either parent.” (p.42). 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 Jucurucu, 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. Jucurucu, 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 striped 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 Jucurucu is not clearly identified. Vivo (1991, locality 26) listed it as “Rio Jucurucu (boca [mouth]) 17°32′S, 39°14′W”, which is a little south of the mouth of the Rio Jucurucu, south of the town of Prado. In the place name index “Localidades da Coleção do Museu de Zoológia de São Paulo,” a compilation by Paulo Emílio Vanzolini, kept in the museum, the following coordinates are given “Rio Jucurucu (= Cachoeira Grande), Bahia (17°15′S, 39°46′W)”, a location on the middle of the southern arm of the Rio Jucurucu, near to the village of Torcida, inland. Kinzey (1982) listed the Rio Jucurucu (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 Jucurucu 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 Jucurucu is otherwise the domain of *C. geoffroyi*.

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.
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 (Itapeci and Belmonte), but they argued that this probably resulted from small, introduced populations of the former. Hybrids possibly occur along the upper Rio Araquai, 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 Valencia, 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 mix of animals 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 M1, 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 (cinzclaro) 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. 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 parphylogy 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 mitigated 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
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 “Kuhliii” 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 trinomium 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, pp.107) 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.).

![Sonograms of representative long calls of Callithrix.](https://bioone.org/journals/Primate-Conservation)
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).

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

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 Kuhlus prior to using the generic, hence Kuhl, 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 generic based upon a personal name in which the correct original spelling terminates with -i, or vice-versa, constitutes an incorrect subsequent spelling, even if the change in spelling is deliberate...” The use of the specific name “kuhlii” with one “i” would, therefore, be incorrect. Coimbra-Filho (1985) referred to the species as *Callithrix kuhlii*.


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 kuhlisi* 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, southeast 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, legs and feet 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*,

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[1] *Note:* The English translation is slightly altered for clarity.
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 ± 1.01 mm, n = 43; mean cranial width (euryon to euryon) 22.92 ± 0.80 mm, n = 44; mean mandible width (bicondylar breadth) 25.6 ± 0.76 mm, n = 43; mean length of upper post-incisor tooth row (mesial surface of left C¹ to distal surface of left M²) 11.89 ± 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, Brazil (Coimbra-Filho 1985, 1990) (Fig. 5). It is possible that its range extended north along the coast to the Rio Paraguacu, 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 Jucurucu, 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 Araçáui (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. penicillata 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 11286, 11288-89. Rio Urucuia, Cachoeira, municipality of Buritis, Minas Gerais. 3 November 1964. Coll. Exp. DZ.


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


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.


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**Appendix I**

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

<table>
<thead>
<tr>
<th>MNRJ = Museu Nacional do Rio de Janeiro, Brazil</th>
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<tbody>
<tr>
<td>MZUSP = Museu de Zoologia, Universidade de São Paulo, Brazil</td>
</tr>
<tr>
<td>USNM = National Museum of Natural History, Washington, DC</td>
</tr>
</tbody>
</table>

| DZ = Departamento de Zoologia, Secretaria de Agricultura do Estado de São Paulo |

1. Alegre (Fazenda), região do Barro Branco, sudeeste de Rio do Meio, Itororó, Bahia, 15°09′S, 39°56′W. Observation by Pinto (1994).


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).


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. Bolandeira (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 Icuiú and Água Doce, Itacuí, Bahia, 14°48′S, 39°54′W. Observation by Pinto (1994).


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).


16. Cotovelho (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. Dendheua, Fazenda 20 km to the east of Una, Una-Arataca road, Una, Bahia, 15°14′S, 39°13′W. Observation by Pinto (1994).


21. 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. jacchus penicillata*.

22. 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*.

23. Itajuiú (Fazenda), Rio Piabanha, 16 km to the north of Itapetínga, Itambé, Bahia, 15°06′S, 40°13′W. Observation by Pinto (1994).

24. Itapetinga (Fazenda), Serra do Felicó, south of Itarantém, Bahia, 15°48′S, 40°09′W. Observation by Pinto (1994).

25. Itaperuçu (Fazenda), Ilhéus, Bahia, 14°55′S, 39°12′W. One specimen in the MRNJ, listed by Mendes (1997) and attributed to *C. kuhlii*. Listed under the general heading of Fortuna (Vaz, 2005).

26. José Deodato Araújo (Fazenda de), 14 km west of Una Una-Arataca road, Una, Bahia, 15°17′S, 39°12′W.

27. Limeira (Fazenda), Sapucaieira, region of the Rio Aguípe, Ilhéus, Bahia, 15°03′S, 39°04′W.

28. Limoério, Fazenda, 10 km from the Nova Canaã-Itajai road, Nova Canaã, Bahia, 14°53′S, 40°08′W. Observation by Pinto (1994).

29. Morro das Pedras (Fazenda), Ilhéus, 14°49′S, 39°02′W. Serviço de Estudos e Pesquisa sobre a Febre Amarela (SEPSFA). September 1944. 

30. 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*.


33. Nova Guaiaquil (Fazenda), vicinity of Rio do Meio, Itororó, Bahia, 15°08′S, 39°57′W. Observation by Pinto (1994).

34. Palmeira (Fazenda), Palmeira, Serra das Guaribas, left bank of the Rio Jequitinhonha, Itapebi, Bahia, 15°55′S, 39°37′W. Observation by Pinto (1994).


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).


40. Pontal dos Ilhéus, 14°49′S, 39°01′W. Attributed to *C. jacchus penicillata* by Knzey (1982; locality 18). Vivo (1991) listed Fazenda Pontal, Repartimento, Ilhéus, with one skin and one skull in the MUZSP, seven skins and five skulls in the MRNJ, attributed to *C. jacchus penicillata*. Cited by Mendes (1997; locality K8) and attributed to *C. kuhlii*.


42. Rio 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 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)”.


46. Rio do Ouro, headwaters of, southeast of Itipupá, Icibui, Bahia, 14°33′S, 39°44′W. Observation by Pinto (1994).

47. Sambaituba, Artagauerá, 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 MRNJ. 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


Appendix 2


MN RJ = 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 Buer-


Combra-Flho


+ 814 skulls.