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A MORPHOLOGICAL ANALYSIS OF SOME SPECIES OF *CALLICEBUS,* THOMAS, 1903 (PITHECIIDAE - CALLICEBINAE)

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Abstract

A chromogenetic field analysis was performed with 25 of 29 of the known species of the genus *Callicebus*. Some species presented polymorphism, such as *C. moloch, C. hoffmansii* and *C. cupreus. C. bernhardi* presents the same distribution of color in chromogenetic fields as *C. moloch*, differing only in pigment amount, mainly in ventral surfaces, suggesting *C. bernhardi* is a junior synonym of *C. moloch*. *C. hoffmansii* presents two distinct phenotypes, but without a geographic barrier between them. *Callicebus cupreus*, *C. dubius* and *C. caligatus* are distinct species.

Key Words: Callicebus, taxonomy, phenotypical polymorphism

Resumo

Uma revisão taxonômica baseada nos campos cromogenéticos foi procedida em 25 das 29 espécies conhecidas do gênero *Callicebus*. Algumas espécies apresentaram polimorfismo como *C. moloch, C. hoffmansii e C. cupreus. Callicebus bernhardi* apresenta o mesmo padrão de distribuição de campos cromogenéticos de *C. moloch*, divergindo somente na quantidade de pigmentos, principalmente na face ventral da pelagem. Assim, *C. bernhardi* deve ser considerado sinônimo júnior de *C. moloch. C. hoffmansii* apresenta dois fenótipos distintos, porém não há uma barreira geográfica entre eles. *C. cupreus, C. dubius* e *C. caligatus* são espécies distintas.

Palabras Clave: *Callicebus*, taxonomia, polimorfismo fenotípico

Introduction

Although new species of *Callicebus* have been described from Brazil and Bolivia during the last decade, few taxonomic studies had been made on this genus during the same period. The first taxonomic review was performed by Elliot (1913), who recognized 22 monotypic species. This arrangement has been modified by several researchers, such as Tate (1939), Thomas (1927), Lönnberg (1939), Cruz-Lima (1945), Vieira (1955) and Cabrera (1958), who proposed more detailed taxonomic arrangements, defined geographical distributions and suggested phylogenetic relationships within the taxon. Hill (1960), influenced by those authors, proposed a more complete taxonomic arrangement. More recently, only Hershkovitz (1990), Kobayashi (1995) and Anselmo (1997) performed taxonomic studies of *Callicebus*. Hershkovitz (1990) based in skull, skeleton morphology and pelage color, recognized 13 species with 25 subspecific taxa, divided among four groups, as listed in Table 1.

Kobayashi (1995) carried a phenetic analysis based on metric skull characters, besides cariotype, pelage coloration and geographic distribution of 23 species and subspecies (*C. oenanthe, C. aureipalatti* and *C. coimbrai* were not included; the last two had not been described at that time). He recognized five species groups (Table 1) and stated these groups are independent lineages since the rates of character differentiation were not significantly different among the nearest related groups. Among these groups, Kobayashi (1995) pointed out a great differentiation rate between *personatus* and *torquatus*, while *donacophilus*, *cupreus*, *moloch* appear more closely related. Concerning the pelage color pattern of the *moloch* group, Kobayashi considered *donacophilus* and *personatus* groups as "no contrasting pattern", burnt yellow for *donacophilus* and blackish to yellowish for *personatus*; the *cupreus* group was defined as "weakly contrasting" and *moloch* and *torquatus* groups as "contrasting ventral surfaces" and "throat with white band", respectively. Roosmalen *et al.* (2002) described two new species (*C. stephennashi* and *C. bernhardi*), and considered five species groups: 1. *torquatus,* 2. *personatus,* 3. *moloch,* 4. *cupreus,* 5. *donacophilus.*

The great individual and population color variation in *Callicebus* raises several doubts and, sometimes, misunderstanding about the taxonomy of this genus. Aquino *et al.* (2008) found two distinctive populations of *Callicebus torquatus* in northeast Peru. Although several characteristics such as the shape of the hair tuft on the throat

(a characteristic of *torquatus* group), color tones on hands and the width of frontal band, seems to be different among those populations, the authors were not confident whether the two populations could be considered as different taxa or not. Heymann *et al.* (2002) also found problems with *Callicebus* phenotypical characterization, notably on the color of the hands. Moore (2009) tested the use of pelage color characters as diagnostic taxonomic markers across the geographic distribution of the *Callicebus* cupreus-group as an example. He found both a clinal variation along a geographic transect, as well as a localized intra-populational variation. He emphasizes that systematists should be careful while considering the relationship between intra-populational variation and geographic distribution. In this

Table 1. Taxonomic *status* synopsis of *Callicebus* as presented by some authors and this work (modified from Roosmalen, 2002).

Hershkovitz (1963)	Hershkovitz (1988, 1990)	Kobayashi (1995)	Groves (2001)	Roosmalen et al, 2002	Auricchio (2005)
	Group *modestus*		**Group** *modestus*		
	C. modestus		*C. modestus*		
	Group *donacophilus*	**Group** *donacophilus*	**Group** *donacophilus*	**Group** *donacophilus*	**Group** *donacophilus*
C. moloch donacophilus	*C. donacophilus donacophilus*	*C. donacophilus donacophilus*	*C. donacophilus*	*C. donacophilus*	*C. donacophilus*
	C. d. pallescens	*C. d. pallescens*	*C. pallescens*	*C. pallescens*	*C. pallescens*
	C. oenanthe		*C. oenanthe*	*C. oenanthe*	*C. oenanthe*
		C. modestus		*C. modestus*	*C. modestus*
	C. olallae	*C. ollalae*	*C. olallae*	*C. olallae*	*C. olallae*
C. m. moloch	**Group** *moloch*	**Group** *moloch*	**Group** *moloch*	**Group** *moloch*	**Group** *moloch*
	C. moloch	*C. moloch*	*C. moloch*	*C. moloch*	*C. moloch*
	C. cinerascens	*C. cinerascens*	*C. cinerascens*	*C. cinerascens*	*C. cinerascens*
C. m. hoffmannsi	*C. h. hoffmannsi*	*C. h. hoffmannsi*	*C. hoffmannsi*	*C. hoffmannsi*	*C. hoffmannsi*
	C. h. baptista	*C. h. baptista*	*C. baptista*	*C. baptista*	*C. baptista*
C. m. brunneus	*C. brunneus*	*C. brunneus*	*C. brunneus*	*C. brunneus*	*C. brunneus*
	C. caligatus			*C. bernhardi*	
	C. dubius	**Group** *cupreus*		**Group** *cupreus*	**Group** *cupreus*
C. m. cupreus	*C. cupreus cupreus*	*C. cupreus cupreus*	*C. cupreus cupreus*	*C. cupreus*	*C. cupreus*
C m. discolor	*C. c. discolor*	*C. c. discolor*	*C. c. discolor*	*C. discolor*	*C. discolor*
C. m. ornatus	*C. c. ornatus*	*C. c. ornatus*	*C. c. ornatus*	*C. ornatus*	*C. ornatus*
	C. personatus personatus		*C. personatus personatus*	*C. caligatus*	*C. caligatus*
			C. coimbrai		
	C. p. melanochir		*C. p. melanochir*	*C. dubius*	*C. dubius*
	C. p. nigrifrons		*C. p. nigrifrons*	*C. stephennashi*	*C. stephennashi*
	C. p. barbarabrownae		*C. p. barbarabrownae*		*C. aureipalatti*
	Group *torquatus*	**Group** *torquatus*	**Group** *torquatus*	**Group** *torquatus*	**Group** *torquatus*
C. torquatus torquatus	*C. torquatus torquatus*	*C. torquatus torquatus*	*C. torquatus torquatus*	*C. torquatus*	*C. torquatus*
C. t. lugens	*C. t. lugens*	*C. t. lugens*	*C. t. lugens*	*C. lugens*	*C. lugens*
	C. t. lucifer	*C. t. lucifer*	*C. t. lucifer*	*C. lucifer*	*C. lucifer*
	C. t. purinus	*C. t. purinus*	*C .t. purinus*	*C. purinus*	*C. purinus*
	C. t. regulus	*C .t. regulus*	*C. t. regulus*	*C. regulus*	*C. regulus*
C. t. medemi	*C. t. medemi*	*C. t. medemi*	*C. medemi*	*C. medemi*	*C. medemi*
		Group *personatus*		**Group** *personatus*	**Group** *personatus*
		C. personatus		*C. personatus*	*C. personatus*
		C. melanochir		*C. melanochir*	*C. melanochir*
		C. nigrifrons		*C. nigrifrons*	*C. nigrifrons*
		C. barbarabrownae		*C. barbarabrownae*	*C. barbarabrownae*
		C. coimbrai		*C. coimbrai*	*C. coimbrai*

article I present an analysis of the color pattern of all *Callicebus* specimens from the main Brazilian collections, in order to evaluate phenotypical polymorphism and the validity of these species using the color pattern of fur and hair as diagnosable characters.

Material and methods

I examined 455 dry skins of 25 species from 136 localities belonging to the following collections: Museu de Zoologia da Universidade de São Paulo (MZUSP - 194 specimens); Museu Nacional do Rio de Janeiro (MNRJ - 97); Museu Paraense Emílio Goeldi (MPEG - 130); Instituto Nacional de Pesquisas da Amazônia (INPA - 10); Instituto Pau Brasil de História Natural (IPBHN - 10; Universidade de Brasília (UnB - 1) and Centro de Primatologia do Rio de Janeiro (CPRJ – 4). Appendix I lists the specimens together with geographic coordinates, label identification and a review of identification as found after this analysis. One specimen of *C. pallescens* and one of *C. caligatus* were studied alive in captivity. Material of *Callicebus medemi, C. oenanthe, C. ollalae, C. modestus* and *C. auriepallati* were not available so these were excluded from this study.

Characters were chosen based on the pelage color of body parts or chromogenetic fields. Following Hershkovitz (1977), these are defined as any part of the pelage showing a particular color pattern from nearby areas, (for instance, the forearm, the back, one sub-apical band in a hair, etc), as shown in Figure 1. I could find chromogenetic fields characters only in pelage, not in hair, so the analysis focused on those. Each specimen was morphologically analyzed and

Table 2. Distinctive characters among *C. cupreus, C. caligatus* and *C. dubius.*

	***C. cupreus* phenotype 1 (most common)**	***C. caligatus***	***C. dubius***
Face	Reddish-cream	Dark reddish brown	Sideburns, sides of head and beard deep red
Forehead	reddish-cream (agouti hair banded with light stripes longer than dark ones)	Frontal Black stripe with no abrupt division with nape	transversal frontal band whitish, with a fine black line of superciliar vibrissae which connects the blackish ears
Crown	reddish-cream (agouti hair banded with light stripes longer than dark ones).	Black (rostral part)	brownish agouti; hairs with 4–5 pheomelanic bands, each alternated with eumelanic band.
Nape	reddish-cream (agouti hair banded with light stripes longer than dark ones).	Dark reddish brown -agouti. Each hair reddish brown with black tip	brownish agouti; hairs with 4–5 pheomelanic bands, each alternated with eumelanic band.
Back	reddish-cream (agouti hair banded with light stripes longer than dark ones).	Black	Brownish agouti. brownish agouti; hairs with 4–5 pheomelanic bands, each alternated with eumelanic band.
Lower back	reddish-cream (agouti hair banded with light stripes longer than dark ones), but washed with brown.	Dark reddish brown -agouti. Each hair reddish brown with black tip	Reddish -brown -agouti brownish agouti; hairs with 4–5 pheomelanic bands, each alternated with eumelanic band
External surface of fore legs and forearms	intense redish brown which can vary to orangish.	Dark reddish brown -agouti. Each hair reddish brown with black tip	Reddish
Back of Hands	Brown, not agouti	Black	Blackish agouti,
Fingers	Brown, not agouti	Black	Contrasting white
Back of Feet	Brown, not agouti	Black	Contrasting white
Base of tail	Reddish-cream (agouti hair banded with light stripes longer than dark ones), but washed with brown.	Black (20%)	Reddish-brown -agouti
Middle tail	Reddish-cream (agouti hair banded with light stripes longer than dark ones), but washed with brown.	Greyish, black/beige or burnt yellow (blackish hairs with 0.7 cm of whitish tip)	Blackish.
Tip of tail	Reddish-cream (agouti hair banded with light stripes longer than dark ones), but washed with brown.	Burnt yellow/ beige brush (INPA 4032)	Contrasting white brush
Ventral surface	Intense reddish brown which can vary to orangish.	Deep reddish-brown agouti. Each hair reddish-brown with black tip;	Hairs of throat blackish agouti; chest, belly and ventral surface of legs and arms reddish or reddish-brown; not banded.

assigned to different chromogenetic pattern groups by comparing the color pattern of 14 regions (shown in Figure 1, plus chest, belly and ventral surface of limbs), considering color tone variation as character states. This variation is due to the pigment present in hairs. Hershkovitz (1977) points out pheomelanin as the pigment responsible for yellows, browns and reds, depending on the amount of it deposited in the hair. Melanin is the pigment which gives black and gray colors to the hair. The analyses were performed by simple visual inspection, for example: when the character was crown with melanin pigment, states could be gray or black. Characters used in this study are listed in Table 2.

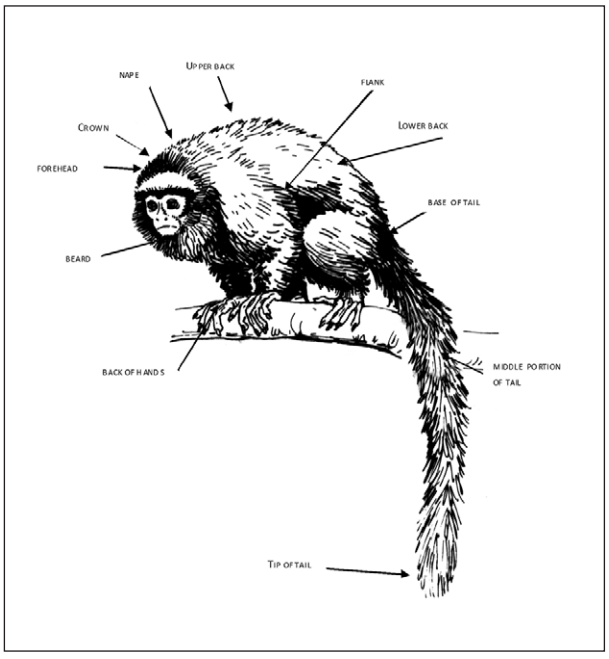

Figure 1. Pelage chromogenetic fields considered for this analysis.

Collecting sites were plotted (Fig. 2) and compared with bibliography. Although almost all *Callicebus* species were included in this analysis (25 of 29 species), only the ones with taxonomic problems are discussed in this paper. Table 3 lists these species and the number of specimens analyzed.

Results and Discussion

Morphological Analysis

1. *C. moloch*/ *C. bernhardi*

Pelage chromogenetic analysis shows *C. moloch* has great color tone variation on several chromogenetic fields, especially on the ventral surface, which ranges from yellow to reddish-brown. I could split the specimens into three phenotypes: "*normal phenotype", "red phenotype"* and *"light phenotype"*. The "normal phenotype" is the commonest (84% of the sample) and has a cream forehead, crown (banded

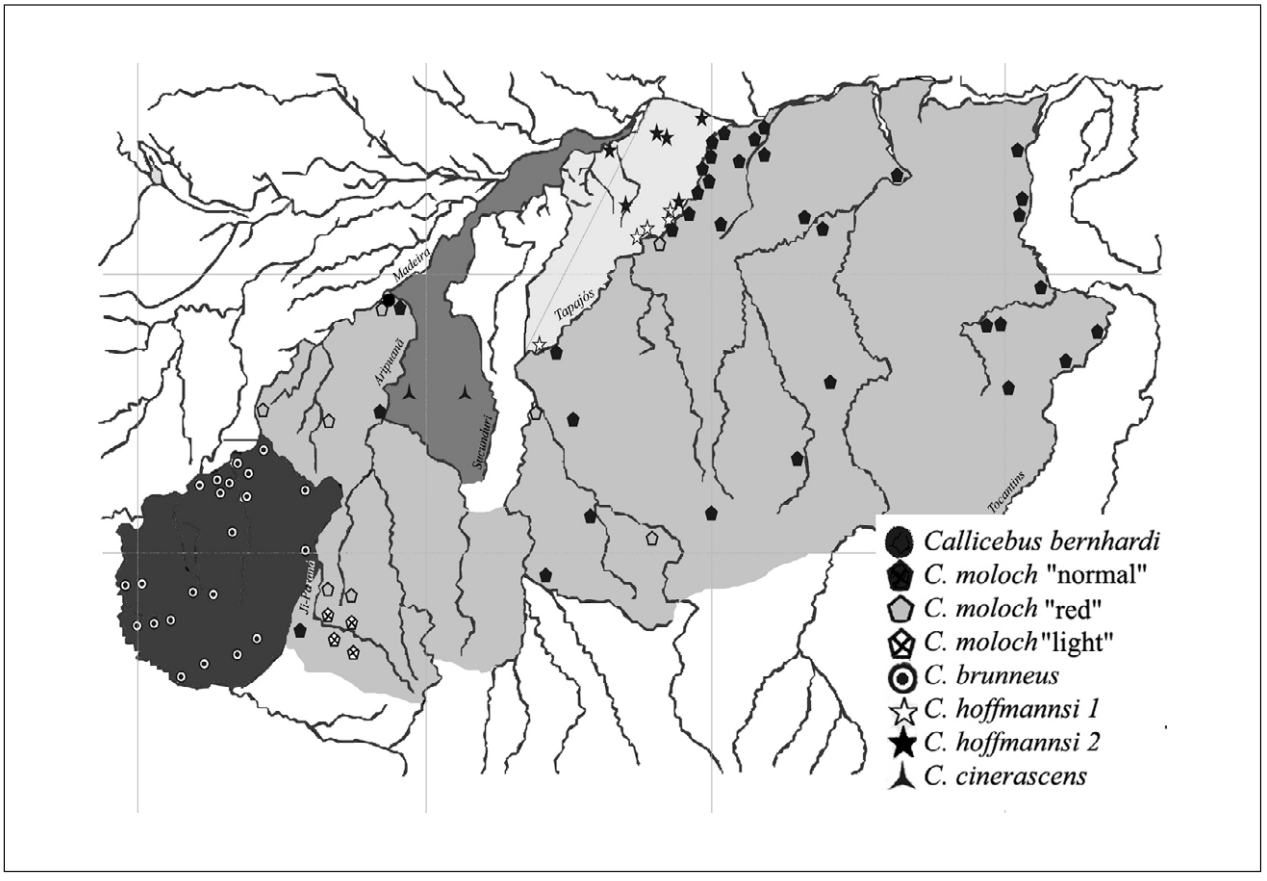

Figure 2. Map of collecting sites of *Callicebus* (*C. bernhardi, C. moloch* (3 forms), *C. brunneus*, *C. hoffmannsi* (2 forms) and *C. cinerascens*). Black arrow indicates a locality where all 3 phenotypes of *C. moloch* appear sympatric. Numbers refer to Appendix I localities.

hair showing light bands broader than dark ones) flanks, dorsal surface of limbs, feet and hands; lower-back light brown with a slight brown stripe along the middle back, slightly darker than the flanks, not washed with brown or it has very little amount of this pigment. The middle portion of tail is very dark (from dark brown to black) and the tip lightening to very light brown or dirty white. Beard, chest, belly and ventral surface of limbs are light orange-brown, more pigmented at the tip of hairs.

The general color pattern of all specimens follows the description above, but specimens IPBHN 207, 208, 209 (loc. 52, Ig Almas, Rio Juruena, extreme north of Apiacás, MT); MZUSP *18956* (loc.53 – RO, Nova Colina Polonoroeste); MZUSP 18964, 20253, *20255*, 20058, 20067 (loc.54 - RO, Nova Brasília Polonoroeste); MPEG 21972 (loc. 112 - PA, Ig. do Patauá, Município de Itaituba); MPEG 22000 (loc. 113 - PA, Apui, BR-230 Humaitá-Itaituba km 17) have the ventral pelage extremely pheomelanized of a live reddish-brown. These represent what I called *"red phenotype"*. A third phenotype, called here *"light phenotype"* has ventral parts much lighter, sort of a lime-yellow (specimens MZUSP 5198 and 5200 from loc. 82 – AM, Bom Jardim, right margin of Amazonas River); MPEG 22014, 22015, 22016, 22017 (loc. 109 – PA, UHE Tucuruí, Tocantins River); MPEG 245 (loc. 95 – PA, São João do Araguaia); MPEG 246 (loc. 94 – PA, Alto Iriri River, Xingu).

Roosmalen *et al.* (2002) described *C. bernhardi* and identified specimens MPEG 22996, 22997 (locality 50 - BR km 150 Apis-Humaitá, right margin of Marmelos River, AM); MPEG 24590 and 24591 (locality 55 - Alta Floresta, MT) as belonging to this taxon. Paratypes of *C. bernhardi* (INPA 4029 and 4033; locality 57 - AM River Mariepauá left aff. River Madeira) show the same chromogenetic pattern as *C. moloch*, with identical chromogenetic fields. These specimens differ only in color tone and pigment amount on the ventral surface, exactly as seen in the *"red phenotype"*. In Roosmalen *et al.* (*op. cit.*), diagnostic characters that distinguish *C. bernhardi* of *C. moloch* are described as follows: "*...by grayish forehead and crown, white ear tufts, and blackish tail with a distinct white pencil*". Actually, there is wide variation in forehead and crown color tone among all 183 specimens of the 3 phenotypes, from grayish to light red-brown, and the description above agrees perfectly with most specimens analyzed of "normal phenotype" as well.

Table 3. Material used for this study.

Species	Skins	Alive
C. moloch "normal phenotype"	154	
*C. moloch "red phenotype" / C. bernhardi**	20	
C. moloch "light phenotype"	9	
C. hoffmannsi	27	
C. brunneus	56	
C. dubius	1	
C. cupreus	70	
C. caligatus	2	1
TOTAL	**339**	**1**

Concerning the auricular tufts, none of 183 specimens of *C. moloch* (3 phenotypes) and those identified as *C. bernhardi* in INPA and MPEG that I could analyze, presented white auricular tufts (including *C. bernhardi* paratypes). Tails of all *"red phenotype"* specimens as well as *C. bernhardi* specimens are identical to *C. moloch*: black with a lighter tip. Drawings of *C. moloch* in Roosmalen *et al.* (2002) do not show a black tail and the whitish back of the hands, not matching all specimens analyzed. Thus, all specimens of the "*normal phenotype", "red phenotype", "light phenotype"* and those described as *C. bernhardi* show the same chromogenetic field pattern, differing, as mentioned, only in the amount of pigment (color tone) of the ventral surface.

Concerning the geographic distribution of *C. moloch* (all phenotypes), it is the broadest among all *Callicebus* species, occurring south of the Amazonas River, between the right margin of Madeira/Ji-Paraná Rivers to the left margin of Tocantins River. *C. moloch* is not found between the right margin of Aripuanã River and the left margin of Abacaxis River, where *C. cinerascens* is found (Noronha, *et al.* 2007). *Callicebus moloch* is found in Rondônia on both margins of the medium/upper Ji-Paraná River (Ferrari, *et al.* 2000), what is confirmed by specimens MZUSP 18956 (RO, Nova Colina Polonoroeste, right margin of Ji-Paraná River 10°48'S61°43'W, *"red phenotype";* MZUSP 18964, 20253, 20255, 20058, 20067 (RO, Nova Brasília Polonoroeste, right margin of Ji-Paraná River – 10°56'S61°20'W *"red phenotype",* and MPEG 19709, 19710, 19712, 19713 (Alvorada d'Oeste, BR 429 linha 64 km 87, left margin of Ji-Paraná River - 11°23'S62°18'W *normal phenotype.* Monção *et. al.* (2008) also assigned specimens they called *C. bernhardi* (here, "*red phenotype*") to 90 km west of Alto Alegre dos Parecis (Chapada dos Parecis, Rondonia).

Roosmalen (2002) states that there is a gap in the range of *Callicebus* at the southern portion of this region, between Sucunduri/Juruena River and Tapajós River. I could not find any specimens in Brazilian museums from this region. Wide rivers such as the Juruena / Teles Pires / Tapajós are no barriers isolating the three phenotypes of *C. moloch.* Gascon *et al.* (2000) observed that wide rivers are not always obstacles to put apart small mammals and frogs as well.

Localities for *C. bernhardi* indicated by Roosmalen *et al.* (2002) are: 51 (AM, Comunidade de Nova Olinda, right margin of Aripuanã River, Novo Aripuanã – holotype, INPA 3929 only skeleton) and 57 (AM, Mariepauá River, right tributary of Madeira River – paratypes of *C. bernhardi*). Specimens MNRJ 2480 and 2481 (from AM, right margin of São João do Aripuanã River) presents *"light phenotype*" and this locality is only 30 km straight line from locality 51 and 60 km from locality 57, mentioned

above, on the same bank of Aripuanã River. In the locality 109 (PA, UHE Tucuruí rio Tocantins) it is possible to find both *"light and normal phenotype*" as can be seen in specimens MPEG 21442, 21443, 22014, 22015, 22016, 22017, 22016 (normal phenotype) MPEG 22018 (light phenotype), one evidence of polymorphism. *"Red phenotype"* can be found far to the east from known localities of *C. bernhardi*. Specimens MPEG 21972 (locality 112- Ig. Patauá, Itaituba, PA), MPEG 22000 (BR 230 Itaituba, PA) and IPBHN 207, 208, 209 (locality 52- Ig. Almas, Juruena River, Apiacás, MT) are *"red phenotype"* (see Appendix I for coordinates). These localities are among others where phenotype can be *normal phenotype* or *light phenotype,* one more evidence of polymorphism.

One specimen from Alta Floresta (locality 55) MPEG 24590, label identificated as *C. bernhardi,* had its DNAmt sequenced and it is more similar to the sequence of IPBHN 207 (from Apiacás, MT), both *"red phenotypes"*. A phylogenetic analysis for *Callicebus* carried by me (to be published elsewhere) shows strong evidence for the three phenotypes of *C. moloch* to be considered a polymorphism of the same taxon. Also, *C. bernhardi* appears as sister group of *C. moloch*. It is possible to recognize a trend to a clinal variation along a east-west transect through the range of the species, with specimens from western localities showing more pigmented ventral parts (phenotype red) and specimens with lighter ventral parts (phenotype light) to the east. "Normal phenotype" is found throughout the range. Moore (2009) found similar results in *C. cupreus*. *C. hoffmannsi* showed similar south-north differences in ventral amount of pigments as can be seen bellow. Based on this, I suggest here *C. bernhardi,* Roosmalen *et al.* (2002), to be considered as a junior synonym of *C. moloch*.

2. *C. hoffmannsi*

Analysis of chromogenetic fields of *C. hoffmannsi* found two phenotypes differing only in the color tones of the ventral parts: *hoffmannsi 1,* yellow similar to that observed in typical *C. moloch*; and *hoffmannsi 2* which looks a very light lime-yellow. Pattern *hoffmannsi 2* is found north of pattern 1, the boundary between them set approximately by latitude 4ºS (Itaituba, Para) (Fig. 2). Despite color differences and non-overlapping ranges, I could not find any geographic barrier or an ecological feature supporting the possibility that *C. hoffmannsi* should be split into two taxa. So, I consider these two phenotypes as polymorphisms of the same species until other evidence of speciation arises.

3. *C. cupreus*

Callicebus cupreus also shows three phenotypes: **Phenotype 1:** forehead and crown reddish-cream (agouti hair banded with light stripes broader than the dark ones). Back and nape almost concolor with crown. Lower back similar, but washed with brown. Tail as back; arms, legs, chest, belly and ventral surface of an intense reddish brown, sometimes orangish. Back of hands and feet are brown, not agouti. **Phenotype 2:** specimens MZUSP11831 and 11832 from Pauini, AM, have arms, legs, chest and ventral surfaces orangish. **Phenotype 3** *C. cupreus* MZUSP7332 from Iquiri River, AM, holotype of *C. cupreus acreanus* and MZUSP5067 and 5068 from Santa Cruz do Eiru River have forehead and crown agouti-brown with black and cream, lighter than described for the phenotype 1, back as *moloch* and lower-back more brownish. Tail is dark-brown, gradually getting lighter to the tip, which is cream. Arms, legs, ventral surfaces and beard are dark reddish-brown, almost dark red.

Six specimens (MPEG 1587, 1588, 1605, 1608, 1609 and 1845) from Amazonas (Rio Javari, Estirão do Equador) are darker than the phenotype 3, described here. Phenotypes are distributed in four localities (Figure 2) that are inside the known distribution of *C. cupreus* and do not show a geographic pattern that could suggest an existence of more than one only taxon. As it was not possible to identify geographical limits that could indicate segregation among taxa, and it was not possible to perform a DNA analysis, definite considerations about the taxonomic status of *C. cupreus* must await, intra-specific color polymorphism being the best explanation for the observed pattern.

4. *C. cupreus, C. caligatus* and *C. dubius*

Grooves (2001) follows Hershkovitz (1990) in *Callicebus* taxonomy, but doubts him concerning some propositions. One of them considers *C. caligatus, C. dubius* and *C. cupreus* as synonyms. Roosmalen *et al.* (2002) described differences among these three species, considering all of them valid, a view I agree based on morphological grounds. All three show several distinctive characters, as pointed out by Roosmalen (2002) and revised here (shown in Table 2), such as the presence or absence of chromogenetic fields, e.g. frontal white and black stripes, tip of tail and white fingers.

Conclusions

C. bernhardi must be considered as a junior synonym of *C. moloch*, since the only difference between them is the amount of pigment in the hairs and it occurs in sympatry with *C. moloch* in several localityes. *C. hoffmannsii* shows two phenotypes with parapatric ranges, but without any defined geographic barrier that could support their assignment as two different taxa. Phenotype variation in *C. cupreus* is polymorphic, and do not show a geographic pattern that could support the idea of splitting it in more than one taxon; *Callicebus cupreus, C. dubius* e *C. caligatus* are distinct species since they present several distinctive characters and allopatric ranges.

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Appendix I

Collecting sites of all specimens analyzed. Label: Taxon indicated in label; Analysis = identification by the author of this article; Specimens = specimens' Number at collection; Listing numbers in bold are those cited in the map of Figure 2.

No	Collecting Locality	Coordinates	Label	Analysis	SPECIMENS
1	Colombia (loctip região de Villavicencio Rio Meta)	04°15'N 73°50'W	*C. ornatus*	*C. ornatus*	MNRJ 2486
2	Ecuador, Rio Anaray	00°30'S 76°22'W	*C. discolor*	*C. discolor*	MNRJ 3917
3	AM Ig. Iá Pq. Nac. Pico da Neblina	00°17'N 66°25'W	*C. lugens*	*C. lugens*	MNRJ 59657
4	AM, Barcelos, Rio Aracá Ig Jauari	00°10'S 63°05'W	*C. lugens*	*C. lugens*	MNRJ 67071
5	AM Ig. Japomeri, Rio Padauiri	00°00'S 64°00'W	*C. lugens*	*C. lugens*	CRB 2570 MNRJ 27070
6	RR Lago da Cobra dir. Rio Mucajaí	01°40'N 60°55'W	*C. torquatus*	*C. lugens*	MZ 9689, 9690
7	AM São Gabriel da Cacheira	00°07'S 67°04'W	*C. lugens*	*C. lugens*	INPA 4066
8	AM Rio Tootobi af.dir. rio Demini	01°40'N 63°34'W	*C. lugens*	*C. lugens*	MPEG 10018
9	AM Rio Mucajaí	02°45'N 62°00'W	*C. torquatus*	*C. lugens*	MPEG 1928, 1929, 1931,1932, 26374
10	PA 54 km S 150 km W de Altamira Gleba 61 lote 02	03°12'N 52°13'W	*C. torquatus*	*C. lugens*	MPEG20181 near Rio Uruará
11	AM, Rio Juruá	06°00'S 68°00'W	*C. regulus*	*C. regulus*	MZUSP 911; MZ911mounted
12	AM, Fonte Boa	02°33'S 66°02'W	*C. regulus*	*C. regulus*	MNRJ 2465, 21047, 25 899
14	AM Lg. Taoaria Grande, Rio Purus	6°30'S 64°15'W	*C. purinus*	*C. purinus*	MNRJ 2461
15	AM Lg. Ayapuá, R. Purus	04°28'S 62°08'W	*C. purinus*	*C. purinus*	MNRJ 2464, 2466, 2470
16	AM Porangaba mg.dir. rio Juruá Porto Walter	8°39'S 72°50'W	*C. cupreus*	*C. cupreus*	MPEG 22998 (black tail), 23000
17	AM Barro Vermelho mg.esq. rio Juruá Eirunepé	06°28'S 68°46'W	*C. cupreus*	*C. cupreus*	MPEG 23001
18	AM São Luiz do Mamoriá rio Purus	07°33'S 66°25'W	*C. cupreus*	*C. cupreus*	MPEG 270 (light colored)
19	Peru Iquitos Parque do MPEG	03°47'S 73°13'W	*C. cupreus*	*C. cupreus*	MPEG 253 (leucometopa), 672, 6874, 6875, 259
20	Peru Rio Marañons Iquitos	04°30'S 73°27'W	*C. cupreus*	*C. cupreus*	MPEG 677
21	AM Rio Javari Estirão do Equador	04°32'S 71°38'W	*C. cupreus*	*C. cupreus* 2	MPEG 1587, 1588, 1605, 1608,1609,1845
22	AC Rio Branco	9°57'S 67°48'W	*C. cupreus*	*C. cupreus*	MPEG 7102, 7103
23	AM Rio Jaquirana (Cach Jaquirana)	8°43'S 66°48'W	*C. cupreus*	*C. cupreus*	MPEG 8903
24	AM Lago Tefé Porto da Castanha	3°34'S 64°47'W	*C. cupreus*	*C. cupreus*	MPEG 13207, 13208, 13211
25	AM Santo Antonio do R. Eiru	07°10'S 70°25'W	*C. cupreus*	*C. cupreus*	MZUSP 4798,4805
26	AM Santa Cruz do R. Eiru	07°30'S 70°49'W	*C. cupreus*	*C. cupreus*	MZUSP 5054, 5057, 5062**,** 5064, 5066, 5067, 5068, 5069, 5070, 5071, 5072, 5073, 5076, 5077, 5081, 5082, 5085, 5086, 5087, 5088, 5089, 5090
27	AM Eirunepé	06°40'S 69°53'W	*C. cupreus*	*C. cupreus*	MZUSP 5052, 5055, 5056, 5058, 5059, 5060, 5061, 5063, 5065, 5074, 5075**,** 5078, 5079, 5080, 5083, 5084, 11534
28	AC Manoel Urbano	08°53'S 69°40'W	*C. cupreus*	*C. cupreus*	MZUSP 11237, 19542

No	Collecting Locality	Coordinates	Label	Analysis	SPECIMENS
29	AC Sena Madureira	09°04'S 68°44'W	*C. cupreus*	*C. cupreus*	IPBHN 820
30	AM, São Paulo de Olivença -Mata Juratuba	03°57'S 68°57' W	*C. cupreus*	*C. cupreus*	MNRJ 21049
31	AM Pauini	07°40'S 66°57'W	*C. cupreus*	*C. cupreus* 2	MZUSP 11831,11832
32	AC Iquiri	09°50'S 67°45'W	*C. cupreus*	*C. cupreus* 2	MZUSP 7332
33	RO EE Antonio Mugica Nava, Porto Velho esq Rio Madeira	09°24'S 64°56'W	*C. dubius*	*C. dubius*	*MZ (no number sat at time)*
35	AM Ig. Bacana marg. Oeste lago Jarí marg dir baixo Purus	04°00'S 61°20'W	*C. caligatus*	*C. caligatus*	INPA 4032; MZUSP 11722(unknown locality)
36	AM Humaitá Lábrea BR 230 km 41 mg.dir rio Ipixuna	07°30'S 63°23'W	*C. cupreus*	*C. caligatus*	MPEG 22011, 22012
37	AM Interfluvio R. Ipixuna e Mucuim no Purus	06°30'S 64°00'W	*C. stephennashi*	*C. stephennashi*	INPA 4030, 4031
38	AM médio e alto rio Purus	05°30'S 63°00'W	*C. stephennashi*	*C. stephennashi*	*INPA (no number sat at time)*
39	Bolivia Sta Cruz de la Sierra Provincia de Cercado	17°60'S 63°20'W	*C. donacophilus*	*C. donacophilus*	MNRJ 5537, 21059, 21060
40	MS Corumbá	19°00'S 57°38'W	*C. donacophilus*	*C. donacophilus*	MZUSP 3355, 3356, 3358, 3359, 3371
41	RO Alto Paraíso. Polonoroeste	09°37'S 63°27'W	?	*C. brunneus*	MZUSP 20075
42	RO Porto Velho	08°47'S 63°55'W	*C. brunneus*	*C. brunneus*	MZUSP 7798**,** 7799
43	RO Santa Bárbara	09°10'S 63°04'W	*C. brunneus*	*C. brunneus*	MZUSP 20141
44	RO Rio Machado Cach Nazaré	08°52'S 62°07'W	*C. brunneus*	*C. brunneus*	MZUSP 20432, 20433**,** 20434,20435; MPEG 22993, 22994, 22995
45	RO Pedra Branca	10°01'S 62°05'W	*C. brunneus*	*C. brunneus*	MZUSP 22897
46	RO Faz. Rio Candeias município Porto Velho	08°57'S 63°38'W	*C. brunneus*	*C. brunneus*	MPEG 10941,10942
47	RO UHE Samuel rio Jamari afl.dir. rio Madeira	08°40'S 63°25'W	*C. brunneus*	*C. brunneus*	**MPEG** 21686,21687, 21688, 21689, 21690, 21691, 21692, 21693, 21694,21695, 21696, 21697, 21698, 21699, 21700, 21701, 21702, 21703, 21704, 21705, 21706, 21707, 21710, 21711, 21748, 21795, 21943, 21944, 21945, 21946, 21947, 21948, 21949, 21954, 21955, 21956, 23035, **MNRJ** 28487, 28488, 28489
48	RO Calama margem direita Rio Ji-paraná	08°03'S 62°53'W	*C. moloch*	*C. brunneus*	MPEG 22006
49	PA Ig. Mundo novo margem direita do médio Rio Iriri	05°25'S 54°25'W	*C. moloch*	*C. moloch*	MPEG21836
50	AM BR-230 Humaitá-Apis km 150 mg.dir. rio Marmelos	07°45'S 61°44'W	*C. bernhardi*	*C. moloch* "red phenotype"	MPEG 22996, 22997
51	AM Com. Nova Olinda dir. R. Aripuanã Novo Aripuana	05°15'S 60°20'W	*C. bernhardi*	*C. moloch* "red phenotype"	INPA 3929 (holotype - only skeleton)
52	MT Apiacás Ig. Almas Rio Juruena	07°40'S 58°05'W	-	*C. moloch* "red phenotype"	IPBHN 207, 208, 209,
53	RO Nova Colina Polonoroeste	10°48'S 61°43'W	*C. moloch*	*C. moloch* "red phenotype"	MZUSP 18956
54	RO Nova Brasília Polonoroeste	10°56'S 61°20'W	*C. moloch*	*C. moloch* "red phenotype"	MZUSP 18964, 20253, 20255, 20058, 20067
55	MT Alta Floresta	09°52'S 56°04'W	*C. bernhardi*	*C. moloch* "red phenotype"	MPEG 24590, 24591
56	AM Com. Nova Olinda Rio Aripuanã	05°31'S 60°25'W	*C. bernhardi*	*C. moloch* "red phenotype"	INPA 3929

No	Collecting Locality	Coordinates	Label	Analysis	SPECIMENS
57	AM Rio Mariepauá aff. esq. Madeira	05°30'S 60°34'W	*C. bernhardi*	*C. moloch* "red phenotype"	INPA 4033 (paratype), 4029 (paratype)
58	AM Prainha Rio Aripuanã	07°16'S 59°19'W	?	*C. cinerascens*	MZUSP 11806, 11807**,** 11808, 11809, 11810, 11811, 11812
59	AM Prainha perto de Cipotuba m dir Rio Aripuanã.	07°16'S 60°20'W	?	*C. cinerascens*	INPA 4085
60	AM Lago do Batista marg dir R. Amazonas I. Tupinambarana	03°15'S 58°15'W	*C. baptista*	*C. baptista*	**MZUSP** 4802**,** 4957, 5141, 5145, 5161, 5162, 5163, 5164, 5168, 5170, 7168, 7169, 7173, 7174, **MNRJ** 5923, 5903, 6003
61	AM Tapaiuna marg dir R. Amazonas I. Tupinambarana	03°27'S 58°18'W	*C. baptista*	*C. baptista*	MZUSP 7166,7167,7171
62	Uíra Curapá	03°20'S 58°17' W	*C. baptista*	não visto	MGMvanR50
63	AM Parintins	02°50'S 56°45'W	*C. moloch*	*C. hoffmannsi*	MPEG 690
64	PA Fordlandia	03°47'S 55°35'W	*C. hoffmannsi*	*C. hoffmannsi* 1	MZUSP 11731, 11839
65	PA Itaituba marg esq R. Tapajós	04°18'S 56°05'W	*C. hoffmannsi*	*C. hoffmannsi* 1	MZUSP 3574, 3575, 3576
66	PA Brasilia Legal , marg esq R. Tapajós	03°55'S 55°35'W	*C. hoffmannsi*	*C. hoffmannsi* 1	MZUSP 11715, 11721, 11726
67	PA Vila Braga Tapajós	04°24'S 56°18'W	*C. hoffmannsi*	*C. hoffmannsi* 1	MPEG 251, MNRJ 2472
68	PA Jacareacanga 17km Rod. Transamazônica	06°15'S 58°00'W	*C. hoffmannsi*	*C. hoffmannsi* 1	IPBHN 444
69	PA Samauma R Tapajós	03°35'S 55°35'W	*C. hoffmannsi*	*C. hoffmannsi* 2	MZUSP 11741, 11745
70	PA Aruã Rio Arapiuns marg esq R. Tapajós	02°40'S 55°50'W	*C. hoffmannsi*	*C. hoffmannsi* 2	MZUSP 5091
71	PA Urucurituba marg esq Rio Tapajós	03°45'S 55°30'W	*C. hoffmannsi*	*C. hoffmannsi* 2	MZUSP 10154, 10155, 11743, 11815, 11833, 19534
72	PA Santa Rosa Ilha de Urucurituba	03°48'S 56°33'W	*C. hoffmannsi*	*C. hoffmannsi* 2	MZUSP 11834, 11835, 11836
73	PA Rio Arapiuns Santarém Tapajós	02°20'S 55°13'W	*C. hoffmannsi*	*C. hoffmannsi* 2	MPEG 587
74	PA Vila Maripá, marg dir R Tapajós	02°39'S 55°57'W	*C. hoffmannsi*	*C. hoffmannsi* 2	MPEG 21444
75	PA Itaituba-Jacareacanga km 19	04°18'S 56°08'W	*C. hoffmannsi*	only skull	MPEG 8499, 8500, 8501, 8502
76	PA Monte Cristo marg dir R. Tapajós	04°05'S 55°38'W	*C. moloch*	*C. moloch*	MZUSP 3567, 3568, 3569, 11817
77	PA Taperinha	02°32'S 54°18'W	*C. moloch*	*C. moloch*	MZUSP 3570; MPEG 4733, 4734, 4735, 4736, 4737, 4738, 4739, 4740, 4743, 4744, 4745, 4746, 4747, 4748, 4749, 4750, 4751, 4752, 4753, 4754, 4755, 4756, 4757, 4758, 4759, 4760, 4761, 4762, 4763, 4764, 4765, 4766, 4767, 4768,4769, 4770, 4778
78	PA Santarém Faz Maruá	02°26'S 54°42'W	*C. moloch*	*C. moloch*	MZUSP 3571, 3572
79	PA Piquiatuba	03°03'S 55°07'W	*C. moloch*	*C. moloch*	**MZUSP** 5142,5153, 5155, 5156,5158, 5160, **MNRJ** 5981, 5979, 5980
80	PA Caxiricatuba R. Tapajós	02°36'S 54°56'W	*C. moloch*	*C. moloch*	MZUSP 5143, 5144, 5146, 5147, 5148, 5149, 5150, 5151, 5152, 5157, 5159, 5165, 5166, 5167, 5169, 24735
81	PA Foz do Curuá	02°23'S 54°05'W	?	*C. moloch*	MZUSP 5196, 5197, 5202
82	PA Bom Jardim dir Rio Amazonas	02°48'S 54°08'W	*C. moloch*	*C. moloch*	MZUSP 5198, 5200

No	Collecting Locality	Coordinates	Label	Analysis	SPECIMENS
83	Pa Cachimbo	09°22'S 54°58'W	*C. moloch*	*C. moloch*	MZUSP 8062
84	PA Fordlandia	03°47'S 55°23'W	*C. moloch*	*C. moloch*	MZUSP 10151, 10153,11716, 11717, 11718, 11719, 11720, 11723, 11724, 11725, 11727, 11728, 11729, 11730, 11732, 11733, 11734, 11735, 11736, 11737, 11738, 11739, 11740, 11742, 11744, 11813, 11814, 11816, 11837, 11838, 11840, 11841, 19690
85	PA Itapoama R. Tapajós	03°15'S 55°00'W	*C. moloch*	*C. moloch*	MZUSP 10152
86	PA Sto Antonio R. Tocantins	02°55'S 49°40'W	*C. moloch*	*C. moloch*	MZUSP 13472 (-= IPBHN 444 breast redish)
87	PA dir Rio Tapajós esq R. Mutuns	06°10'S 57°35'W	*C. moloch*	*C. moloch*	IPBHN 203
88	MT R. Arinos, aff dir R. Juruena	10°35'S 58 o00'W	*C. moloch*	*C. moloch*	MZUSP 11244 (SP Zoo), MNRJ 2915, 2923
89	PA Largo do Souza Rio Iriri	04°00'S 53°03'W	?	*C. moloch*	MZUSP 25441, 25442, 25443
90	PA Boca do rio Bacajá	03°25'S 51°48'W	?	*C. moloch*	MZUSP 25444, 25445
91	PA, Santarém, Rio Curuatinga, Aff Rio Curuauna	02°55'S 54°35'W	*C. moloch*	*C. moloch*	MNRJ 11590, 11593
92	PA, Alto Cururu	07°45'S 57°27'W	*C. moloch*	*C. moloch*	MNRJ 23867
93	PA, Rio Xingu	07°00'S 53°00'W	*C. moloch*	*C. moloch*	MNRJ 54834, 54835, 54836
94	PA Alto rio Iriri Xingu	08°20'S 53°30'W	*C. moloch*	*C. moloch* "light phenotype"	MPEG 246
95	PA São João rio Araguaia	06°14'S 48°23'W	*C. moloch*	*C. moloch* "light phenotype"	MPEG 245
96	PA Igarapé João Ribeiro mg.esq. rio Iriri	03°55'S 53°20'W	*C. hoffmannsi*	*C. moloch*	MPEG 21837, 21883
97	Luzilândia rio Araguaia Prox. Itaipava	06°41'S 48°50'W	*C. moloch*	*C. moloch*	MPEG 10932
98	PA Luzilândia rio Araguaia Xinguara	06°56'S 49°54'W	*C. moloch*	*C. moloch*	MPEG 10933, 10939
99	PA Serra Norte Carajás N1	06°0'S 50°16'W	*C. moloch*	*C. moloch*	MPEG 10943, 10944,11843
100	PA Serra Norte Carajás N2 área de manganês	06°00'S 50°00'W	*C. moloch*	*C. moloch*	MPEG 11832
101	PA 170 km S de Tucuruí Saúde mg.esquerda rio Tocantins	05°18'S 49°17'W	*C. moloch*	*C. moloch*	MPEG 12175, 12176
102	PA Santarém-Cuiabá Itaituba BR 165 zona Sul	04°05'S 54°55'W	*C. moloch*	*C. moloch*	MPEG 12627
103	PA Santarém Rod BR-163 km125 Flora do Tapajós. =78	03°27'S 55°10'W	*C. moloch*	*C. moloch*	MPEG 26406
104	MT Apiacás	09°30'S 57°05'W	*C. moloch*	*C. moloch*	*IPBHN 208, 209*
105	Alvorada d'Oeste BR 429 linha 64 km 87	11°23'S 62°18'W	*C. moloch*	*C. moloch*	MPEG 19709, 19710, 19712, 19713
106	AM, São João, R. Aripuanã	05°29'S 60°25'W	*C. moloch*	*C. moloch*	MNRJ 2480, 2481
107	PA, Santarém, Belterra = 80	02°39'S 54°57'W	*C. moloch*	*C. moloch*	MNRJ 5494
108	AM, Foz do Rio Castanho (R Roosevelt)	07°33'S 60°42'W	*C. moloch*	*C. moloch*	MNRJ 2482, 2484, 2485
109	PA UHE Tucuruí rio Tocantins	03°40'S 49°40'W	*C. moloch*	*C. moloch*	MPEG21442, 21443, 22014, 22015, 22016, 22017, 22016
109a	PA UHE Tucuruí rio Tocantins	03°40'S 49°40'W	*C. moloch*	*C. moloch* "light phenotype"	MPEG 22018

No	Collecting Locality	Coordinates	Label	Analysis	SPECIMENS
110	PA Mun Tucuruí Sítio Calandri acima da barragem mg esq Rio Tocantins	03°50'S 49°42'W	*C. moloch*	*C. moloch* "light phenotype"	MPEG 22015, 22016
111	PA, Ipanema, beira da Rodagem esquerda Santarém = 78	02°47'S 54°55'W	*C. moloch*	*C. moloch*	MNRJ 11588, 11591, 11592
112	PA Ig. do Patauá af. esq. Rio ?? Município de Itaituba	04°16'S 55°48'W	*C. moloch*	*C. moloch* "red phenotype"	MPEG 21972
113	PA, Apui, BR-230 Humaitá-Itaituba km 17	07°35'S 62°50'W	*C. moloch*	*C. moloch* "red phenotype"	MPEG 22000
114	(loctip 30 milles north Concepción, Paraguai)	22°50'S 57°27'W		*C. pallescens*	*Criad. Velho Jatobá*
115	Ba, Mirorós - Faz Conceição	11°24'S 42°17'W	*C. barbarabrownae*	*C. barbarabrownae*	UNB 1510
116	SE, Cristinapolis, Faz. Cruzeiro	11°28'S 37°45'W	*C. personatus*	*C. coimbrai*	MNRJ 30550
117	BA, (loctip Morro Dárara ou Faz Arara)	14°00'S 40°00'W	*C. melanochir*	*C. melanochir*	MZUSP 3884
118	MG Teófilo Otoni	17°52'S 41°28'W	*C. personatus*	*C. personatus*	MZUSP 2712, 2713, 2714
119	MG Baixo R. Suaçui	18°47'S 41°45'W	*C. personatus*	*C. personatus*	MZUSP 5839, 5931, 5932
120	ES Colatina	19°32'S 40°37'W	*C. personatus*	*C. personatus*	MZUSP 2219, 2220, 2221, 2222, 2223, 2224, 2225, 2226, 2227
121	ES Rio Doce	19°30'S 40°30'W	*C. personatus*	*C. personatus*	MZUSP 2409, 2410, 2411, 2412, 2413
122	ES Sooretama	19°00'S 40°00'W	*C. personatus*	*C. personatus*	MZUSP 11142, 11148, 111152, 111164, 11711, 11712, 11713, 11714, 11803, 11804, 11805
123	MG, Passos, Foz do Brejo, São João da Glória	20°42'S 46°37'W	*C. personatus*	*C. personatus*	MNRJ 21065, 21066, 25898
124	ES, São Domingos, Mata 10 de Agosto, Faz 10 de Agosto	19°08'S 40°38'W	*C. personatus*	*C. personatus*	MNRJ 21054, 21052, 21053
125	ES, Lagoa Juparaua, Sant´anna	19°22'S 40°07'W	*C. personatus*	*C. personatus*	MNRJ 2478
126	ES, Estrada Linhares, São Matheus km 54	19°15'S 40°05'W	*C. personatus*	*C. personatus*	MNRJ 21051
127	ES, Rio São José, Braço do Sul	19°05'S 40°40'W	*C. personatus*	*C. personatus*	MNRJ 54782, 54788
128	MG, Ituete, Rio Poço	19°25'S 41°18'W	*C. personatus*	*C. personatus*	MNRJ 11986
129	RJ Itatiaia	22°31'S 44°32'W	*C. nigrifrons*	*C. nigrifrons*	MZUSP 7426, 7427, 7428, 7429, 7430,19548
130	SP Serra da Cantareira	23°32'S 46°37'W	*C. nigrifrons*	*C. nigrifrons*	IPBHN 318
131	SP Itatiba	23°00'S 46°50'W	*C. nigrifrons*	*C. nigrifrons*	IPBHN 605, IPBHN 1016, IPBHN 1017
132	RJ, Itatiaia, Chevap - Funil	22°30'S 44°34' W	*C. personatus*	*C. nigrifrons*	MNRJ 25897
133	Cabeceiras do Paranatinga		*C. personatus*	*C. personatus*	MNRJ 3008
134			*C. personatus*	*C. personatus*	MNRJ 2479
135			*C. melanochir*	*C. melanochir*	MNRJ 11049
136			*C. purinus*	*C. purinus*	CPRJ 005