

On the Taxonomic History and True Identity of the Collared Titi, *Cheracebus torquatus* (Hoffmannsegg, 1807) (Platyrrhini, Callicebinae)

Hazel Byrne¹, Anthony B. Rylands², Stephen D. Nash³ and Jean Philippe Boubli⁴

¹Department of Anthropology, University of Utah, UT, USA

²Global Wildlife Conservation, Austin, TX, USA

³Department of Anatomical Sciences, Health Sciences Center, State University of New York, Stony Brook, NY, USA

⁴School of Science, Engineering and the Environment, University of Salford, Manchester, UK

Abstract: The collared titi, *Cheracebus torquatus*, is paradoxically the least well-defined of the so-called “*torquatus* group” of Neotropical titi monkeys. Since its description by Hoffmannsegg in 1807, it has been re-characterized numerous times. In this study, the true identity of *Cheracebus torquatus* is assessed based on a review of its taxonomic history and the observation of 100 skins from across the genus *Cheracebus*, including the holotype for *C. torquatus*. We propose that the *C. torquatus* type specimen and type description fit most closely with widow monkeys found south of the Rio Solimões between the rios Juruá and Purus, and we conclude that *purinus* Thomas, 1927, is a junior synonym of *torquatus*. This necessarily invalidates the *torquatus* type locality, as defined by Hershkovitz, of Codajás, north (left) bank of the Solimões, and we thus restrict the type locality to Aiapuá, left bank of the Rio Purus, Brazil. The left bank Rio Solimões populations that were previously classified as *C. torquatus* (*sensu* Hershkovitz) are here included as *lugens*, and we redefine *C. lugens* to include all *Cheracebus* found north of the Solimões-Japurá-Caquetá. We discuss the broad phenotypic variation found across *C. lugens* specimens and the existence of three *C. lugens* lineages in molecular phylogenies, as well as issues with the classification of other forms recognized by Hershkovitz. To conclude, we currently consider the genus *Cheracebus* to comprise five widow monkey species—*torquatus* (formerly *purinus*), *regulus*, *lucifer*, *medemi* and *lugens*.

Key words: *Cheracebus*, widow monkeys, collared titis, *torquatus*, *purinus*, Callicebinae, Pitheciidae

Introduction

The genus *Cheracebus* Byrne *et al.*, 2016, subfamily Callicebinae, is currently considered to comprise six species of titi monkeys, collectively known as the collared titis or widow monkeys for their overall dark pelage coloration and contrasting white collar. They occur in the Amazon and Orinoco basins in Brazil, Colombia, Ecuador, Peru, and Venezuela, from the foothills of the Eastern Cordillera of the Andes, east to the left banks of the Rio Branco and lower Rio Negro, north of the Rio Amazonas-Solimões, and the left bank of the Rio Purus, south of the Rio Amazonas-Solimões (Fig. 1) (Hershkovitz 1990; Byrne *et al.* 2018). *Cheracebus* are among the least studied of the callicebine taxa and were previously in the genus *Callicebus* (see Byrne *et al.* 2016). Their distinction from other titis, however, has long been

recognized. *Cheracebus torquatus* was, for example, one of just two polytypic titi species acknowledged in Hershkovitz’s first appraisal of the taxonomy of the titi monkeys in 1963, and the six subspecific forms subsequently recognized by Hershkovitz (1990) were separated into the “*torquatus* species group” (*torquatus*, *lugens*, *medemi*, *lucifer*, *regulus*, and *purinus*).

Hershkovitz’s seminal works on titi monkey taxonomy in 1988 and 1990 were based on his examination of over 1,000 museum specimens but he evidently missed some which were crucial to his analysis. For the widow monkeys, the most notable of these was the type specimen of *torquatus* Hoffmannsegg, 1807. Hershkovitz (1988, 1990) based his species hypothesis for *torquatus* largely on the previous work of taxonomists, Oldfield Thomas and Einar Lönnberg. In fact, apart from *medemi* (described by Hershkovitz in 1963), the

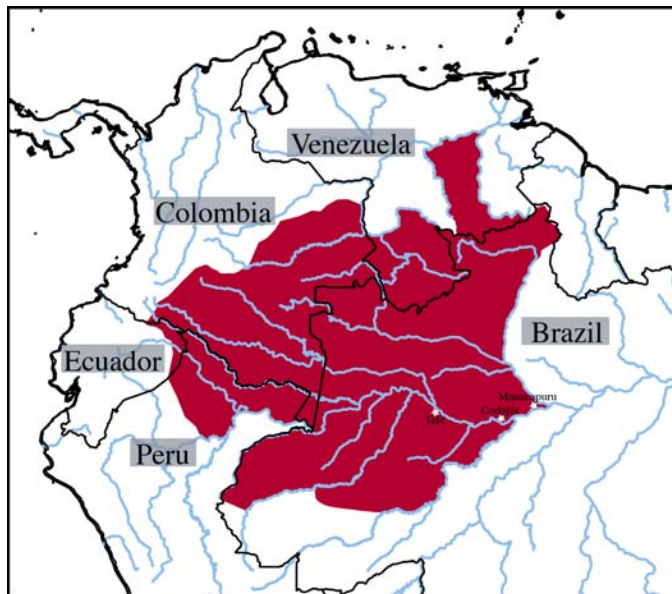


Figure 1. Approximate geographic distribution of the widow monkeys, genus *Cheracebus*. Modified from Byrne *et al.* (2018).

arrangement for *Cheracebus* taxa proposed by Hershkovitz (1988, 1990) was similar to the classification suggested by Thomas (1927a).

In 1914, Thomas recognized three species: *torquatus*, *lugens*, and his newly described taxon, *lucifer*. Subsequently, Thomas (1927a, 1927b) described *purinus* and *regulus* (as well as *ignitus*, not currently recognized), and designated all widow monkey taxa as subspecies of *C. torquatus*. In his first review of the Callicebinae, Hershkovitz (1963) described a new subspecies, *C. torquatus medemi*, and classified *purinus*, *lucifer*, *regulus* and *ignitus* as synonyms of *C. torquatus torquatus*. In his later publications, Hershkovitz (1988, 1990) resurrected *purinus*, *lucifer* and *regulus* as subspecies of *C. torquatus*, and classified *ignitus* as a synonym of *lucifer*. The only major change to the species-level taxonomy of *Cheracebus* in the 30 years since Hershkovitz's reviews was the elevation of all six subspecies to species (Van Roosmalen *et al.* 2002; Groves 2005).

Despite being the first titi taxon described, *torquatus* is the least well-defined of the widow monkeys and, since its description, it has been re-characterized and redefined numerous times. The confusing taxonomic history of *Cheracebus torquatus* is confounded by the lack of an explicit type locality. Thomas (1927a) was the first to suggest that *torquatus* occurred around the lower Solimões and Negro, and Lönnberg (1939) subsequently proposed that the type description for *torquatus* (as summarized by Wagner in 1855) matched specimens in the Stockholm museum from Codajás, left bank of the Rio Solimões. Following Lönnberg (1939), Hershkovitz (1988, 1990) restricted the type locality for *torquatus* to Codajás, and indicated a distribution along the left bank of the Solimões, in a southern, east-west sliver of the Negro-Solimões interfluvium in Brazil. Notably, it is evident that none of these taxonomists had examined the *torquatus* type specimen and, in the absence of an explicit type locality, they relied seemingly entirely upon the description of the type

specimen (or the summary by Wagner 1855; p.119) to define *torquatus*. The progression of *torquatus* from a reddish brown *purinus*-like form, as it was originally described by Hoffmannsegg (1807), to a duller *lugens*-like form through the taxonomic literature over the past 200 years seems like an unfortunate taxonomic version of the children's game known as "Telephone" (in the USA).

Here we address the uncertainty surrounding the identity and validity of *torquatus* through a review of the taxonomic history, including an assessment of the original type description and of the holotype that is in the Museum für Naturkunde (Natural History Museum), Berlin.

Methods

We examined museum specimens at the British Museum of Natural History, London (BMNH); the Field Museum of Natural History, Chicago (FMNH); and the Instituto Nacional de Pesquisas da Amazônia (National Institute of Amazonian Research) Manaus (INPA). We also examined photos of specimens maintained in other collections: Museum für Naturkunde (Natural History Museum), Berlin (MNB) (*torquatus* holotype); Naturhistoriska Riksmuseet (Royal Museum of Natural History), Stockholm (NRM); Museu Nacional (National Museum of Brazil), Rio de Janeiro (MNRJ) (note, two MNRJ specimens were seen in hand while at the FMNH); Smithsonian National Museum of Natural History, Washington, DC (USNM); American Museum of Natural History, New York (AMNH); Museum National d'Histoire Naturelle (National Museum of Natural History), Paris (MNHN); Instituto de Desenvolvimento Sustentável Mamirauá (Mamirauá Institute for Sustainable Development), Tefé (IDSM); and the Museu Paraense Emílio Goeldi (Goeldi Museum), Belém (MPEG).

A total of 100 *Cheracebus* specimens were assessed for this work (Table 1). We focused primarily on assessing specimens considered to belong to *torquatus* (*sensu* Hershkovitz 1990) ($N = 13$) and *purinus* ($N = 14$), as well as *lugens* ($N = 35$). For comparison, we also considered *lucifer* ($N = 15$), *regulus* ($N = 12$), and *medemi* ($N = 11$) specimens that were at hand but they are not discussed here in detail.

For information on the molecular dataset used for the phylogenetic analyses, see the section "Molecular evidence." Additional details of the specimens examined can be found in the supplementary material (http://www.primatesg.org/storage/pdf/PC34_Suppl_Mat_Byrne_et_al_C_torquatus_2020.pdf).

The Type Locality of *torquatus*

Callitrix [sic] *torquata* was described by Johann Centurius Hoffmannsegg in 1807 (p.86), the first description of a widow monkey. The description was based on a single type specimen collected prior to 1806 by Friedrich Wilhelm Sieber, his personal collector, and placed in the MNB. In his description of *torquatus*, Hoffmannsegg (1807) stated

Table 1. List of all museum specimens assessed for this study including ID, species from the label or museum catalogue, species assigned here based on Hershkovitz (1990), and species assigned here after the taxonomic changes in this article, and locality number in Figure 3. Detailed information on the collection locality is presented in Table S1.

| Museum or Field ID | Museum code | Species label or museum catalogue | Assigned species <i>sensu</i> Hershkovitz | Assigned species updated | Locality # see Fig. 3 |
|--------------------|-------------|-----------------------------------|---|--------------------------------|-----------------------|
| ZMB-265 | MNB | <i>torquatus</i> | <i>purinus</i> | <i>torquatus</i> | NA |
| 38885 | FMNH | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 4 |
| 1851.7.12.7 | BMNH | <i>torquatus</i> | <i>purinus</i> | <i>torquatus</i> | 5 |
| 1926.5.5.21 | BMNH | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 4 |
| CTGAM154 | INPA | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 3 |
| CTGAM195 | INPA | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 3 |
| CTGAM209 | INPA | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 3 |
| MN-2464 | MNRJ | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 4 |
| MN-2461 | MNRJ | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 2 |
| 631211 | NRM | <i>torquatus</i> | <i>purinus</i> | <i>torquatus</i> | 2 |
| 631214 | NRM | <i>torquatus</i> | <i>purinus</i> | <i>torquatus</i> | 2 |
| USNM-518222 | USNM | <i>torquatus</i> | <i>purinus</i> | <i>torquatus</i> | 5 |
| USNM-105539 | USNM | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 1 |
| M-78961 | AMNH | <i>purinus</i> | <i>purinus</i> | <i>torquatus</i> | 5 |
| 35076 | FMNH | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | NA |
| 1926.5.5.22 | BMNH | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 7 |
| 1925.12.11.8 | BMNH | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 6 |
| 1842.4.29.15 | BMNH | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | NA |
| MN-23865 | MNRJ | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 612103 | NRM | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 621045 | NRM | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 621046 | NRM | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 621104 | NRM | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 622023 | NRM | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 631039 | NRM | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 641040 | NRM | <i>torquatus</i> | <i>torquatus</i> | cf. <i>lugens</i> ₁ | 8 |
| 620501 | NRM | <i>torquatus</i> | <i>torquatus?</i> | cf. <i>lugens</i> ₁ | 6 |
| 88246 | FMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 16 |
| 88247 | FMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 16 |
| 89479 | FMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 14 |
| 88248 | FMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 15 |
| 35144 | FMNH | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | NA |
| 1933.10.11.1 | BMNH | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | NA |
| 1928.7.9.1 | BMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 10 |
| 1928.11.3.1 | BMNH | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | 23 |
| 1928.11.3.2 | BMNH | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | 23 |
| 1951.714 | BMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 18 |

| | | | | | |
|---------------|------|------------------|--------------------|--------------------|----|
| 1855.12.24.44 | BMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | NA |
| 1899.9.11.1 | BMNH | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 17 |
| CTGAM733 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 12 |
| CTGAM734 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 12 |
| CTGAM753 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 12 |
| CCM105 | INPA | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | 19 |
| JPB123 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 21 |
| JPB124 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 21 |
| JPB136 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 22 |
| JPB160 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 19 |
| JPB161 | INPA | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 19 |
| JPB81 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 11 |
| CRB2696 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 10 |
| CRB2697 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 10 |
| CRB2698 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 10 |
| CRB2667 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 20 |
| CRB2570 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 20 |
| CRB2205 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 20 |
| CRB2668 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 20 |
| CRB2434 | MNRJ | <i>lugens</i> | <i>lugens</i> | <i>lugens</i> | 21 |
| 640403 | NRM | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | 13 |
| 640404 | NRM | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | 13 |
| 36619 | MPEG | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | 9 |
| 37152 | MPEG | <i>torquatus</i> | <i>lugens</i> | <i>lugens</i> | 9 |
| MO-1997-1573 | MNHN | <i>amictus</i> | <i>lugens</i> | <i>lugens</i> | NA |
| 70698 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70699 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70700 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70692 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70693 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70694 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70695 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70696 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 70697 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 25 |
| 84551 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 26 |
| 70691 | FMNH | <i>medemi</i> | <i>medemi</i> | <i>medemi</i> | 24 |
| 86978 | FMNH | <i>lucifer</i> | <i>cf. lucifer</i> | <i>cf. lucifer</i> | 27 |
| 86979 | FMNH | <i>lucifer</i> | <i>cf. lucifer</i> | <i>cf. lucifer</i> | 27 |
| 1914.3.1.1 | BMNH | <i>lucifer</i> | <i>lucifer</i> | <i>lucifer</i> | 29 |
| 1914.3.1.2 | BMNH | <i>lucifer</i> | <i>lucifer</i> | <i>lucifer</i> | 28 |
| 1927.3.6.7 | BMNH | <i>lucifer</i> | <i>lucifer</i> | <i>lucifer</i> | 34 |
| 1927.8.11.7 | BMNH | <i>lucifer</i> | <i>lucifer</i> | <i>lucifer</i> | 34 |
| 1927.8.11.4 | BMNH | <i>ignitus</i> | <i>lucifer</i> | <i>lucifer</i> | 34 |
| 1934.6.14.2 | BMNH | <i>torquatus</i> | <i>lucifer</i> | <i>lucifer</i> | 31 |
| CTGAM703 | INPA | <i>torquatus</i> | <i>lucifer</i> | <i>lucifer</i> | 32 |

| | | | | | |
|--------------|-------|------------------|----------------|----------------|----|
| CTGAM726 | INPA | <i>torquatus</i> | <i>lucifer</i> | <i>lucifer</i> | 32 |
| CTGAM727 | INPA | <i>torquatus</i> | <i>lucifer</i> | <i>lucifer</i> | 32 |
| 630127 | NRM | <i>torquatus</i> | <i>lucifer</i> | <i>lucifer</i> | NA |
| 640219 | NRM | <i>torquatus</i> | <i>lucifer</i> | <i>lucifer</i> | NA |
| USNM-307380 | USNM | <i>torquatus</i> | <i>lucifer</i> | <i>lucifer</i> | 30 |
| ICA0015 | IDSMS | <i>lucifer</i> | <i>lucifer</i> | <i>lucifer</i> | 33 |
| 1927.8.11.6 | BMNH | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |
| 1927.3.6.8 | BMNH | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |
| 1927.8.11.5 | BMNH | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |
| 1928.4.27.7 | BMNH | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |
| 1928.4.27.8 | BMNH | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |
| 1927.8.11.63 | BMNH | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |
| JT051 | IDSMS | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 35 |
| JT053 | IDSMS | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 35 |
| JT054 | IDSMS | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 35 |
| JT071 | IDSMS | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 35 |
| MN-21047 | MNRJ | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |
| MN-2465 | MNRJ | <i>regulus</i> | <i>regulus</i> | <i>regulus</i> | 36 |

Footnote 1: cf. *lugens* refers to Phenotype C i.e., *torquatus* (*sensu* Hershkovitz 1990)

that the specimen was encountered in the unknown and little-frequented wilderness (“O Certão,” p.91) of the interior of the province of Pará, and this is all that is recorded. In 1807, Pará, or “Grão-Pará,” was a Portuguese province that extended far inland from its capital, Belém, covering an enormous stretch of Amazonian South America including the current states of Pará and Amazonas, and the entire distribution of *Cheracebus* within Brazil (Olson 1991). The province of Amazonas, created in 1850, was turned into a state in 1889, and its separation more than halved the original province of Pará.

It appears that this inexplicit type locality caused significant confusion among taxonomists subsequent to the division of the provinces of Pará and Amazonas. Schlegel (1876) suggested that the actual type locality of *torquatus* was the right bank of the mouth of the Rio Tocantins, Pará. His suggestion was followed by Elliot (1913) and Cabrera (1958) but questioned by Cruz Lima (1945) and Hill (1960). Widow monkeys of the genus *Cheracebus* are entirely absent from modern-day Pará and, thus, Thomas (1927a; p.345) defined the “Lower Rio Negro and Lower Solimões” as the distribution of *torquatus*. This hypothesis was somewhat corroborated by Lönnberg (1939) based on an analysis of specimens collected from Codajás (left bank of the Rio Solimões), and formed the basis for the classifications by Hershkovitz (1988, 1990) and Van Roosmalen *et al.* (2002). Hill (1960) suggested that the type locality could be Tefê (right, south bank of the Solimões), but this proposal received little further attention. Given the great phenotypic variation found in many callicebine taxa, the lack of type locality has proven to be detrimental to confirming the true identity of *torquatus*.

Type description and holotype

The type description for *torquatus* is in German (Hoffmannsegg 1807; p.89) and is broadly summarized as follows: The overall pelage coloration agrees with that of a horse chestnut, but with some variation in the color of the body. The back of the head (occiput), neck, back, sides to the elbows, thighs, lower legs, and base of the tail are chestnut in color. However, the head towards the eyebrows, sideburns, forearms to the wrist, feet and terminal half of the tail are black-brown to black. The ventral side, extending under the ears, inside of the arms to the elbows, and inner legs, is foxy-red or rust-colored. The striking yellowish-white collar is about an inch in width and curves upwards becoming thinner towards the ears, resembling the shape of a few-days-old moon. The terminal two-thirds of the forehands also show this pale yellowish-white color. The hairs of the blackish parts as well as of the head, legs, and underside are mostly uniformly colored (monochrome), at the base somewhat paler. However, the hairs on the back, the shoulders and the sides are annulated with one or a few yellowish-white rings.

Thus, the overall picture of *torquatus* (*sensu* Hoffmannsegg 1807) from this description is of a reddish-brown dorsum with pale yellowish-white banding/flecking on the hairs, a uniform foxy-red underside, a clear well-defined throat collar, pale hands, and blackish-brown to black feet, forearms, forehead, sideburns, and terminal half of the tail.

The type specimen for *torquatus* is housed at the MNB. We were able to examine four clear photographs of this specimen (Fig. 2, A–D). These photos show that the specimen



Figure 2. The holotype for *Cheracebus torquatus* (Hoffmannsegg, 1807): A) dorsal; B) ventral; C) face and crown; D) collar. Photos by Christiane Funk at the MNB.

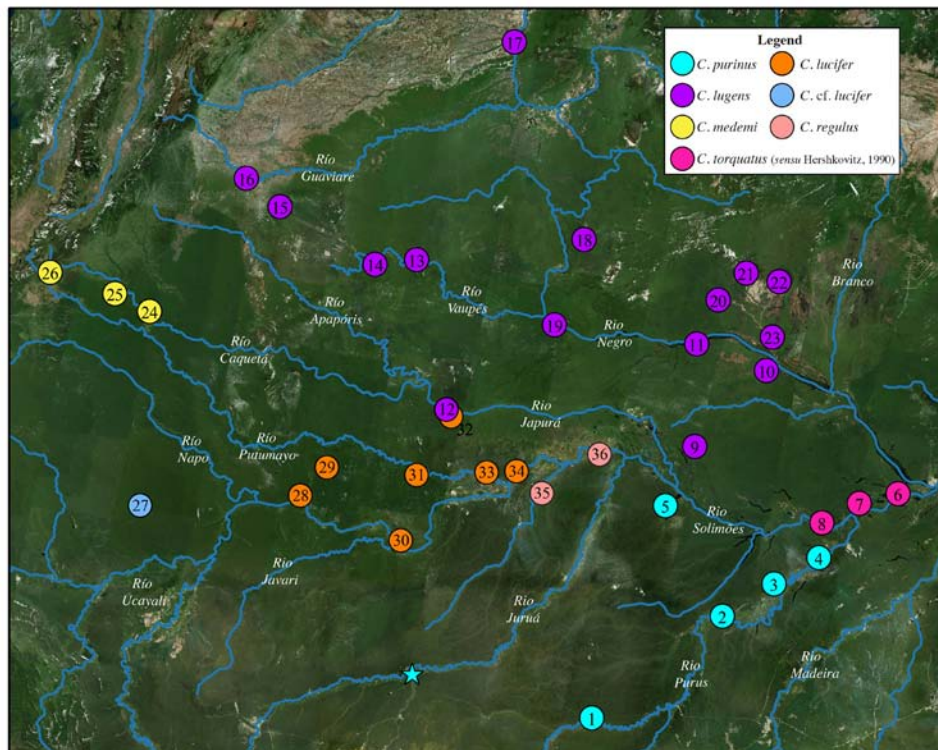


Figure 3. Map showing the collection localities of museum specimens assessed in this study. Numbers correspond to those in Table 1 and Table S1 in the Supplementary File. Note, some localities are loosely estimated and some are too general to be depicted (see full locality information in Table S1). The blue star marks the location an individual was photographed on the right bank of the Rio Tarauaca.

has lost half of the tail, one forehand, and several digits on the other hand, and overall the pelage is in poor condition. It is still possible, however, to distinguish the main characters described by Hoffmannsegg (1807). In agreement with the type description, the specimen shows an overall strong reddish-brown (similar to Chestnut to Morocco Red [Ridgway 1912]), near uniform on the head (including the crown) and legs, but with pale yellowish flecking on the back and, more strikingly, on the flanks. The ventral side is a bright fox/rusty red (similar to Mars Orange to Orange Rufous [Ridgway 1912]). The throat collar is buffy-whitish and well-developed, as might be expected given the name “*torquatus*” (Latin for collared), which gave rise to the taxon’s common name, the collared titi. The hands appear to be a more greyish buffy-white than the collar, although it is difficult to be certain of the original color given the extent of degradation and possible bleaching in this area. The sideburns, forearms, and feet are black.

Taxonomic History of *Cheracebus torquatus*

Oldfield Thomas (1914, 1927)

Shortly after Hoffmannsegg’s description of *torquatus* (1807), Humboldt (1811) described *Simia lugens* from San Fernando de Atabapo in Venezuela, as a primarily blackish form with white hands and a white throat collar. Humboldt’s impression of the titi monkey reminded him of the dress typical of widows in the local communities there, hence the moniker “widow monkey.” Most of the contributions to widow monkey taxonomy in the 1800’s focused on validating the distinctions between *torquatus*, *lugens*, and *Simia amicta* É. Geoffroy Saint-Hilaire, 1812 (from “Brazil”), the last treated as a synonym of *lugens* by Thomas (1914) and of *torquatus* by Hershkovitz (1990) and Groves (2001).

It was not until the early 20th century, after assigning all titi monkeys to the genus *Callicebus* in 1903, that Oldfield Thomas (1914, 1927a) established the basis for the subsequent classifications of *Cheracebus* taxa. In 1914, prior to the description of *purinus*, *regulus* and *ignitus*, Thomas defined *torquatus* as all red-bellied forms without mentioning other diagnostic characters or commenting on its distribution. At this time, Thomas (1914) recognized *lugens* as the entirely blackish form, placing *amicta* and *vidua* Lesson, 1840, both with black bellies, as synonyms, and described *lucifer*—similar to *lugens* but with a chestnut-rufous, rather than black, tail. This classification of three species was based on six specimens from the BMNH, two of each taxon.

Thomas (1927a) subsequently described *purinus* and *regulus*, but considered all five taxa as subspecies of *torquatus*. In this review, Thomas gave more explicit diagnostic characters for each of these taxa and a sentence on their proposed distribution. The only specimens mentioned in this later work are the holotype specimens of *purinus* and *regulus*, with *purinus* described as the red-bellied form with pale-banded dull brown (“grizzled greyish, the hairs ringed with black and buffy”) dorsal pelage, based on a single specimen

(1926.5.5.21). In a key provided to distinguish the taxa, Thomas (1927a; p.510) wrote that both *purinus* and *torquatus* show a “deep rufous” underside and tail mixed reddish with black but *torquatus* has a “uniform dark chestnut-reddish” dorsum, in contradiction with the evident pale banding on the holotype specimen for this taxon and detailed in the type description. Many specimens of *purinus* Thomas, 1927, are a good match to the type description for *torquatus*, outlined in the previous section “Type description and holotype.” The other taxa were described by Thomas (1927a) as showing a blackish underside, varying in the coloration of the back, crown, and/or tail. His suggestion for the distribution of *torquatus* was the lower Rio Negro and lower Solimões, and for *purinus*, lower Purus, south of the Solimões.

Later the same year, Thomas (1927b) described *ignitus* based on a specimen from the “Rio Tonantins” (1927.8.11.4) as another reddish-bellied form which he proposed was closely allied to *torquatus*. Most authors since have considered *ignitus* as a junior synonym of *lucifer* and it is not currently recognized as a valid taxon (e.g., Hershkovitz 1990). Here, we focus on *torquatus* and *purinus* but we discuss this anomalous *ignitus* type specimen in the section “The reddish-bellied form, *ignitus* Thomas, 1927.” Across these three short reviews, Thomas (1914, 1927a, 1927b) mentions a total of 12 specimens housed at the BMNH upon which his suggestions are based.

Thomas apparently never saw the type specimen of *torquatus*, and in 1914, he refers to two specimens in the BMNH as *torquatus*, both of which are still housed there and were examined by HB. One specimen (1851.7.12.7) is a juvenile, consisting solely of the upper torso (head and arms), collected at Ega, now Tefé (Amazonas, Brazil), which is on the right (south) bank of the Solimões within the current proposed distribution of *purinus* (locality 5 on Fig. 3). It shows a dark brown-rufous dorsal pelage, a brighter red underside clearly defined from the dorsal pelage, and a well-developed thick collar. This specimen was not mentioned in 1927 when Thomas divided the red-bellied phenotypes and described *purinus*; however, notably, it does not show the dull brown “grizzled” dorsal pelage of the *purinus* type specimen that Thomas apparently relied upon to distinguish between these taxa. Here, we follow Hershkovitz (1990) in labeling this incomplete specimen as *purinus*; however, it is not considered in detail.

The collection locality for the other *torquatus* specimen (1842.4.29.15) is given as the Rio Negro. It has a dark mahogany red dorsal pelage (Fig. 4; panel A). On the back, the hairs have a mahogany reddish base with red and blackish bands towards the tip (distal 1/3) (Fig. 5; panel A). Although the banding pattern is rather subtle, the hairs are evidently not uniform as indicated by Thomas (1927a) in his key for *torquatus*. The ventral side is primarily dull rusty reddish-brown (similar to Amber Brown to Burnt Sienna [Ridgway 1912]) with a blackish tip on most hairs such that the ventral pelage does not contrast particularly strongly with the dorsal side except for a clearer/brighter reddish area on the hind legs

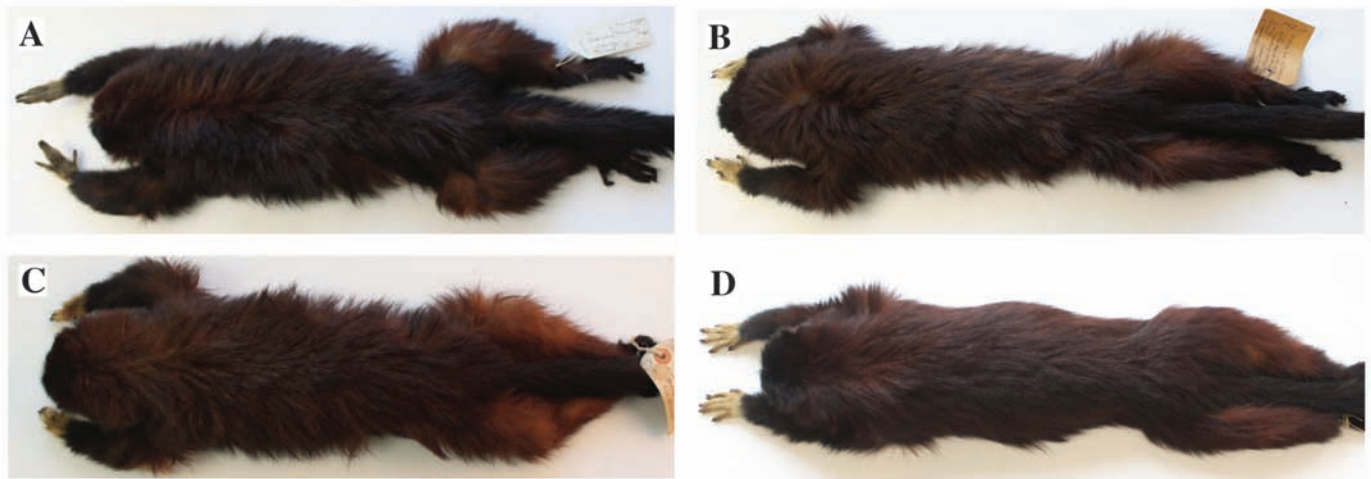


Figure 4. Dorsal view of specimens of *Cheracebus torquatus* (*sensu* Hershkovitz 1990): A) Rio Negro, BMNH (1842.4.29.15); B) Lago do Arara, BMNH (1926.5.5.22); C) Manacapurú, BMNH (1925.12.11.8); D) Codajás, MNRJ (MN-23865).

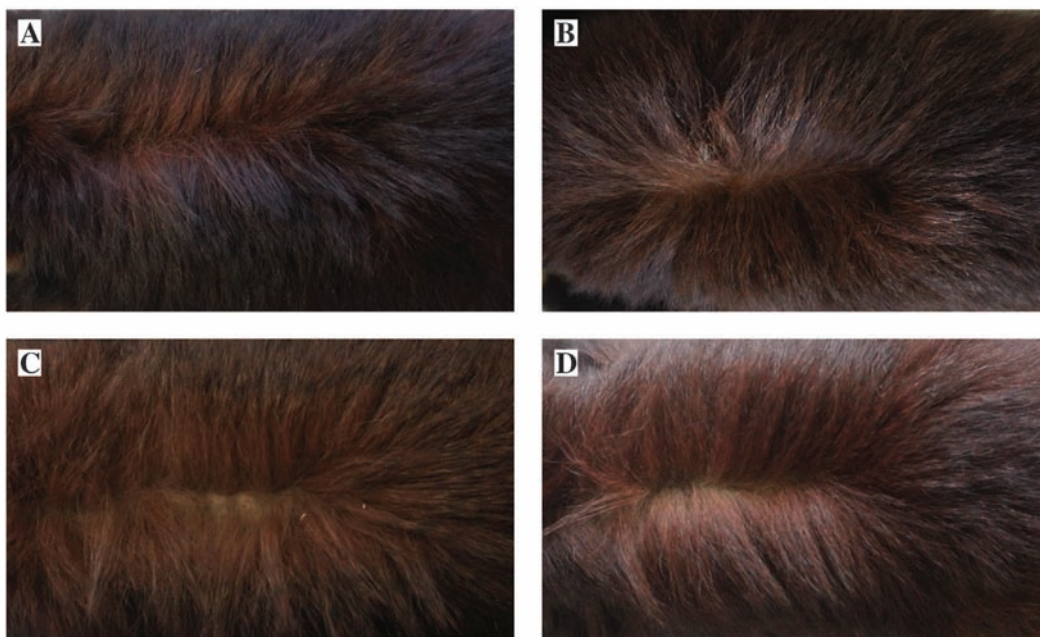


Figure 5. Banding pattern on the hair shaft at the shoulders/nape of specimens of *Cheracebus torquatus* (*sensu* Hershkovitz 1990): A) Rio Negro, BMNH (1842.4.29.15); B) Lago do Arara, BMNH (1926.5.5.22); C) Manacapurú, BMNH (1925.12.11.8); D) Codajás, MNRJ (MN-23865).

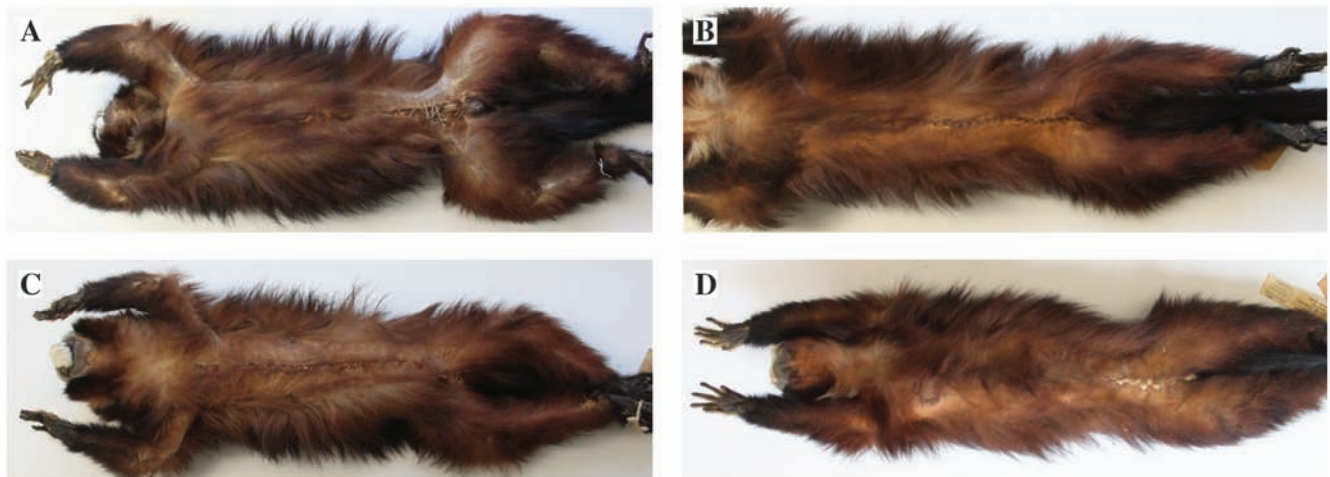


Figure 6. Ventral view of specimens of *Cheracebus torquatus* (*sensu* Hershkovitz 1990): A) Rio Negro, BMNH (1842.4.29.15); B) Lago do Arara, BMNH (1926.5.5.22); C) Manacapurú, BMNH (1925.12.11.8); D) Codajás, MNRJ (MN-23865).

(Fig. 6; panel A). The collar is very thin (Fig. 7; panel A), and the hands are dark buffy-whitish. It has a black forehead that contrasts slightly with the deep dark reddish posterior crown (Fig. 8; panel A). It seems that this specimen formed the basis for Thomas's hypothesis regarding the locality and identity of *C. torquatus*. Many of these pelage characters do not match the *torquatus* type; the overall color of the dorsal pelage is much darker/blacker toned than the overall "chestnut" of the *torquatus* type; the dorsal hairs do not have pale yellowish banding (rather showing black banding); the ventral pelage is not uniformly reddish colored, rather it is browner, duller/darker and less clearly marked from the dorsum owing to the black tips; and the collar is very thin. This nonspecific specimen locality ("Rio Negro") is not mapped in Figure 3, however, the river itself is labeled. Note, in the aforementioned Figures 4 through 8, panels B, C and D are other specimens assigned to *torquatus* by Hershkovitz (1990) and discussed in more detail in the section "Summary of *torquatus* Specimens (*sensu* Hershkovitz 1990)."

Einar Lönnberg (1939)

In 1939, Einar Lönnberg published a detailed analysis of seven specimens he had received at the NRM collected at Codajás, on the left (north) bank of the Solimões, in Brazil (locality 8 on Fig. 3). Lönnberg (1939) gives an excellent description of the pelage coloration of these specimens and the individual variation between them, which are consistent with our own limited observations of these specimens from photos (Fig. 9; A–F), as well as with other similar specimens from this region assessed in hand in other collections. A summarized version of the general pattern as described by Lönnberg (1939; p.2) is as follows: The back is mahogany brown in some specimens, but less reddish in others, it could be called dark rufous brown; posterior of the crown is very dark reddish, approaching "Claret Brown," but variable in different specimens, sometimes the same shade as the back; the ventral side, extending to upper parts of arms and legs, is rufous brown, resembling "Burnt Sienna" (Ridgway 1912) in some specimens, or more like chestnut in others; the collar is little developed, the white hairs (sometimes slightly yellowish) are broadly tipped with pale orange rufous, and in some specimens, the white is entirely substituted by this color; the hands are ochre yellow; the forehead, anterior crown, sideburns, arm to the elbows (sometimes higher), and feet (sometimes up to the knee or higher) are black; in most specimens, there is a narrow border of white hairs surrounding the face; the tail is exteriorly black, but the hair base is dark reddish or brownish (not visible), especially in the proximal portion of the tail. Lönnberg also gives a detailed explanation for variation in overall coloration of the pelage on the back from mahogany to dark rufous brown; in some specimens, the hair darkens from a mahogany red middle section; in others, the hairs are "annulated with various shades of rufous on more or less pronounced black."

Although Lönnberg's description of these Codajás specimens appears to be a good representation, his suggestion that

the pelage color pattern essentially agrees with the original description by Hoffmannsegg (1807) is problematic. Not only did Lönnberg himself not see the type specimen, he did not read the original type description but, instead, a short, summary by Wagner (1855). The description as given by Wagner (1855) states that the upper side is chestnut-brown, becoming black on the lower parts of the limbs and terminal half of the tail; the underside is foxy-red, almost rust-colored; the collar is yellowish-white and stretches from ear-to-ear across the throat, the hands are of the same color. Although Wagner's description is accurate in the information it gives, it omits much of the detail of Hoffmannsegg's description, for example, regarding the strong definition of the collar, a distinguishing feature between the *torquatus* type and these Codajás specimens. Wagner's summary also entirely excludes some important aspects such as the pale/yellowish banding on the back and shoulders of the *torquatus* type, which is not found in the Codajás specimens.

Furthermore, it appears that the subjectivity of the terms used to describe the coloration of the *torquatus* type has caused some issues. For example, Lönnberg's description of the Codajás specimens as having a rufous brown (Burnt Sienna [Ridgway 1912]) to chestnut ventral pelage suggests a more brownish coloration than foxy-red or rust-colored, and indeed the Codajás specimens in the NRM are typically more brownish ventrally than the *torquatus* type. In a similar manner for the dorsal pelage, the chestnut color in the descriptions of *torquatus* suggest a lighter reddish tone than the darker mahogany or brown rufous of the Codajás specimens. Comparing Lönnberg's description and images of the Codajás skins (Fig. 9) to Hoffmannsegg's original description of *torquatus* and images of the type (Fig. 3), it is apparent that these Codajás specimens do not "essentially" agree with the *torquatus* type, illustrating the subjectivity of terms used to describe colors even when employing color standards such as those by Ridgway (1912), for example reddish brown tones as chestnut, mahogany, rufous or claret. It also seems peculiar that a species named for its collar (*torquatus*; collared titi) by Hoffmannsegg (1807) would have a "little developed" collar, as noted by Lönnberg in his description of the Codajás specimens (1939; p.2).

Lönnberg was aware of the work of Thomas (1914, 1927a), mentioning these studies in his paper, and the general concordance in the conclusions of these two taxonomists apparently solidified this view of the identity of *torquatus* as the left bank Solimões populations found around Codajás, despite neither having seen nor assessed the type specimen.

Philip Hershkovitz (1963, 1988, 1990)

In Hershkovitz's first appraisal of the Callicebinae in 1963, he recognized only three subspecies of *C. torquatus*: *C. t. lugens*, *C. t. medemi*, and *C. t. torquatus*. He assessed just 21 *Cheracebus* specimens in the collections at the Field Museum (FMNH) in Chicago—five *lugens*, eleven of his newly described taxon *medemi*, and five further specimens (one from Lago de Ayapuá, Amazonas, Brazil; two from no

precise location, Brazil; and two from Santa Lucia, Nanay, Loreto, Peru). Across these latter five specimens, Hershkovitz suggested that there was an “apparent absence of features for consistently distinguishing the populations on one side of the Solimões from the other” (p.47) and they were each classified as *torquatus*. The hypothetical distribution of the subspecific form *torquatus* (*sensu* Hershkovitz 1963) extended from the Rio Purus west to the Rio Juruá (and possibly Rio Javari/Río Yavari) south of the Solimões; to the “north of the Solimões, known from Codajás and between the rios Solimões and Japurá” (p.56); and into Colombia and Peru between the middle Río Caquetá, the Río Marañón and lower Río Tigre. Thomas’s taxa, *lucifer*, *regulus*, and *purinus* were here included as synonyms of *C. t. torquatus*. Hershkovitz (1963; p.48) suggested that *C. t. torquatus* populations could be “distinguished from *medemi* and *lugens* by their more reddish color and by their contrastingly whitish or yellowish hands or fingers.” He proposed to restrict the type locality of *C. t. torquatus* to Codajás [Codajás], north bank of Rio Solimões, Amazonas, Brazil, citing both Thomas (1927a) and Lönnberg (1939). Thus, as of 1963, Codajás was viewed as the type locality for the reddish subspecies *torquatus*, which as recognized, was otherwise distributed to the south of the rios Caquetá-Japurá and Solimões.

This view of the diversity of widow monkeys largely prevailed until Hershkovitz’s subsequent revisions in 1988 and 1990, in which he recognized six taxa, reinstating *lucifer*, *regulus*, and *purinus* as valid subspecific forms of *torquatus*. Hershkovitz (1990) developed this classification based on his analysis of 178 *Cheracebus* specimens, over half of which were *lugens* (N = 96), with 18 specimens of *torquatus* and 11 of *purinus*. He gave explicit hypothetical distributions and diagnostic characters for each of these lineages, and restricted *torquatus* to a thin, east-west section along the left (north) bank of the Solimões, between the Negro-Solimões interfluvium in Brazil (western limits not defined).

Recent changes: Marc van Roosmalen

Van Roosmalen *et al.* (2002) redefined *torquatus*, modifying some diagnostic characters, and extended the distribution of *torquatus* through the Negro and Solimões-Japurá interfluvium in Brazil, west to the rios Vaupés and Apaporis in Colombia, with *lugens* distributed broadly elsewhere east of the Rio Branco (north of the Solimões-Japurá-Caquetá). This contrasted with the restricted range along the left bank of the Solimões proposed earlier for *torquatus* by Hershkovitz (1988, 1990). As indicated by Van Roosmalen (2003), it would seem that this is based on a broad interpretation of the map provided by Hershkovitz (Fig. 3, 1963) for *torquatus*, just excluding the supposed distribution of *purinus*, *regulus*, and *lucifer*.

Molecular evidence suggests that *Cheracebus* individuals collected on the left bank of the Rio Japurá and right bank of the Rio Negro (i.e., *torquatus sensu* Van Roosmalen *et al.* 2002) do not form a clade to the exclusion of *lugens* collected to the left (north) bank of the Negro (Byrne 2017).

In addition, *Cheracebus* individuals in the regions newly attributed to *torquatus* can be phenotypically similar to those elsewhere classified as *lugens*. Phenotypic and molecular evidence, therefore, suggest that *torquatus* and *lugens* (*sensu* Van Roosmalen *et al.* 2002) are not monophyletic taxa. This topic is discussed in more detail in the section “Phenotypes found north of the Solimões-Japurá-Caquetá.” Here, we primarily discuss *torquatus* as defined by Hershkovitz (1990). Most of the specimens he labeled as *torquatus* appear to be somewhat distinguishable from other *Cheracebus* individuals found north of the Solimões-Japurá-Caquetá, primarily in the reddish brown ventral color and the weak or diffused collars in most specimens.

Van Roosmalen *et al.* (Fig. 35, 2002) also mapped, enigmatically, a new species with no name in the interfluvium of the lower rios Purus and Madeira, south at least to the Rio Ipixuna, a right bank tributary of the Rio Purus—an extension to the then known range of the genus *Cheracebus*. A similar map that also indicated a new species for the Purus-Madeira interfluvium was presented on his website (Van Roosmalen 2003). According to Van Roosmalen (2003), the identification of collared titis between the lower rios Purus and Madeira was based on sightings “on the north bank of the Lago Jari, near the island of Fortaleza (coordinates 05°00'S, 62°27'W) in the high dryland forest behind the town of Berurí, and at km 253 along the BR-319 that connected Manaus (Carreiro-da-Várzea) with Humaitá and Lábrea and nowadays is accessible only as far as the Rio Igapó-Açú.” To add to the confusion, however, on this website, Van Roosmalen (2003) described (in the text) this Purus-Madeira form as *torquatus* Hoffmann-segg (rather than a new, unnamed species), while maintaining the type locality as Codajás, on the north bank of the Rio Solimões (as per Hershkovitz 1963, 1990). He suggested that an unnamed species (not *torquatus*), closely aligned to *lugens*, was found in the region between the rios Negro-Vaupés and Solimões-Japurá-Apaporis, which is the opposite of what is depicted in both of these maps (Van Roosmalen *et al.* 2002; Van Roosmalen 2003). An apparently corrected map in Van Roosmalen (2020), however, confined the distribution of *torquatus* entirely to the Purus-Madeira interfluvium—aligning it with the collared titis south of the Rio Solimões—with an unnamed, new species (not *torquatus*) indicated this time for the region between the rios Negro-Vaupés and Solimões-Japurá-Apaporis (as was mentioned on his 2003 website, but not illustrated in the accompanying map).

The only existing evidence that a *Cheracebus* lineage exists between the rios Purus and Madeira is the two sightings described by Van Roosmalen (2003). Judging by his detailed description, the Lago Jari location was evidently of a pet. The Berurí locality it seems was the sighting of an individual in the wild. In light of unpublished results from a survey expedition led by WCS Brazil in 2011 (Röhe 2012), it is possible that Van Roosmalen might have mistaken another titi (*Plecturocebus caligatus*) that occurs in this region for a collared titi monkey. In this expedition, JPB and collaborators conducted 12 line-transect censuses of primates

along the BR-319 federal highway that dissects the Purus-Madeira interfluvium. The 12 transects were placed between the km 165 and 300 of the BR-319 highway, including the Agro-Extractivist Settlement Project (PAE) Tupana Igapó Açú, the Sustainable Development Reserve Igapó-Açú, and the Nascentes do Lago Jari National Park. In total, the sampling effort amounted to 400 km of walked transects where all seven primates known from this region were detected, including multiple sightings of *Plecturocebus caligatus*. There were no records of *Cheracebus*. There are no known sightings of *Cheracebus* in this region among locals in nearby communities (Castanho, Igapó-Açú). We include the above explanation of Van Roosmalen's (2003, 2020) hypotheses for clarity; however, in this article, we focus on Van Roosmalen *et al.*'s (2002) classification of widow monkeys, which has been highly influential to subsequent studies on *Cheracebus*.

Van Roosmalen *et al.* (2002) and Groves (2005) treated all six *Cheracebus* taxa as species, and there have been no peer-reviewed publications proposing modifications to the species-level taxonomy of the widow monkeys since. Although some authors continue to refer to Hershkovitz (1990)—Haugaasen and Peres (2005), Casado *et al.* (2007), and Aquino *et al.* (2008), for example—it is Van Roosmalen *et al.*'s (2002) taxonomic arrangement and distributions that are most commonly referenced and they are used for the assessments on the IUCN Red List (but see also updated distributions in Byrne *et al.* 2018, Suppl. File 2).

Summary of *torquatus* Specimens (*sensu* Hershkovitz 1990)

In this section we summarize the pelage coloration of specimens labeled as *torquatus* by Hershkovitz (1990), excluding specimens we consider to be *lugens*. The 18 specimens Hershkovitz (1990) considered as *torquatus* were as follows (see also Table 1, and Suppl. File, Table S1): eight Codajás specimens (seven from the NRM and one from MNRJ; locality 8 on Fig. 3); two specimens from Manacapuru (one each from the BMNH and NRM; locality 6 on Fig. 3); one from the Lago do Arara (BMNH; locality 7 on Fig. 3); two from the Rio Negro (BMNH); one purchased in Manaus and two of unknown provenance in the FMNH; and two of unknown provenance from the MNHN. The MNHN could find only one specimen—the *amicta* holotype, which was in poor condition with possible discoloration (pale patches). Based on the images received, this MNHN specimen is a *lugens*. The NRM provided images for their eight specimens. The rest of these specimens assigned to *torquatus* by Hershkovitz (1990) were assessed in person by HB (see Table 1, and Suppl. File, Table S1).

One specimen of unknown provenance (label says “Rio Negro?”) found in the FMNH (35144) was identified by HB as *lugens* (blackish dorsal and ventral pelage), and HB was unable to locate/identify a second *torquatus* specimen of unknown provenance in the FMNH. One Rio Negro

specimen in the BMNH (1933.10.11.1) has a dark red and blackish banded pattern in the dorsal hairs; however, it has a darkish belly, a very well-developed thick collar, and blackish proximal (base) portion to the dorsal hairs. It is also considered to be *lugens* (Phenotype B; see section below “Phenotypes found north of the Solimões-Japurá-Caquetá”). Thirteen of the 18 specimens are considered here, but for the NRM Codajás specimens (open skins) we primarily verified the description from Lönnberg, see section “Einar Lönnberg (1939).”

Our own descriptions of *torquatus* are based on the specimens viewed in person. Most of the characters agree with Lönnberg's summary of the Codajás *torquatus* specimens and here we focus our discussion on the most important diagnostic characters. Specimens of *torquatus*, as defined by Hershkovitz (1990), generally show a reddish to reddish brown section towards the proximal portion of the dorsal hairs, while the distal section (tip) is banded between a similar reddish coloration and blackish to dark brownish (darker and less reddish than the base color), essentially blackish bands on reddish or reddish brown (Fig. 5; A–D). The overall color is a dark mahogany-red to dark brown rufous, and relatively well banded to weakly banded, although the FMNH specimen purchased in Manaus appears near uniform (Fig. 4; A–D). Most specimens show a dull rusty brownish-red ventral coloration with some blackish or brown tipped hairs on the chest/belly, as well as a buffy whitish proximal section to the hair shaft in some areas on some specimens, giving rise to the “washed” ventral appearance (Fig. 6; A–D). The ventral coloration extends onto the outer hind legs, but usually appears clearer reddish (not black tipped, without a pale base, and less brownish) in coloration on the hind legs than the ventral region. The collar is either weakly developed and not clearly differentiated/demarcated from the ventral coloration (tipped with reddish), or very thin (Fig. 7; A–D). A new illustration of this lineage by Stephen Nash is presented in Figure 10.

There is variation in the dorsal coloration among *torquatus* specimens viewed in hand. The MNRJ Codajás specimen (MN-23865), the BMNH specimens from Manacapuru (1925.12.11.8), Lago do Arara (1926.5.5.22) and Rio Negro (1842.4.29.15) [described in the section “Oldfield Thomas (1914, 1927)”], and the specimen purchased in Manaus from the FMNH (35076), agree with Lönnberg's description of the dark mahogany reddish Codajás specimens (Fig. 4; A–D). These specimens typically show red mahogany on the proximal portion (base) of the hair and alternating reddish and dark brown or blackish at the distal portion (tip) (Fig. 5; A–D). The BMNH Manacapuru specimen has the palest reddish coloration at the hair base and is banded on the tips, resulting in the most distinct banding pattern and strongest overall reddish coloration (Figs. 4 and 5; panel C). The Lago do Arara specimen and the FMNH specimen are the darkest overall, the former is faintly banded and it has a thin but relatively defined collar (Figs. 5 and 7; panel B), while the latter fades from buffy to dark reddish to a darker tip (no banding).

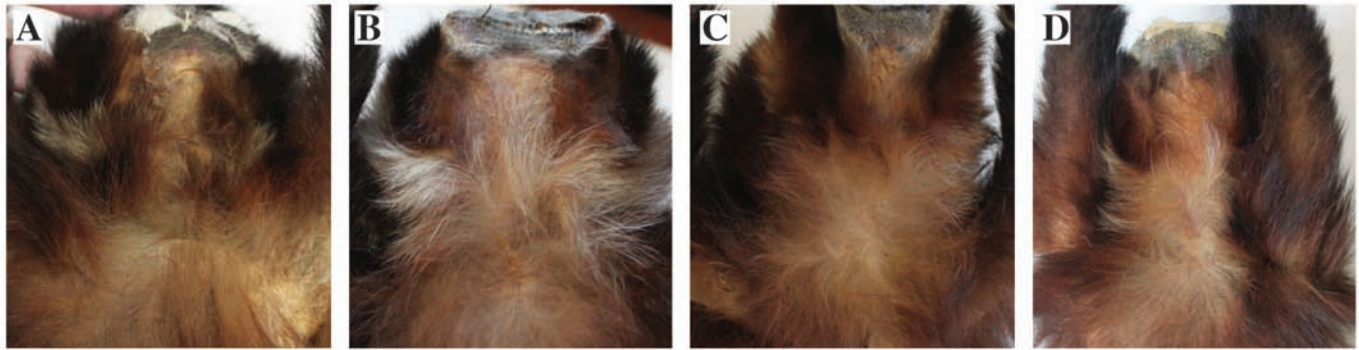


Figure 7. View of the throat collar of specimens of *Cheracebus torquatus* (*sensu* Hershkovitz 1990): A) Rio Negro, BMNH (1842.4.29.15); B) Lago do Arara, BMNH (1926.5.5.22); C) Manacapurú, BMNH (1925.12.11.8); D) Codajás, MNRJ (MN-23865).

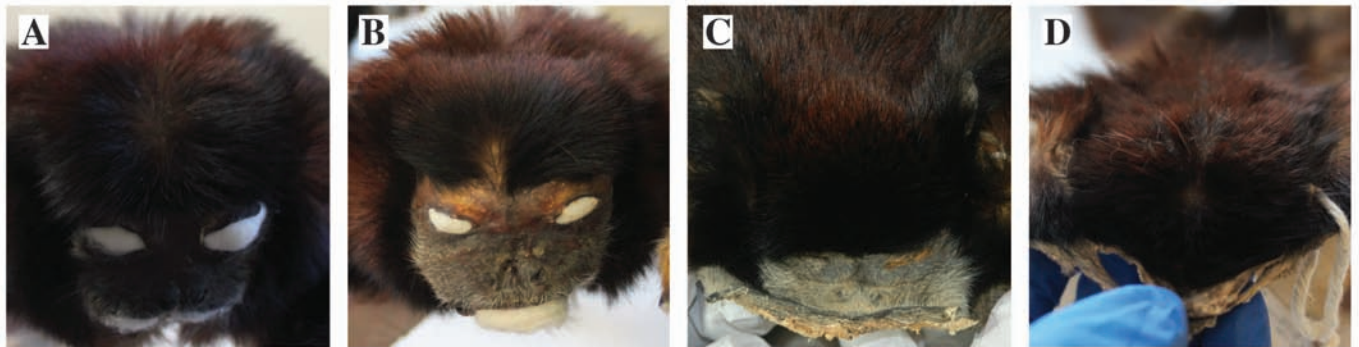


Figure 8. View of the forehead and crown of specimens of *Cheracebus torquatus* (*sensu* Hershkovitz 1990): A) Rio Negro, BMNH (1842.4.29.15); B) Manacapurú, BMNH (1925.12.11.8); C) Codajás, NRM (621046) (photo by Daniela Kalthoff at the NRM); D) FMNH (35076).

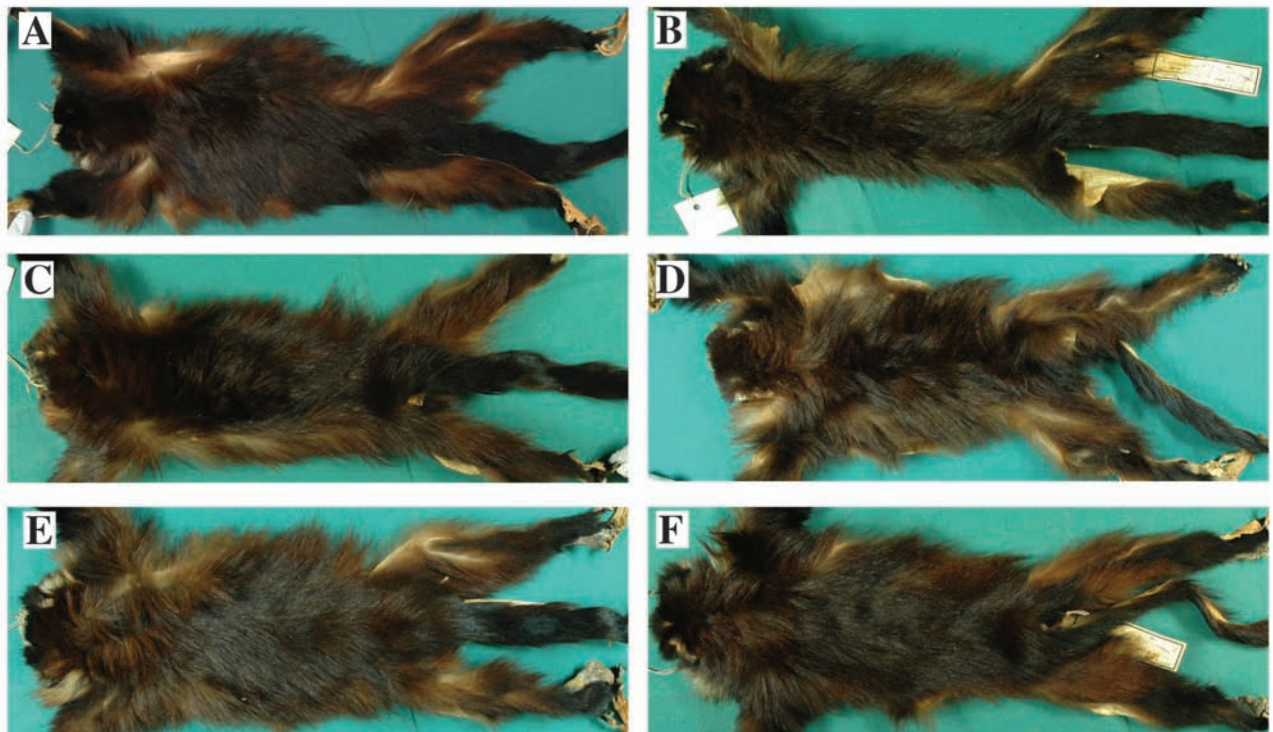


Figure 9. Dorsal view of open-skin specimens of *Cheracebus torquatus* (*sensu* Hershkovitz 1990) from Codajás at the NRM: A) 621045; B) 621046; C) 621104; D) 622023; E) 631039; F) 641040. Photos by Daniela Kalthoff at the NRM.

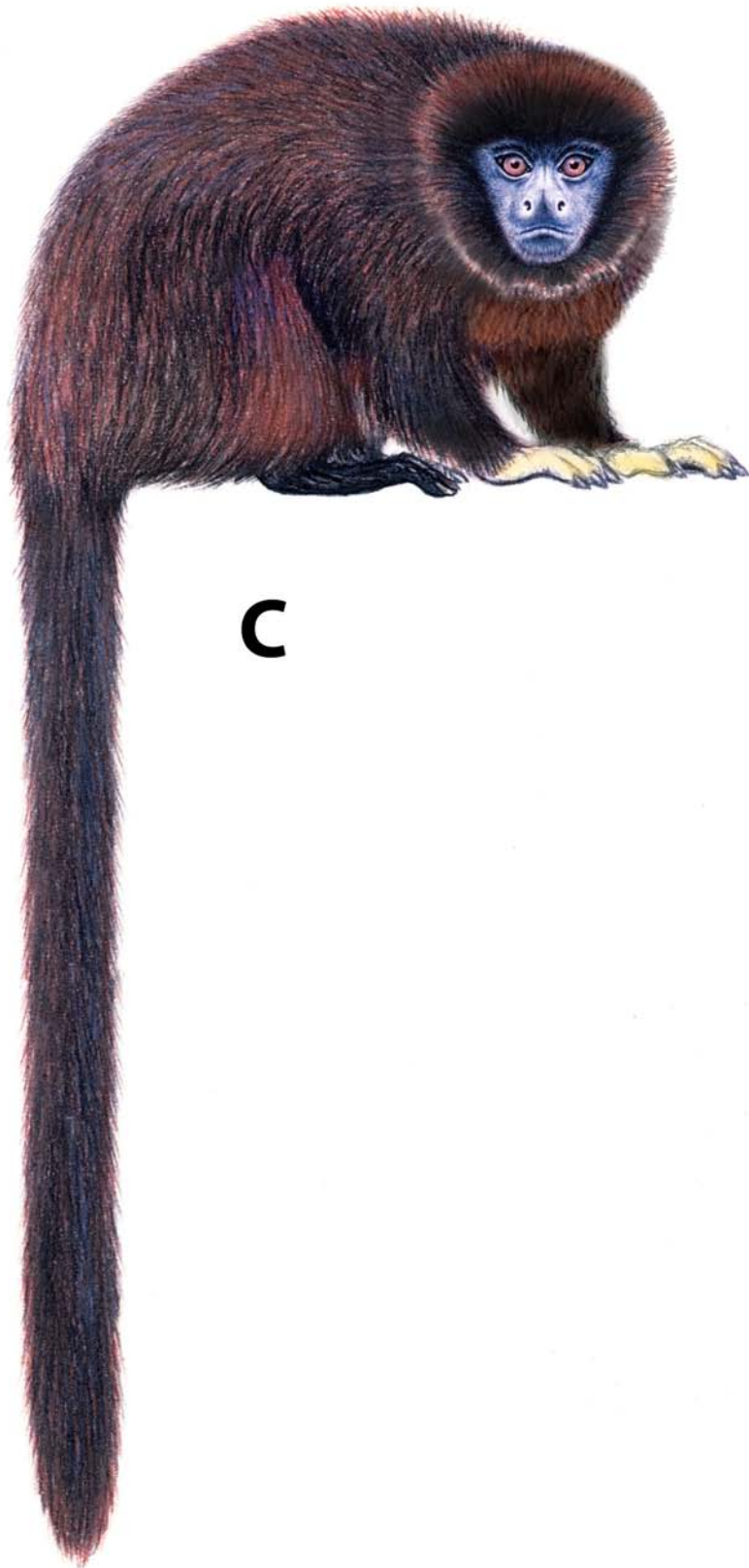


Figure 10. New illustration of *Cheracebus torquatus* (*sensu* Hershkovitz 1990) by Stephen Nash ©.

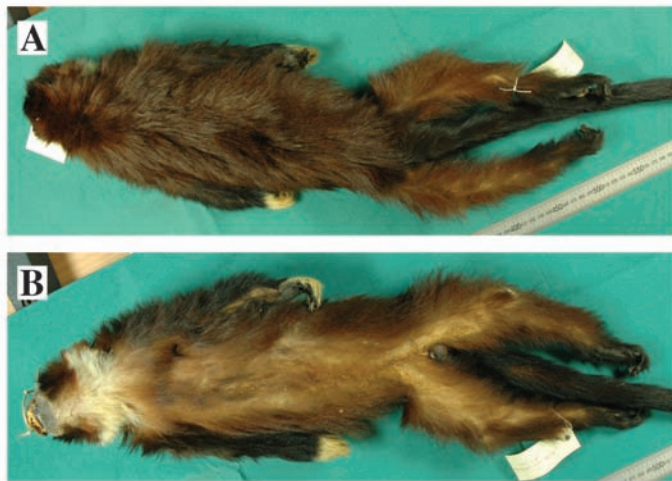


Figure 11. A specimen at the NRM (620501) with collection locality as Manacapurú, identified as *Cheracebus torquatus* by Hershkovitz (1990): A) dorsal; B) ventral. Photos by Daniela Kalthoff at the NRM.

All specimens show a thick black region across the forehead and usually into the anterior crown, with the posterior crown as deep dark reddish or similar in color to the dorsum, as described by Lönnberg (1939) (Fig. 8; A–D).

Based on images, the NRM Manacapurú specimen (620501) is distinct in its brown rufous appearance, which appears browner (less reddish) than the aforementioned specimens and lighter than many of the Codajás specimens from NRM. It appears to have a faint banded pattern on the dorsal hairs (Fig. 11; panel A); however, the images received did not allow for a detailed assessment of the banding pattern. It also has a well-developed and clearly defined collar (Fig. 11; panel B). This specimen is anomalous among specimens labeled as *torquatus* by Hershkovitz (1990) in its gross similarity to *purinus*.

Summary of *purinus* Specimens

In this section we summarize the pelage coloration of *purinus* specimens. Hershkovitz (1990) included 11 *purinus* specimens in his analysis, of which we lacked images of one (a “Lago Aiapuá” specimen in the MNRJ). Although Hershkovitz specified three specimens from “Lago Aiapuá” in MNRJ, only two could be located in their database, and this is possibly an error as he gives the total as 11 *purinus* specimens, rather than 12. We reviewed 13 specimens in all (seven in hand, six from photos), including 10 of the *purinus* specimens examined by Hershkovitz (1990), as well as three additional specimens in INPA which were also used in the molecular datasets of Byrne *et al.* (2016) (and others) and the mitochondrial phylogeny here (see section “Molecular evidence”). While the BMNH specimen from Tefé (Ega; 1851.7.12.7) is most likely to be a *purinus*, we do not consider this incomplete specimen in detail as it is a juvenile and consists solely of the upper torso.

Across the specimens examined, the color of the dorsal region varies greatly from dull brown to reddish chestnut to even brighter red with more or less pigmented yellowish

to golden flecking/banding (Fig. 12; A–F). The main factor impacting the overall speckled or “grizzled” appearance is the degree of contrast between the darker brown to reddish bands versus the paler bands on the distal portion of the dorsal hairs (Fig. 13; A–D). The type specimen (1926.5.5.21) is the most strikingly speckled of all, owing to the strong contrast between pale yellowish bands on dark dull brown (Figs. 12 and 13; panel A). In the lighter dull brown or more rufous brown specimens (e.g., MN-2461, MN-2464), the yellowish banding on the dorsal hairs is still relatively strong and these specimens are evidently speckled overall (Fig. 12, panels B and C; Fig. 13, panel B). The distinct Bordeaux red chestnut (similar to Bordeaux to Chestnut [Ridgway, 1912]) of the unique USNM 105539 shows golden-yellowish banding on more reddish hairs resulting in a somewhat subtler speckled appearance (Fig. 12, panel F; Fig. 13, panel D), while the reddish-brown/chestnut specimens (FMNH 38885, USNM 518222) appear to be the most uniformly colored owing to the weaker contrast between the deep golden (to near pale rufous) bands on brown or reddish-brown coloration (Fig. 12, panels D and E; Fig. 13, panel C). The speckled appearance is often the more notable on the flanks (Fig. 14; A–D).

In the center of the back at the shoulders/nape, the bottom non-banded portion of the hairs usually take a similar coloration to the darker bands at the tip, though the very base can be buffy whitish (Fig. 13). At the edge of the flanks towards the ventral coloration, the mid to lower proximal section of the hair shaft often becomes reddish like the ventral color (also into a buffy whitish base) (Fig. 15). Thus, there can be 4 or more colors on a single dorsal hair, varying slightly across the shoulders/dorsum and flank, and greatly across specimens, giving rise to the significant variation in overall dorsal appearance described above.

In most specimens, the crown is bright reddish such that there is a strong contrast between the coloration of the nape/dorsum and the crown (Fig. 16; A–C); however, in the more reddish or reddish-brown specimens (e.g., FMNH 38885, both USNM specimens), the contrast is lacking or the crown is a similar color to the dorsum (Fig. 16; D–F). In nearly all specimens the reddish coloration of the ventral pelage, which extends onto the outer hind legs, is clearly differentiated and demarcated from the dorsal pelage (Fig. 17; B–F), with the exception of the type specimen (Fig. 17; panel A). The exact ventral coloration varies from a brighter fox/rusty red (found in most specimens), to paler orange (MNRJ-2461) (Fig. 17; panel B), to deep reddish (in the holotype, 1926.5.5.21, which has duller brown beneath the collar) (Fig. 17; panel A), to more brownish (CTGAM195).

All specimens show black pelage in the following areas: on the feet, sometimes coming onto the lower legs, sometimes only the toes, and the MNRJ specimen (MN-2461) from Lago de Tauariá has some white hairs on the toes (Fig. 17; panel B); on the forearms above the pale hands, but the extent varies from just at the lower section around the wrist to covering most of the forearms; and the forehead and sideburns. In some specimens the black forehead band is very



Figure 12. Dorsal view of specimens of *Cheracebus purinus*: A) Holotype, Aiapuá, BMNH (1926.5.5.21); B) Lago Tauariá, MNRJ (MN-2461) (photo by João Oliveira at the MNRJ); C) Lago Aiapuá, MNRJ (MN-2464); D) Lago Aiapuá, FMNH (38885); E) Tefê, USNM (518222); F) Rio Mamoriá-mirim, USNM (105539). Credit, panels E and F: Catalog number USNM (518222, 105539), Department of Vertebrate Zoology, Smithsonian Institution, photos by Kate D. Sherwood.

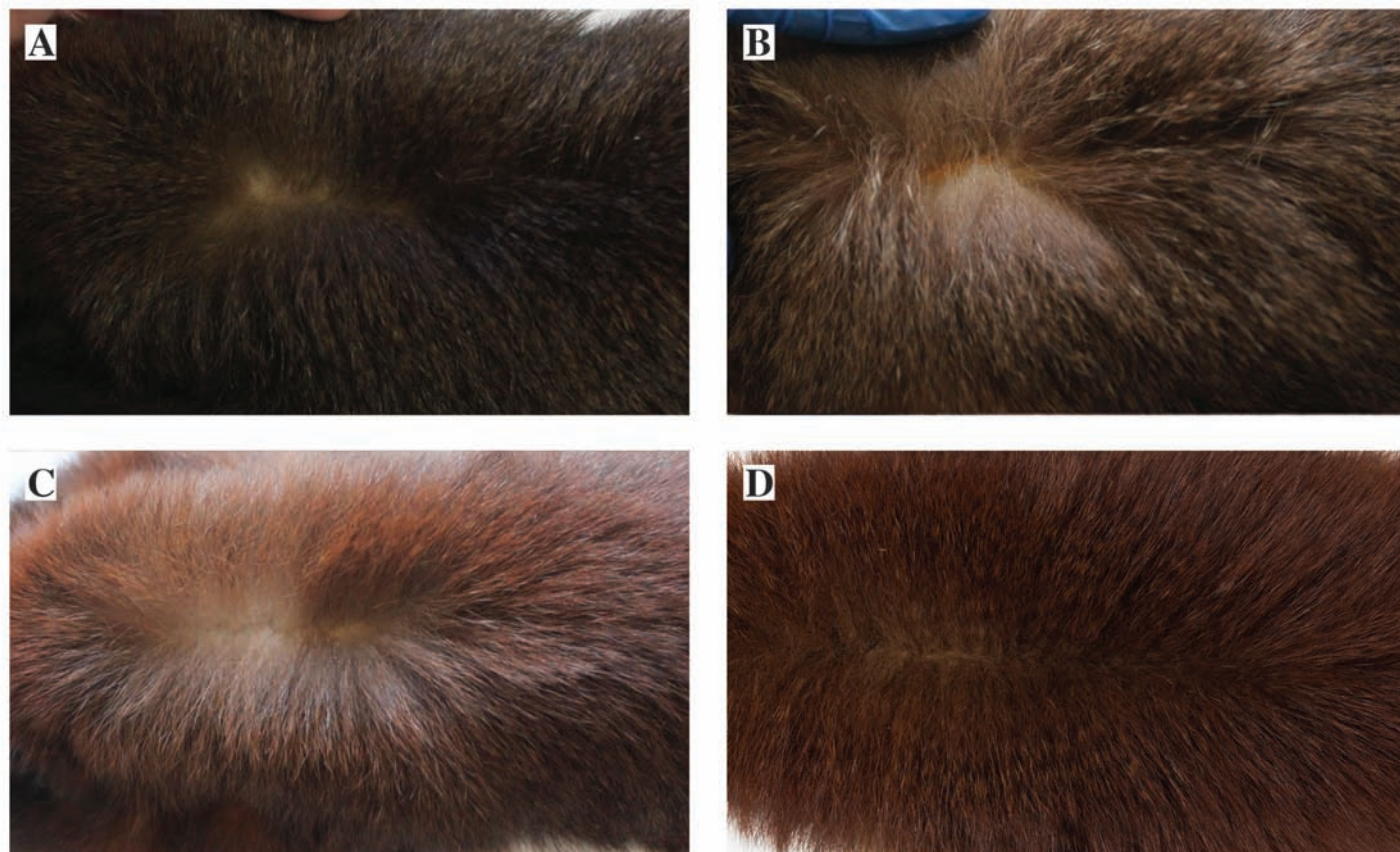


Figure 13. Banding pattern on the hair shaft at the shoulders/nape of specimens of *Cheracebus purinus*: A) Holotype, Aiapuá, BMNH (1926.5.5.21); B) Lago Aiapuá, MNRJ (MN-2464); C) Lago Aiapuá, FMNH (38885); D) Rio Mamoriá-mirim, USNM (105539). Credit, panel D: Catalog number USNM (105539), Department of Vertebrate Zoology, Smithsonian Institution, photos by Kate D. Sherwood.



Figure 14. Side view of the flanks of specimens of *Cheracebus purinus*: A) Lago Aiapuá, MNRJ (MN-2464); B) Lago Aiapuá, FMNH (38885); C) Tefé, USNM (518222); D) Rio Mamoriá-mirim, USNM (105539). Credit, panels C and D: Catalog number USNM (518222, 105539), Department of Vertebrate Zoology, Smithsonian Institution, photos by Kate D. Sherwood.



Figure 15. Banding pattern on the hair shaft on the flanks of a *Cheracebus purinus* specimen from the MNRJ (MN-2464).

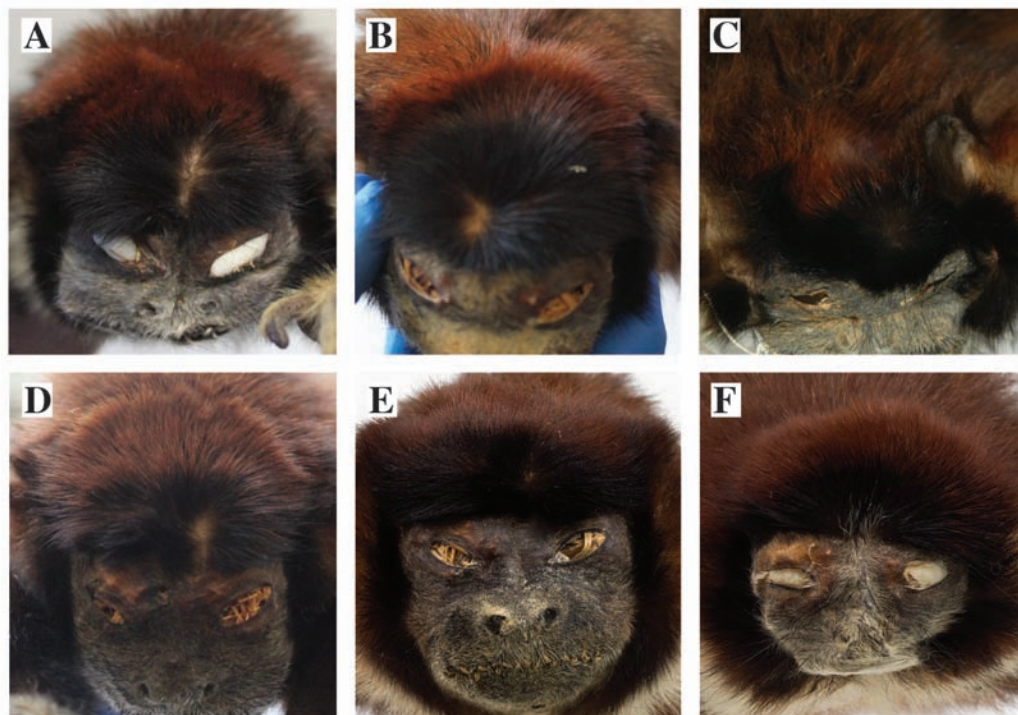


Figure 16. View of the forehead and crown of specimens of *Cheracebus purinus*: A) Holotype, Aiapuá, BMNH (1926.5.5.21); B) Lago Aiapuá, MNRJ (MN-2464); C) Jaburu, NRM (631211) (photo by Daniela Kalthoff at the NRM); D) Lago Aiapuá, FMNH (38885); E) Tefé, USNM (518222); F) Rio Mamoriá-mirim, USNM (105539). Credit, panels E and F: Catalog number USNM (518222, 105539), Department of Vertebrate Zoology, Smithsonian Institution, photos by Kate D. Sherwood.



Figure 17. Ventral view of specimens of *Cheracebus purinus*: A) Holotype, Aiapuá, BMNH (1926.5.5.21); B) Lago Tauariá, MNRJ (MN-2461) (photo by João Oliveira at the MNRJ); C) Lago Aiapuá, MNRJ (MN-2464); D) Lago Aiapuá, FMNH (38885); E) Tefé, USNM (518222); F) Rio Mamoriá-mirim, USNM (105539). Credit, panels E and F: Catalog number USNM (518222, 105539), Department of Vertebrate Zoology, Smithsonian Institution, photos by Kate D. Sherwood.

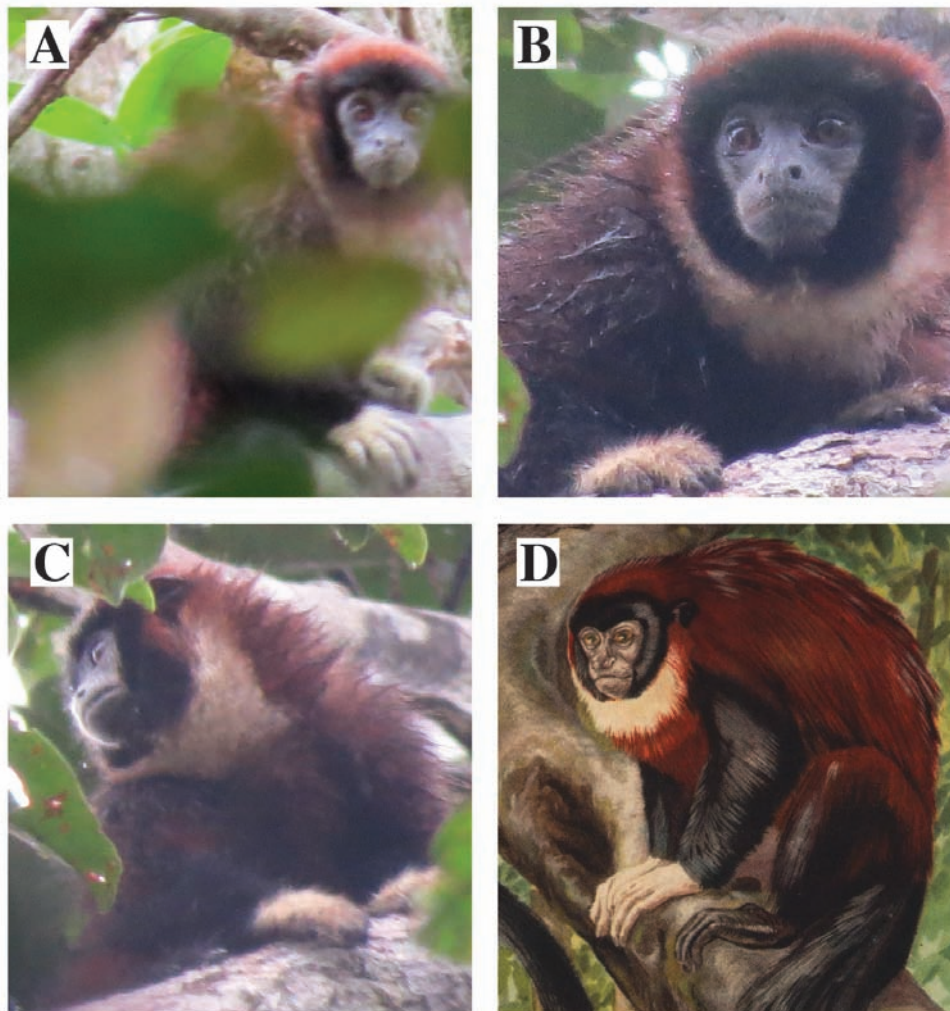


Figure 18. Bright red wild *Cheracebus purinus* (A, B, C) and comparison to an illustration of *Cheracebus torquatus* by Cruz Lima (1945) (D). Photos (panels A, B, C) by Ivan Batista da Silva.

thin and hardly distinguishable (e.g., FMNH 38885) (Fig. 16; panel D), while in others it is much thicker, extending into the anterior crown region and contrasting strongly with the bright posterior crown (e.g., MNRJ-2464, CTGAM154) (Fig. 16; A–C). The tail appears blackish mixed with reddish (base of the hair is reddish with a black distal portion), particularly in the proximal tail.

All specimens show yellowish hands, though the exact coloration is variable from yellowish-white through to golden. One USNM specimen (518222) shows the pale coloration solely on the fingers, with the rest of forehands blackish (Fig. 17; panel E). The whitish to pale yellowish collar is well-developed and very clearly defined, extending to the ear base, thicker in some specimens, and nearly bib-like in one USNM specimen (105539) (Fig. 17; panel F).

The distinct Bordeaux-red USNM specimen (105539) was collected around the Rio Mamoriá, farther south than any other *purinus* specimens examined (locality 1 on Fig. 3). A reddish individual is also presented in figures 39 and 40 in Van Roosmalen *et al.* (2002; p.34), a pet from Camaruã, near the mouth of the Tapuá with the Purus. Images obtained of a wild bright-reddish *Cheracebus* individual (Fig. 18; A–C), pictured to the right (east) bank of the Rio Tarauaca (marked with a blue star on Fig. 3), also with a broad collar, suggests that even stronger red phenotypes may exist farther southwest in the Juruá-Purus interfluvium, and strongly exemplifies how extensively incomplete our knowledge of these under-studied primates is still to this day. The similarity between this individual and an illustration by Cruz Lima (1945; plate XXIX), identified as *Callicebus torquatus torquatus* (Hoffmannsegg), is quite striking (Fig. 18; panel D).

Is *purinus* Thomas, 1927, a Junior Synonym of *torquatus* Hoffmannsegg, 1807?

As outlined through the section “Taxonomic history of *Cheracebus torquatus*,” the main hypothesis regarding the identity of *torquatus* Hoffmannsegg, 1807, is based largely on the work of three taxonomists—Thomas (1914, 1927a), Lönnberg (1939) and Hershkovitz (1963, 1990)—none of whom saw the holotype specimen of *torquatus*. The diagnostic characters for *torquatus* (*sensu* Hershkovitz 1990) are based on the phenotype of some *Cheracebus* individuals found in the region attributed to *torquatus* by these authors, rather than the type specimen or the type description. It is evidently highly doubtful, however, that the type specimen for *torquatus* belongs to the lineage that the moniker *torquatus* now specifically represents. We do not believe that there is strong evidence in support of Codajás as the type locality for this taxon. It was proposed by Hershkovitz (1963) based on the work of Lönnberg (1939), who had read only a summarized version of the type description provided by Wagner (1855). We do not agree with the supposed affinity of the *torquatus* holotype with the Codajás or other left (north) bank Solimões specimens separating it as such from those south of the Solimões between the rios Juruá and Purus

known as *purinus*. In this section, we argue that the *torquatus* holotype and type description match most closely to specimens currently classified as *purinus*.

Broadly across all specimens, *purinus* and *torquatus* (*sensu* Hershkovitz 1990) can be typically distinguished as follows (see also Table 2): the well-defined whitish collar in *purinus* versus thin/weak/diffused collar in *torquatus* (except the NRM Manacapuru specimen) (Figs. 7 and 17); the pattern on the dorsal hairs in *purinus* varies from dull brown to reddish with pale yellowish to deep golden (to near pale rufous) bands and a strongly to weakly banded appearance (could be described as yellowish or golden on dull brown to reddish), while the pattern in *torquatus* is typically red to reddish brown with black to brownish bands and mid-faintly banded to near uniform appearance (could be described as black to brownish on reddish to reddish brown) (Figs. 5 and 13); the ventral coloration in *purinus* is brighter red and more clearly differentiated from the dorsal region in most specimens (although some are partially brownish, notably the type), while *torquatus* are typically more brownish and, in many specimens, the ventral hairs are washed with darker tips and a buffy base (Figs. 6 and 17). Thus, overall *purinus* and *torquatus* (*sensu* Hershkovitz 1990) often share broadly similar colors in the same chromatic fields of the pelage, but at a finer scale there are differences that distinguish the two (Table 2).

In a key, Hershkovitz (1990; pp.78–80) described the diagnostic characters for *torquatus* as “hairs of back and sides weakly banded to uniformly reddish brown; throat collar weakly defined, sometimes absent” while for *purinus* he proposed “hairs of back and sides strongly to faintly banded; throat collar contrastingly colored buffy, yellowish, or whitish, the collar extending to ear base,” and for both taxa “chest and belly reddish or reddish brown.” Hershkovitz then suggested that *torquatus* was distinguished from *purinus* by the “blackish crown not sharply demarcated from mahogany nape, hairs of back uniformly colored or faintly banded” and *purinus* from *torquatus* by “reddish brown crown sharply contrasted with blackish forehead, marked agouti pattern of back, throat collar well developed and sharply defined from surrounding parts” (pp.82–83). Using Hershkovitz’s key and distinguishing features that appear to be a decent representation of these taxa according to our own observations (excluding the details of the crown, which do not seem to hold true entirely, see below), the *torquatus* type specimen very evidently falls under *purinus*.

Importantly, there is variation in the color and contrast of the crown versus the forehead and nape in *torquatus* (as also suggested by Lönnberg 1939) and *purinus* specimens (Figs. 8 and 16). Although the crown can be brighter red and more contrasting in *purinus*, specimens with a more reddish toned dorsum, and/or a thinner black forehead band, lack such contrast. The crown typically becomes deep reddish brown more posteriorly in *torquatus*, usually with a thick black section from the forehead to anterior crown (Fig. 8), while in *purinus* the black coloration is often restricted to a thinner forehead band, only becoming thicker such that it extends into the

Table 2. Summary of the main pelage characters distinguishing *Cheracebus* taxa.

| Species (<i>sensu</i> Hershkovitz 1990) | <i>Cheracebus purinus</i> | <i>Cheracebus torquatus</i> | <i>Cheracebus torquatus</i> | <i>Cheracebus lugens</i> | <i>Cheracebus lugens</i> |
|---|--|---|---|---|--|
| Species (this study) | <i>Cheracebus torquatus</i> | <i>Cheracebus cf. lugens</i> | <i>Cheracebus torquatus</i> | <i>Cheracebus lugens</i> | <i>Cheracebus lugens</i> |
| Phenotype ID | NA | Phenotype C | Phenotype C | Phenotype B | Phenotype A |
| Dorsum: overall color | Highly variable from dull brown to reddish brown to reddish | Dark mahogany-red to dark brown rufous | Dark mahogany-red to dark brown rufous | Dark mahogany-red to claret brown | Blackish to dark brown without reddish tones |
| Dorsal hair shaft pattern: proximal | Dull brown to reddish brown to reddish (sometimes a buffy base) | Reddish to reddish brown | Reddish to reddish brown | Dark brown to blackish (sometimes a buffy base) | Blackish or dark brown |
| Dorsal hair shaft pattern: distal | Dull brown to reddish brown to reddish with yellowish to golden bands | Banded reddish/reddish brown and brown/blackish | Banded reddish/reddish brown and brown/blackish | Uniform dark reddish/reddish brown, or banded reddish/reddish brown and dark brown/blackish | Blackish or dark brown |
| Dorsal hair shaft pattern: summary | Yellowish/golden bands on brown to reddish brown to reddish | Brown/blackish bands on reddish/reddish brown | Brown/blackish bands on reddish/reddish brown | Dark reddish/reddish brown bands on brown/blackish | Largely uniform blackish or dark brown |
| Dorsal hair banding | Very distinctly speckled to weakly banded | Mildly to weakly banded, to near uniform | Mildly to weakly banded, to near uniform | Weakly banded to uniform | Uniform or very faint |
| Ventrum (chest, belly) | Usually uniform bright fox/rusty reddish, though can be deeper red, or more brownish | Dull rusty brownish-red, dark tipped, sometimes a pale base, “washed” | Dull rusty brownish-red, dark tipped, sometimes a pale base, “washed” | Dark brown/blackish | Blackish |
| Distinction between ventral and dorsal colors | Clearly differentiated | Slightly differentiated | Slightly differentiated | None or subtle | None |
| Collar: definition | Well-developed and clearly defined | Weakly developed and often tipped with reddish, or very thin | Weakly developed and often tipped with reddish, or very thin | Well-developed and clearly defined along the center chin | sometimes runs |
| Forehead | Blackish (though sometimes very thin) | Blackish (usually into anterior crown) | Blackish (usually into anterior crown) | Blackish | |
| Crown | Bright reddish and strongly contrasting with dorsum, or similar to dorsum | Posterior: deep dark reddish or similar to dorsum | Posterior: deep dark reddish or similar to dorsum | Usually similar to dorsum or slightly redder | |
| Hands | Yellowish | Yellowish | Yellowish | Yellowish | |
| Forearms | Blackish (extent variable) | Blackish (extent variable) | Blackish (extent variable) | Blackish | |
| Feet | Blackish (+ sometimes lower legs) | Blackish (+ sometimes lower legs) | Blackish (+ sometimes lower legs) | Blackish, sometimes with some pale hairs on toes | |
| Legs | Same as ventral color, blends into the dorsal color on the outer upper hindlegs | Clearer reddish than ventral coloration (less brownish / dark tipped), blends into the dorsal color on the outer hindlegs | Clearer reddish than ventral coloration (less brownish / dark tipped), blends into the dorsal color on the outer hindlegs | Blackish to dark brown | |
| Tail | Black mixed with reddish (reddish base to hair shaft, black tip) | Black mixed with reddish (reddish base to hair shaft, black tip) | Black mixed with reddish (reddish base to hair shaft, black tip) | Blackish | |

anterior crown in a few specimens (for example, MNRJ-2464, CTGAM154) (Fig. 16). In addition, the initial key suggests, accurately, that both *torquatus* and *purinus* can be weakly banded, but the subsequent distinguishing features suggests that *purinus* is always strongly banded (“marked agouti”). As discussed, the exact coloration of the bands on the dorsal hairs influences how “marked” the agouti patterns of the back appear such that some *purinus* specimens are much less distinctly banded (Fig. 13; A–D).

In light of the variation seen across both these lineages, in some cases it may be difficult to confidently identify certain specimens without further supporting evidence such as reliable information on collection location or molecular data. An example is the anomalous Manacapuru specimen from the NRM (620501) that shares traits with *torquatus* (*sensu* Hershkovitz 1990) and *purinus* (Fig. 11; A and B). Even considering this phenotypic variation, however, we argue that both the type description and the type specimen for *torquatus* Hoffmannsegg, 1807, are strongly consistent with the characters presented in *purinus* specimens rather than those of *torquatus* (*sensu* Hershkovitz 1990). The well-defined collar, brighter reddish ventral coloration clearly differentiated from the dorsal pelage and not washed with darker tipped hairs or a buffy proximal section, and the evident yellowish bands to the back and flanks on the *torquatus* type (Fig. 2), noted in the original description, are characters more strongly or solely seen in *purinus* specimens. Overall, the *torquatus* holotype appears most similar to the more reddish *purinus* specimens, including a specimen from Lago Aiapuá (FMNH 38885; locality 4 on Fig. 3), the Bordeaux red specimen from Rio Mamoriá (USNM 105539; locality 1 on Fig. 3), and the specimen from Lake Tefé (USNM 518222; locality 5 on Fig. 3). The *torquatus* holotype, however, is possibly more distinctly “agouti” with paler yellowish bands than these specimens. The FMNH specimen also matches some details in the *torquatus* type description closely, which can no longer be clearly distinguished in the degraded *torquatus* holotype specimen, mainly the thin blackish forehead (Fig. 16; panel D). When the *torquatus* holotype is considered alongside all *purinus* and *torquatus* specimens, it fits well within the variation found across *purinus* but would be considered a very strong outlier and more extreme phenotype than even the most distinct of the specimens assigned to *torquatus* by Hershkovitz (e.g., NRM 620501 from Manacapuru). With the evidence available, we consider the *torquatus* holotype as a member of the same lineage currently classified as *purinus*. Although this idea is drawn out in the most detail in the present discussion, it is evident that other taxonomists have shared this view, for example, Hill (1960) suggested that the type locality for *torquatus* (*sensu* Hoffmannsegg 1807) could be Tefé (right/south bank Solimões, within the hypothetical distribution for *purinus*; see locality 5 on Fig. 3), but this received little further attention.

As noted above (section on “Recent changes: Marc van Roosmalen”), Van Roosmalen *et al.* (Fig. 35, 2002)

indicated that collared titis occur east of the Rio Purus to the Rio Madeira (south of the Solimões), which was based on apparent sightings in two locations. Van Roosmalen (2003, 2020) subsequently indicated that, independent of any consideration regarding *purinus*, they were the true *torquatus* of Hoffmannsegg (1807), thus aligning *torquatus* with collared titis to the south of the Solimões around the Rio Purus. As mentioned, apart from Van Roosmalen’s report, there is no confirmation that widow monkeys are found between the rios Purus and Madeira. Furthermore, the illustration for *torquatus* by Stephen Nash in Van Roosmalen *et al.* (2002) is based on photographs of a pet from Tefé (within the distribution of *purinus*) that has a reddish-chestnut dorsal color (Fig. 19). The lighting is poor, however, and there appear to be paler bands on the dorsal hairs and this individual is considered to be a *purinus* with a reddish phenotype. Although Van Roosmalen’s hypotheses can be confusing to follow and, unfortunately, explicit supporting evidence or explanations are rarely presented, it is clear that we are in broad agreement regarding two things: that *torquatus* (*sensu* Hoffmannsegg 1807) is closely aligned with widow monkeys found south of the Solimões, towards the eastern limit of their distribution around the Purus; and that widow monkeys found on the left (north) bank of the Solimões in the Solimões-Japurá-Negro interfluvium (*torquatus sensu* Hershkovitz 1990) are not *torquatus* (*sensu* Hoffmannsegg 1807) but, rather, aligned with *lugens* (as discussed in the following section, “How to classify *torquatus* (*sensu* Hershkovitz 1990)?”).

Notably, we consider the holotype for *purinus* (collected at “Solimões, Rio Purus, Ayapuá”; locality 4 on Fig. 3) to be the most distinct *purinus* specimen from the holotype and type description for *torquatus*, and also from other *torquatus* specimens (*sensu* Hershkovitz 1990). In comparison to the *torquatus* type, the *purinus* type sits at the opposite end of the spectrum of variation described above for *purinus* specimens, and is itself an outlier. Overall, the *purinus* holotype shows the dullest (greyish) brown coloration with a strikingly speckled agouti appearance (Figs. 12 and 13; panel A). The posterior ventral region is deep reddish but with brownish below the collar on the chest (Fig. 17; panel A), not the chestnut dorsal coloration and brighter red ventral coloration described for *torquatus* by Hoffmannsegg (1807). It seems that this is the only *purinus* specimen that was assessed by Thomas (1927a). Thomas previously classified the more reddish incomplete specimen from Tefé (Ega) at the BMNH (1851.7.12.7) as *torquatus* (1914) and did not mention it subsequently when he described *purinus*. Given that Thomas (1927a) considered only the single type specimen, it becomes more evident how he missed the broader association between the *torquatus* type description and *purinus*, aligning the description instead with specimens collected to the north of the Solimões despite the lack of yellowish banding mentioned by Hoffmannsegg (1807) and the weakly defined collars in these specimens. Thomas (1914, 1927a, 1927b) noted a total of twelve *Cheracebus* specimens, although it is possible he also saw additional specimens at the BMNH. He

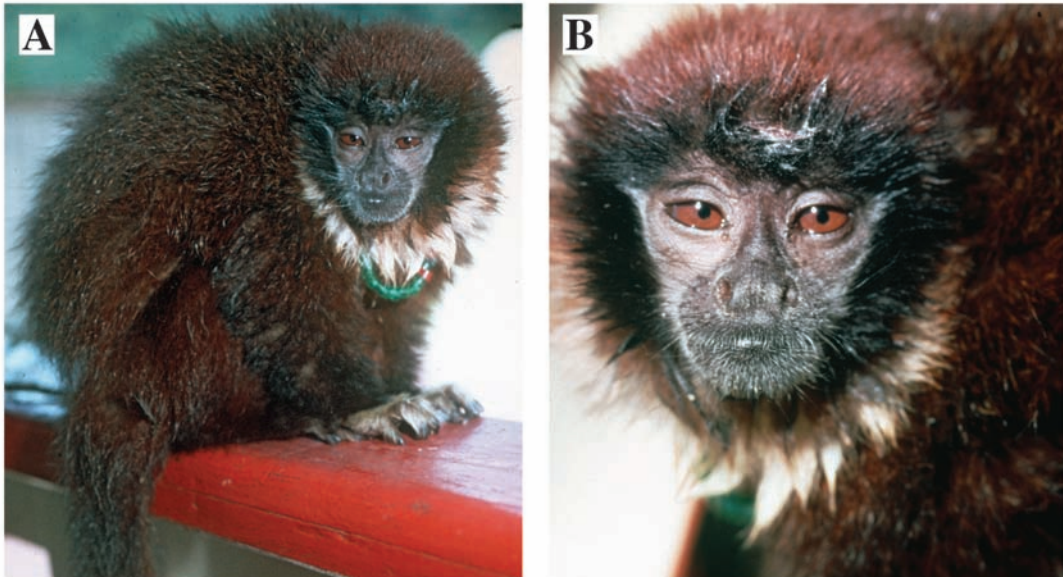


Figure 19. Images of a captive individual/pet from Tefè that Stephen Nash based his illustration of *Cheracebus torquatus* upon for Van Roosmalen *et al.* (2002). Photos by Russell A. Mittermeier.



Figure 20. New illustrations of *Cheracebus torquatus* (formerly *purinus*) by Stephen Nash ©. The image on the left represents the more reddish chestnut specimens including the *torquatus* holotype. The image on the right represents the duller browner specimens.

therefore formally described four taxa and defined six distinct taxa as subspecies of *C. torquatus* based solely on these few specimens (including *ignitus*). Despite the fact that his species hypotheses could not have considered the great phenotypic variation found across these lineages, they were hugely influential for the classifications of subsequent taxonomists.

The two *purinus* from the NRM were also assessed by Lönnberg (1939). In light of the variation found across *Cheracebus* specimens from the same region, he suggested that the difference between these individuals and some Codajás specimens is relatively minor and, although he followed Thomas (1927a), he questioned whether all lineages will hold true when more specimens are assessed. Lönnberg (1939; p.4) noted that the hairs on the back are “ringed” in both *purinus* specimens, but the brown dorsal coloration of one is rather similar to that of one of the Codajás specimen. Lönnberg (1939) evaluated two specimens in hand that were arguably a closer match than the Codajás specimens to even Wagner’s (1855) summary of Hoffmannsegg’s type description for *torquatus*. Despite speculating on the similarity between these *purinus* specimens and some Codajás specimens, he never suggested that they could be *torquatus* (*sensu* Hoffmannsegg, 1807), instead noting the concordance of his hypothesis regarding the identity of *torquatus* with that of Thomas (1927a). Later, Hershkovitz (1990) primarily discussed the work of Lönnberg (1939) and Thomas (1927a) in his classification of *torquatus*, solidifying this view of its identity and affinity with specimens collected on the left bank of the Solimões. Cruz Lima (1945, p.182) also commented on the similarity between some *purinus* specimens in the MNRJ and the description of the Codajás specimens by Lönnberg (1939).

In light of the broad phenotypic variation seen within *Cheracebus* taxa, multiple sources of evidence (phenotypic, molecular and/or reliable locality data) may be required to resolve the identity of some specimens/populations of *Cheracebus*, particularly those that differ from the main broadly accepted phenotype for each lineage. Of the *torquatus* specimens assessed, we consider the anomalous *torquatus* specimen with the collection locality as Manacapuru (NRM 620501; locality 6 on Fig. 3) to be the closest in phenotype to some *purinus* specimens, showing a reddish-brown banded dorsal coloration and a well-defined collar (Fig. 11). We viewed this specimen in photos only and it is possible that some characters are not evident or appeared differently in these images. The main differences to most *purinus* specimens, however, appeared to be the lack of speckled appearance owing to the absence of evident pale bands to the dorsal hairs and a more brownish-red ventral coloration that is less clearly marked from the dorsal pelage. It is also important to note that older collections of Amazonian specimens are often assigned to the nearest named locality and without acknowledgement of the side of the river they were collected on. Manacapuru is a town on the Solimões, just west of Manaus, with much river boat (*recreio*) traffic, and a plausible explanation for this specimen is that it was a pet brought from a

distant locality elsewhere along the Solimões. The collection locality of this NRM specimen as Manacapuru was influential in the classification of it as *torquatus* (*sensu* Hershkovitz 1990), but given both the great phenotypic variation found in *Cheracebus* lineages and the aforementioned doubts with the locality as the true provenance, it is difficult to be certain of its validity.

In the past 30 years in particular, as a result of the seminal work of Hershkovitz (1990), *torquatus* has generally been considered as more akin to *lugens*, *lucifer*, and even *medemi*, than to *purinus*. Unfortunately, the true identity of *torquatus* (*sensu* Hoffmannsegg 1807) has been obscured in its progression in the taxonomic literature over the past 200 years from a red-bellied *purinus*-like form to a duller/darker *lugens*-like form.

We conclude that the *torquatus* holotype and original type description by Hoffmannsegg (1807) fit most closely with specimens collected between the rios Juruá and Purus, the lineage currently classified as *purinus* Thomas, 1927, and not with the widow monkeys on the left (north) bank of the Solimões in the Solimões-Japurá-Negro interfluvium (i.e., *torquatus sensu* Hershkovitz 1990). For this reason, we consider *Callicebus torquatus purinus* Thomas, 1927, to be a junior synonym of *Cheracebus torquatus* Hoffmannsegg, 1807. This necessarily invalidates the type locality restriction of *torquatus* by Hershkovitz (1963, p.56) to “Codajás, north bank of Rio Solimões, Amazonas, Brazil.” The original type locality was the province of Pará, which in 1807 extended through today’s Brazilian states of Pará and Amazonas. We propose to restrict the type locality of *Cheracebus torquatus* to Aiapuá (Ayapuá) left (west) bank of the Rio Purus, Amazonas, Brazil (locality 4 on Fig. 3). This is the well-defined type locality of *purinus* Thomas, 1927, and there are at least three other specimens from this region in other museum collections in addition to the *purinus* type (1926.5.5.21); one reddish-brown specimen in the FMNH (38885) that shows good overall likeness to the *torquatus* type (though less reddish dorsally); and another two at the MNRJ (MN-2464 and MN-2462, the latter was not assessed here as images were not received). The three specimens assessed from this locality provide a good representation of the variation in pelage coloration found across this taxon (e.g., Fig. 12; Panels A, B, and D). New illustrations of this lineage by Stephen Nash are presented in Figure 20; a reddish-chestnut phenotype with a less contrasting crown, similar to the *torquatus* holotype, is summarized in panel A, and a duller/browner phenotype with a brighter, more contrasting red crown is summarized in panel B.

It may seem somewhat unfortunate that a taxonomic name that has as complicated a history as *torquatus* should take precedence over the more clearly defined taxon, *purinus*, but Article 23 (“Principle of Priority”) of the International Code of Zoological Nomenclature (ICZN) states this is a necessity. The complexity of this situation primarily stems from the convoluted history of the name *torquatus* (discussed in detail in the section “*Torquatus*: An identity crisis?”) rather

than any particularly long-standing usage of the name *purinus*, which has only become more clearly established since Hershkovitz's 1990 revision and its elevation to species status (Van Roosmalen *et al.* 2002). Prior to this, *purinus* was considered a junior synonym of a more broadly distributed *torquatus* (which also included *lucifer* and *regulus*) for several decades (Hershkovitz 1963).

In summary, we consider *Cheracebus torquatus* (common name: the collared titi) the valid name for the widow monkey lineage distributed between the rios Juruá and Purus, Amazonas, Brazil, that was previously classified as *purinus* (Fig. 21).

How to Classify *torquatus* (*sensu* Hershkovitz 1990)?

Based on currently available evidence, we suggest that the lineage classified as *lugens* Humboldt, 1811, should also include *torquatus* (*sensu* Hershkovitz 1990), and here we propose to redefine *lugens* to represent all *Cheracebus* found north of the Solimões-Japurá-Caquetá, from the foothills of the Eastern Cordillera of the Andes, east to the left banks of the Rio Branco and lower Rio Negro (see Fig. 21).

Phenotypes found north of the Solimões-Japurá-Caquetá

Our primary justification for this classification is that the variation found across *torquatus* (*sensu* Hershkovitz 1990) could be considered a continuation of, or closely related to, the phenotypes found across *Cheracebus* individuals classified as *lugens*. The dorsal coloration is variable across *lugens* specimens from blackish to dark brownish to dark reddish, either uniform or banded (Fig. 22; A–H). In this section, we characterize the variation in pelage coloration found across specimens found north of the Solimões-Japurá-Caquetá into three general phenotypes (Table 2), but note that many individuals do not fit neatly into these phenotypic categories, with many intermediates. We provide the A and B phenotype definitions primarily to summarize some of this diversity in a manner that aids comprehension of the text.

Phenotype A is typical *lugens*-like with black or dark brown dorsal and ventral pelage without strong reddish tones (Fig. 22; A and B). In these overall dark *lugens* individuals, the hair is largely monochrome blackish or dark brown, or with very faint dark bands, but the dorsum appears largely uniform (Fig. 23; A and B) (Table 2). This is the phenotype most commonly associated with *lugens*. Specimens that are good representations of this phenotype include FMNH 89479, 1928.11.3.2 (NHM), JPB136 (INPA), and JPB81 (MNRJ).

Phenotype B has a dark reddish *lugens*-like appearance with a dark mahogany reddish to claret brown-toned dorsum and a darkish belly (Fig. 22; E–H). The dorsal coloration in this phenotype can be achieved through faint banding between dark reddish or reddish brown and dark brown or blackish on the distal portion of the hairs (with a black or dark brownish proximal portion, sometimes with dark buffyish) (Table 2). Some specimens are uniform dark reddish on the distal portion (tip) of the hair (JPB123, for example, fades from a buffy base to brownish to reddish around the shoulders/nape)

(Fig. 23; E–H). The banding on Phenotype B is subtler than a similar phenotype found in some *lucifer* specimens (*ignitus*-like) that have more striking red bands/flecking. Specimens that are good representations of this phenotype include JPB123 (INPA), JPB160 (INPA), CTGAM733 (INPA), and 1933.10.11.1 (NHM).

Phenotype C is typical *torquatus*-like (*sensu* Hershkovitz 1990) as described in previous sections of this article. The characters found among specimens labeled as *torquatus* (*sensu* Hershkovitz 1990) that are not commonly found elsewhere among *lugens* are the weak/diffuse collar of many individuals versus the well-defined collar of phenotypes A and B, and the more reddish-brown ventral coloration (which extends onto the outer thighs) that is often washed with dark tipped hairs (more clearly differentiated from the dorsal coloration than Phenotype B but less than the lineage formerly known as *purinus*), whereas the ventral color in *lugens* phenotypes A and B varies from blackish to brownish, not more reddish-brown than the dorsal region (Fig. 24; A–F) (Table 2).

New illustrations of *lugens* phenotypes A and B by Stephen Nash, along with the previously mentioned/shown illustration for Phenotype C (see Fig. 10), are presented together in Figure 25.

Although variable, specimens of *lugens* (Phenotype B) from within the Negro-Solimões interfluvium in Brazil, as well as elsewhere north of the Solimões-Japurá-Caquetá, can show a similar dark reddish tone to the dorsal coloration (though typically darker) resulting from a blackish or dark brownish with reddish or reddish-brown pattern to the dorsal hairs, as seen in most specimens of Phenotype C (*torquatus sensu* Hershkovitz 1990). The primary difference in the dorsal pelage is that the proximal portion of the hair in most Phenotype C specimens is similar to the more reddish coloration banded at the tip (Fig. 5), while in Phenotype B *lugens* the proximal portion of the hair is typically similar to the darker coloration (or sometimes darker in the middle with dark buffy at the base) (Fig. 23). In Phenotype C (*torquatus sensu* Hershkovitz 1990), the pattern could be summarized as dark bands on reddish hairs (giving rise to a general dorsal appearance that is often more notably reddish), while in Phenotype B it tends to be reddish bands on brown/blackish hairs (if banded) (Table 2). Both phenotypes can show little to no banding (especially at the shoulder, where it was primarily assessed), instead dorsal hairs can fade from a buffy base to brown to reddish (Phenotype B, for example, JPB123), or a buffy base to reddish to brownish (Phenotype C, for example, FMNH 35076).

Notably, despite labeling two specimens from the BMNH with a collection locality of the Rio Negro as *torquatus*, Hershkovitz (1990) proposed a hypothetical distribution for *torquatus* that was restricted immediately along the left (north) bank of the Solimões, excluding the rest of the Negro-Solimões interfluvium, i.e., the region around the Rio Negro. One of these specimens (1933.10.11.1) is banded reddish and blackish dorsally, but not reddish at the base of the hair, and is brownish ventrally with a thick, well-developed collar. It is

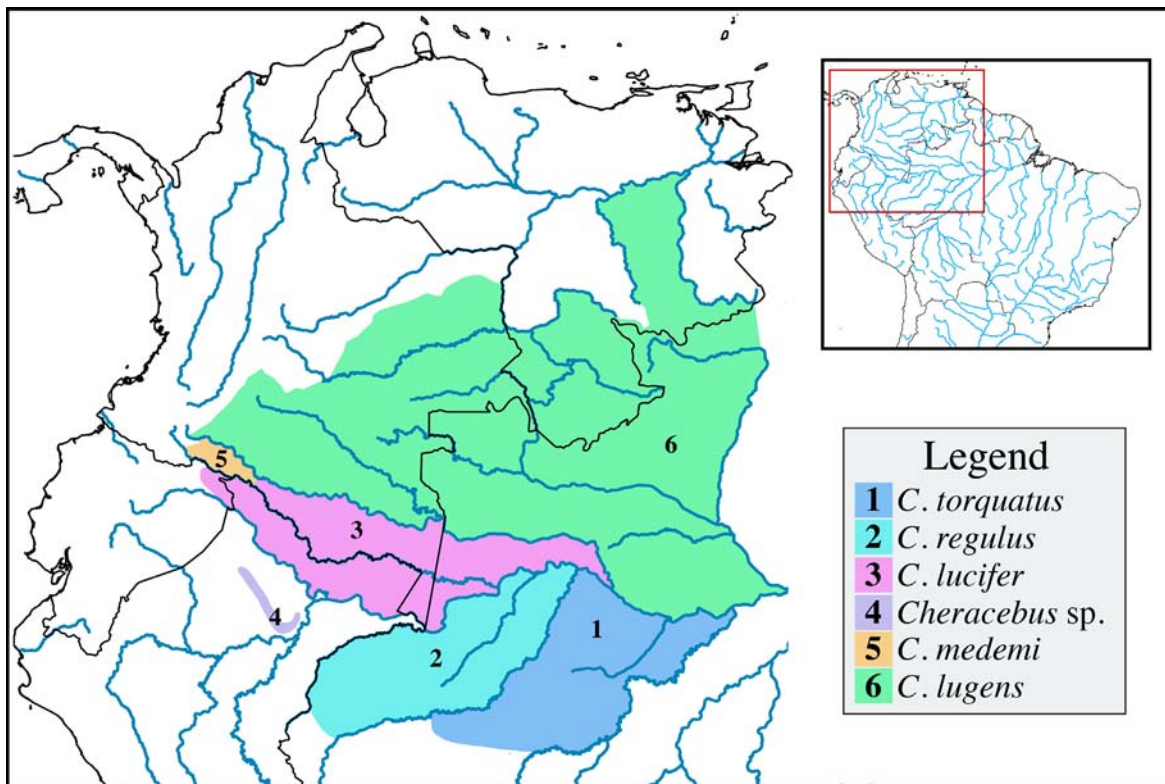


Figure 21. Hypothetical geographic distributions for species of the genus *Cheracebus*. Modified from Byrne *et al.* (2018; Suppl. File 2).



Figure 22. Dorsal view of specimens of *Cheracebus lugens*: A) Guaviare, Colombia, FMNH (89479); B) Right bank Rio Negro, Brazil, MNRJ (JPB81); C) Rio Yatua, Venezuela, BMNH (1951.714); D) Right bank Rio Negro, Brazil, MNRJ (CRB2698); E) Unknown location, BMNH (1855.12.24.44); F) Left bank Rio Negro, Brazil, MNRJ (CRB2667); G) Left bank Rio Negro (Serra do Aracá), Brazil, INPA (JPB123); H) Left bank Rio Japurá, Brazil, INPA (CTGAM753). Photos (panels B, D, F) by João Oliveira at the MNRJ.

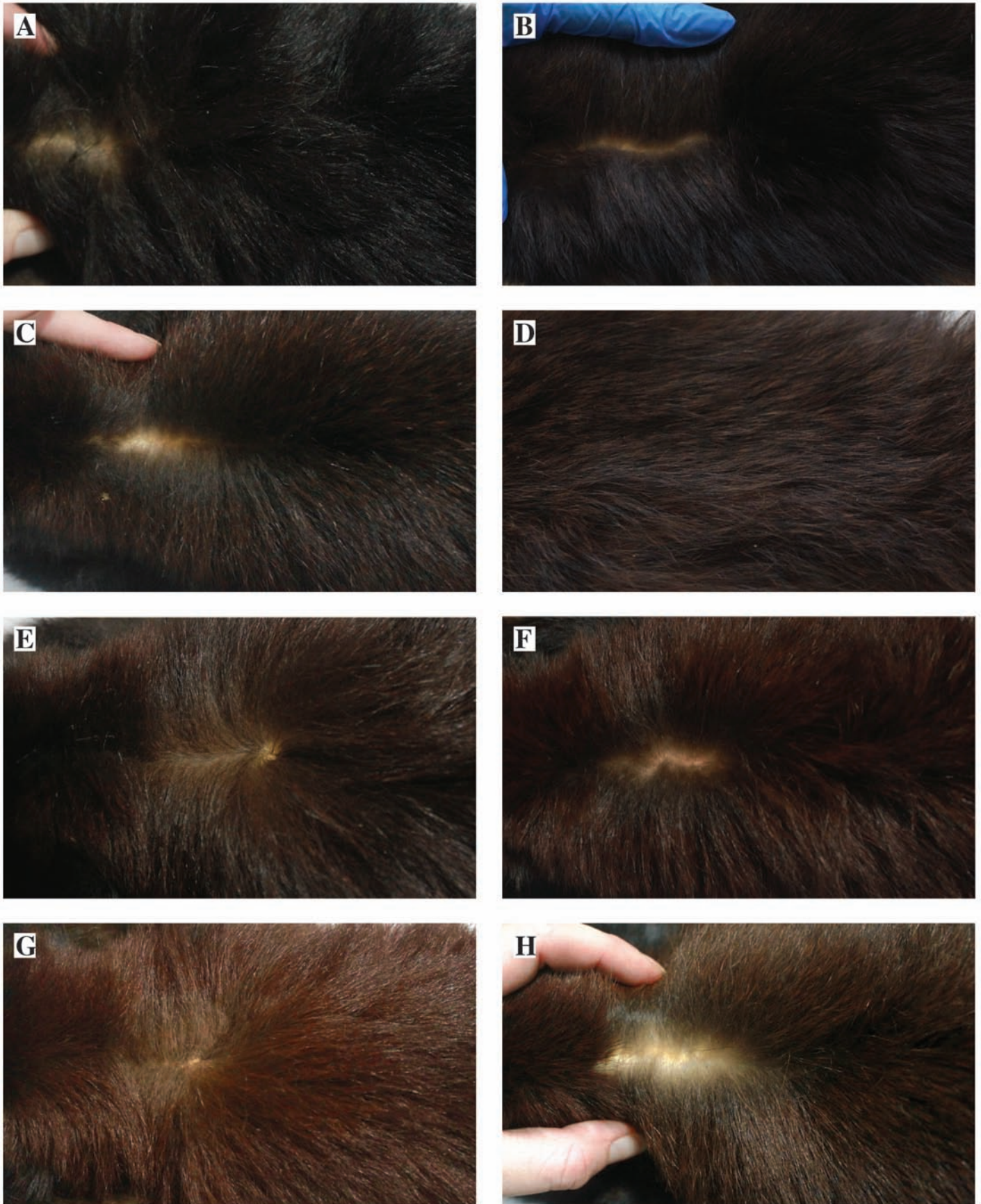


Figure 23. Coloration of the hair shaft at the shoulders/nape of specimens of *Cheracebus lugens*: A) Left bank Rio Negro, INPA (JPB136); B) Guaviare, Colombia, FMNH (89479); C) Left bank Rio Japurá, Brazil, INPA (CTGAM733); D) Guaviare, Colombia, FMNH (88247); E) Left bank Rio Negro (Serra do Aracá), Brazil, INPA (JPB124); F) Left bank Rio Negro, Brazil, INPA (JPB160); G) Left bank Rio Negro (Serra do Aracá), Brazil, INPA (JPB123); H) Left bank Rio Japurá, Brazil, INPA (CTGAM753).

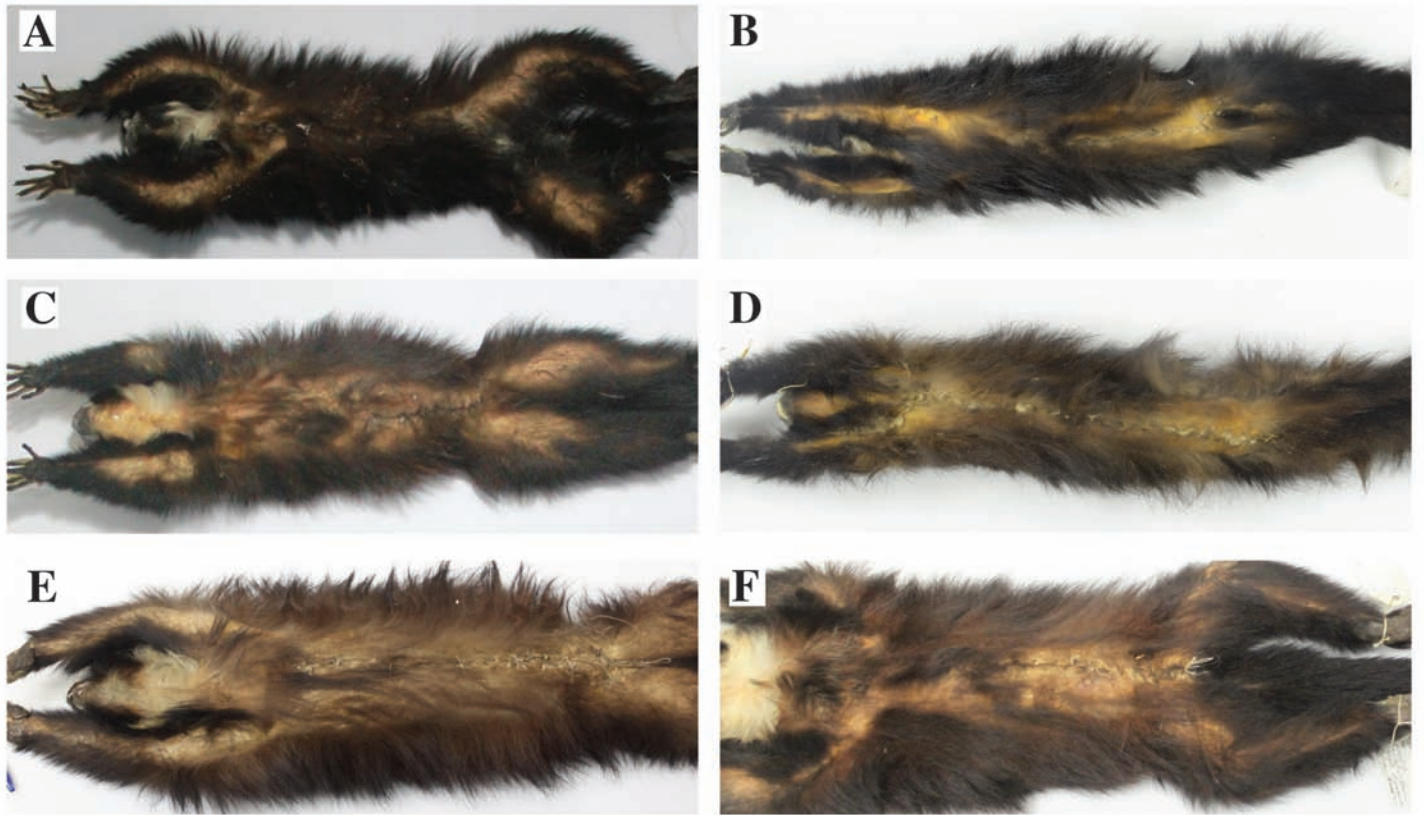


Figure 24. Ventral view of specimens of *Cheracebus lugens*: A) Left bank Rio Negro, INPA (JPB136); B) Right bank Rio Negro, Brazil, MNRJ (JPB81); C) Left bank Rio Japurá, Brazil, INPA (CTGAM753); D) Right bank Rio Negro, Brazil, MNRJ (CRB2698); E) Unknown location, BMNH (1855.12.24.44); F) Rio Yatua, Venezuela, BMNH (1951.714). Photos (panels B, D) by João Oliveira at the MNRJ.



Figure 25. New illustrations of *Cheracebus lugens* by Stephen Nash © including typical blackish *lugens* (Phenotype A; panel A), reddish *lugens* (Phenotype B; panel B), and Phenotype C (i.e., *torquatus sensu* Hershkovitz 1990) (cf. *lugens*; panel C) (also presented in Fig. 10).

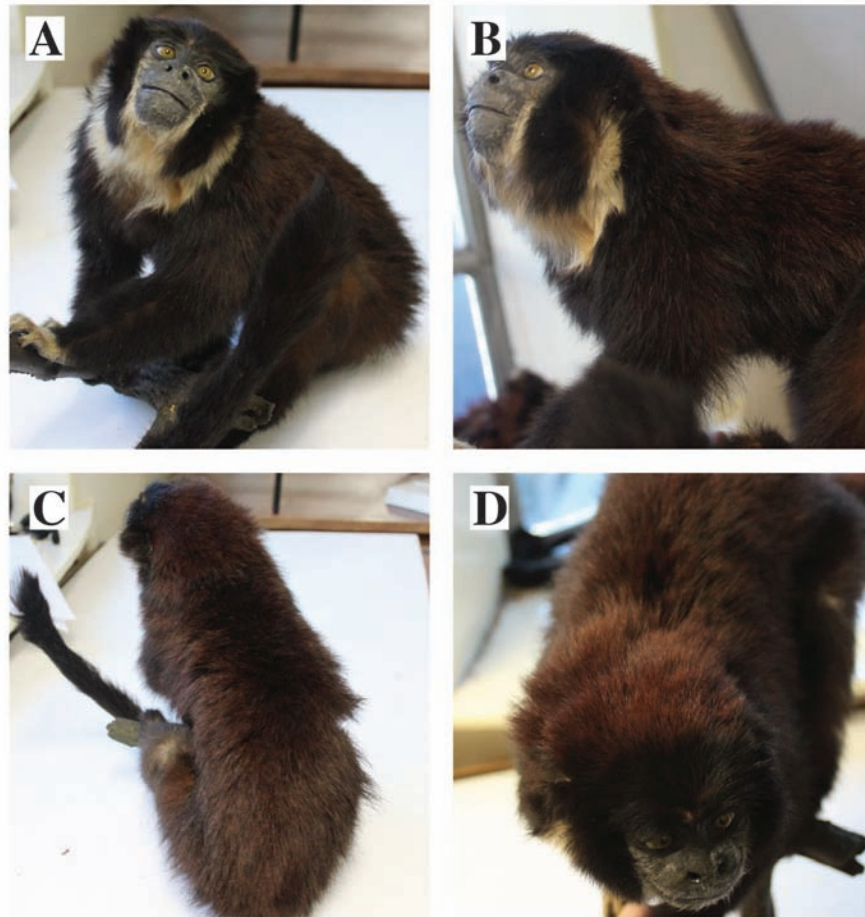


Figure 26. Phenotype B *Cheracebus lugens* specimen mounted at the BMNH (1933.10.11.1) from the Rio Negro: A) frontal; B) side; C) dorsal; D) crown.



Figure 27. Phenotype B *Cheracebus lugens* specimens from Serra do Aracá after collection: A) dorsal view of JPB123; B) dorsal view of JPB124; C) ventral view of JPB123; D) ventral view of JPB124.

considered to be Phenotype B *lugens* and was excluded from our discussion of *torquatus* (*sensu* Hershkovitz 1990) in this study (Fig. 26; A–D). The other BMNH Rio Negro specimen (1842.4.29.15) agrees with Phenotype C (i.e., *torquatus sensu* Hershkovitz 1990); the ventral pelage is dark-tipped reddish-brown, and the proximal portion of the dorsal hair is mahogany red with the distal portion faintly banded between this color and blackish (Figs. 4, 5, and 6; panel A). This specimen has a thin but decently defined collar (Fig. 7; panel A). The collection locality for this specimen suggests that Phenotype C individuals may not be restricted to the region along the left bank of the Solimões.

There are four comparatively recently collected specimens from the right bank of the Rio Negro, Barcelos, Amazonas, in the MNRJ (localities 10 and 11 on Fig. 3). One specimen is mostly blackish with thin subtle brownish banding on the dorsal hair and dark ventral coloration (Phenotype A; JPB81) (Figs. 22 and 24; panel B). Two specimens are dark brownish dorsally without evident banding; however, the base portion of the dorsal hairs appear to be a paler coloration, with some reddish-brown to brownish on the outer thighs (CRB 2696, 2697), each with defined collars. The fourth specimen shows a dorsal region with banding between reddish brown and duller dark brown, reddish-brown on the outer thighs and mixed in the ventral region with patches of darker and buffyish hairs, and a very reduced/diffused collar (but this is possibly partially a result of specimen preparation) (Figs. 22 and 24; panel D). These specimens were only viewed in full-body dorsal and ventral photos and thus detailed examination of the banding pattern on the hairs was not possible; however, the reddish-brown on the outer thighs in three of these specimens, possibly as well as the reduced collar of the fourth specimen, are *torquatus*-like characters (*sensu* Hershkovitz 1990). Despite the variation, these individuals form a clade in the molecular phylogeny (cytb) of Boubli *et al.* (2005) and Casado *et al.* (2007), sister to *lugens* collected on the left bank of the Negro in the MNRJ. One of these right bank Rio Negro specimens (JPB81) was included in the molecular phylogenies of Byrne *et al.* (2016), and RADseq phylogenies of Byrne (2017), and all of the right bank Negro specimens are included in the mitochondrial phylogenies presented here, discussed below in the subsection “Molecular evidence.” Given the above, there is a lack of clarity surrounding the limits to Phenotype C individuals (*torquatus sensu* Hershkovitz 1990) in that they may be intermixed more broadly across the Negro-Solimões interfluvium with other red-toned (dark-bellied) and darker/typical *lugens* (Phenotypes B and A, respectively), as well as intermediate forms.

Van Roosmalen *et al.* (2002) extended the distribution of *torquatus* (*sensu* Hershkovitz 1990) through the Negro-Solimões-Japurá interfluvium in Brazil, west to the rios Vaupés and Apaporis in Colombia, contrasting with the restricted region along the left bank of the Solimões proposed by Hershkovitz (1988, 1990). As indicated by Van Roosmalen (2003), it would seem that this is based on a broad interpretation of

an earlier map provided by Hershkovitz (Fig. 3, 1963), just excluding the supposed ranges of *purinus*, *regulus*, and *lucifer*. Although his maps (Van Roosmalen *et al.* 2002; Van Roosmalen 2003) imply that this hypothetical lineage between the Solimões-Japurá-Apaporis and Negro-Vaupés was *torquatus* (*sensu* Hershkovitz 1990), the website text (Van Roosmalen 2003) suggests that he thought this was an unnamed form closely allied to *lugens*, aligning *torquatus* instead with *Cheracebus* populations around the Rio Purus, as discussed. This was clarified more recently in Van Roosmalen (2020). Regardless of the classification, no description of the diagnostic traits was given for this hypothetical lineage between the rios Solimões-Japurá-Apaporis and Negro-Vaupés, nor any justification for separating it from phenotypically similar individuals found outside this region. Neither dark reddish *lugens* (Phenotype B) nor typical blackish *lugens* (Phenotype A) seem to correspond to these limits—both appear to be found within this region, as well as elsewhere north of the Solimões-Japurá-Caquetá.

Three Phenotype B individuals (CTGAM 733, 734, 753) were collected around the same locality on the left (north) bank of the Japurá in Brazil, near the border with Colombia (locality 12 on Fig. 3), slightly west of the limits to *torquatus* according to Hershkovitz (1990). These specimens show a progression in coloration on the dorsal regions from rich dark reddish (similar to Claret Brown to Chestnut [Ridgway 1912]) with faint banding (appearing more uniform) (Figs. 22 and 23; panel H) to darker brown with a lesser reddish tone and slightly more evident contrast between the reddish and darker bands. The white hairs from the collar in these three specimens, as well as the Phenotype B Rio Negro specimen from the NHM (1933.10.11.1) (Fig. 26), also run along the center of the upper throat connecting with the border of whitish hairs around the lower face.

Two individuals belonging to the same social group (JPB 123, 124) collected at Serra do Aracá (left bank/north of the Rio Negro; locality 21 on Fig. 3) also show dark brownish and reddish coloration to the dorsal hairs, though one (JPB123) is much brighter and more uniformly reddish towards the nape/shoulders (Fig. 27, A–D; see also Fig. 22, panel G; Fig. 23, panels E and G), in addition to an individual (JPB160) collected farther west at São Gabriel da Cachoeira (also left bank Rio Negro; locality 19 on Fig. 3). Thus, it appears that less blackish/brownish and more reddish forms of *lugens* are found across its distribution, or at least in various distinct geographic regions. Furthermore, typical blackish Phenotype A *lugens* individuals are also found between the rios Solimões-Japurá-Apaporis and Negro-Vaupés (for example, the aforementioned JPB81 specimen from the right bank of the Rio Negro). Phenotypic evidence, therefore, suggests that *torquatus* (*sensu* Van Roosmalen *et al.* 2002), i.e., the lineage Van Roosmalen later considered an unnamed form (2020), is not a valid taxon, and this is corroborated by molecular data, discussed below in the section “Molecular Evidence.”

Defler (Fig. 4, 2012) also showed that *lugens* is highly phenotypically variable across Colombia, with dark reddish

brown and more light brown-rufous coloration seen in some individuals. Even reddish-bellied forms appear to be found in various regions, for example, a specimen in the BMNH (1951.714) from the Rio Yatua on the left bank of the Casiquiare, Venezuela (locality 18 on Fig. 3), which has a very dark reddish-black dorsum, and a more brownish red that is tipped/mixed with blackish on the ventral side (Fig. 24; panel F).

Over time, across the taxonomic literature, the image of *torquatus* has been modified from a red-bellied *purinus*-like form with a red chestnut dorsum (its true affinity), to a less distinctly red-bellied form with weak collar and a darker dorsum (i.e., Phenotype C, typical of the left bank Solimões populations; *torquatus sensu* Hershkovitz 1990), to an enigmatic *lugens*-like form with no explicit description (i.e., *torquatus sensu* Van Roosmalen *et al.* 2002). In summary, the lineage referred to as *torquatus* by Hershkovitz (1990), and others, is here considered a geographically distributed phenotype (referred to as Phenotype C) found, along with others, between the rios Negro and Solimões in Brazil that belongs within the widely distributed *lugens* clade, typically (but not consistently) with a reddish proximal coloration to the dorsal hairs, a more reddish-brown ventral coloration with black-tipped hairs (more distinct from the dorsal region than other *lugens*, but less so than *purinus*) and a more diffuse (or thinner) collar than Phenotypes A and B.

Although it is certainly possible that Phenotype C populations (*torquatus sensu* Hershkovitz 1990) may represent a distinct lineage that deserves recognition, more data are required regarding the diversity (both phenotypic and molecular) of populations north of the Solimões-Japurá-Caquetá in order to justify the naming of a new taxon. We consider this to be the most conservative classification; however, it is concordant with the phenotypic and molecular evidence available. Molecular data suggest that multiple distinct lineages may exist in the clade north of the Solimões-Japurá-Caquetá, but available evidence shows little concordance with reddish Phenotype B versus blackish Phenotype A individuals and it is not possible to give hypothetical geographic limits at present without more data from across this region, especially from Colombia. Regardless of the exact classification we assign to the lineage previously known as *torquatus sensu* Hershkovitz 1990), we do not believe that this Phenotype C matches the type specimen and description given for *torquatus* by Hoffmannsegg (1807), as discussed in detail in the previous sections. We suggest that Phenotype C (*torquatus sensu* Hershkovitz 1990) should be identified as *Cheracebus* cf. *lugens* until more data are available to support or refute its proposed affinity to *lugens*.

Molecular evidence

The molecular data generated thus far for *Cheracebus* includes mitochondrial and nuclear loci generated using traditional Sanger sequencing techniques from: *lugens* specimens collected at various locations north of the Rio Negro in Brazil (including the Serra do Aracá specimens noted above; specifically, localities 19, 20, 21 and 22 on Fig. 3);

lugens specimens collected from the right bank of the Rio Negro (localities 10 and 11 on Fig. 3) (primarily JPB81, which forms a clade based on the cytochrome b locus with the other variable individuals collected in this region [Casado *et al.* 2007; Boubli *et al.* 2005]); *lugens* specimens collected to the left bank of the Rio Japurá (locality 12 on Fig. 3), near the border with Colombia (CTGAM 733, 734, 753); *lucifer* specimens collected at the same location on the right bank of the Japurá (locality 32 on Fig. 3); and *torquatus* (i.e., formerly *purinus* Thomas, 1927; referred to as *torquatus* throughout the remainder of this section) specimens collected at the Abufari Biological Reserve on left bank of the Rio Purus (locality 3 on Fig. 3). See a breakdown of the main molecular studies including these specimens in Table S1 of the Supplementary File. Although we have samples for other wild-caught and museum specimens, we have yet to sequence some of these individuals. Some of the same lineages are also represented in the RADseq phylogenies of Byrne (2017), the results of which are discussed alongside the mitochondrial phylogeny results below.

Molecular phylogenies generated using mitochondrial data currently available for these *Cheracebus* lineages, some of which were unpublished but all of which were collected previously for other studies/projects (following the methods described in Byrne *et al.* 2018), were included herein to summarize the phylogenetic relationships across these lineages. Previously unpublished sequences were deposited in GenBank under the accessions MT461028 to MT461058, and MT465103 to MT465114 (Suppl. File, Table S2). See the supplementary file for detailed information on dataset preparation, accession numbers, and tree reconstruction methods. Phylogenetic inference was conducted using maximum-likelihood (ML) and Bayesian methods on a data matrix consisting of the cytochrome *b* (CYTB) locus and partial cytochrome oxidase I (COI) locus (Dataset A), as well as a second alignment that also included the non-coding, highly variable D-Loop region (Dataset B).

Two consistent patterns from across our various molecular phylogenies are noted here. Across all molecular phylogenies generated to date, *Cheracebus lucifer* is sister to *torquatus* (formerly *purinus*), while *lugens* is sister to this clade [(*lucifer*+*torquatus*) vs. *lugens*] (Figs. 28 and 29), suggesting that the Solimões-Japurá-Caquetá may be the major dividing barrier for *Cheracebus* (see also Byrne 2017; Byrne *et al.* 2018). This topology is particularly surprising given the general phenotypic affinity between *lucifer* and *lugens*. Specimens collected at the same location on opposing sides of the Rio Japurá (localities 12 and 32 on Fig. 3) are broadly similar in phenotype, although showing some distinguishing features—the *lucifer* specimens (CTGAM 703, 726, 727), for example, have more striking/contrasting banding on the dorsal hairs (giving a more agouti appearance, similar to *torquatus* [formerly *purinus*]). While it is possible that populations farther east along the Japurá-Solimões than sampled in this study (i.e., around Codajás and Manacapuru) are members of the clade comprised of *lucifer* + *regulus* + *torquatus*

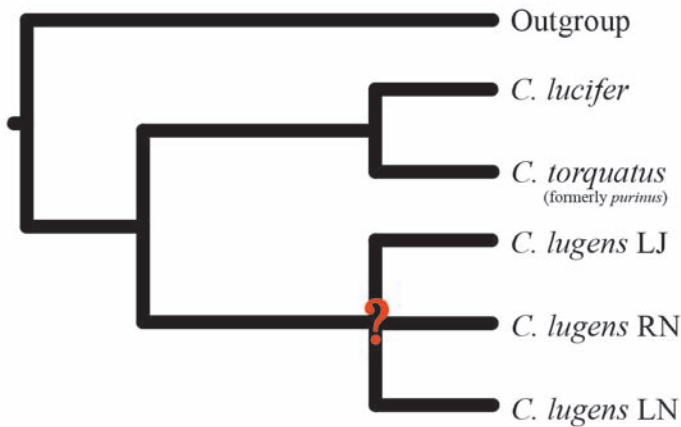


Figure 28. Graphic reconstruction summarizing the relationship among lineages of *Cheracebus* across various phylogenies inferred to date. LJ = Left bank Rio Japurá; RN = Right bank Rio Negro; LN = Left bank Rio Negro.

(formerly *purinus*) or other populations elsewhere that defy this pattern, this scenario is considerably less likely than two monophyletic clades divided by the Solimões-Japurá-Caquetá, as suggested by the molecular data generated to date.

Secondly, molecular evidence suggests that there are multiple distinct lineages within the clade north of the Solimões-Japurá-Caquetá classified here as *lugens*. Three distinct geographically-distributed lineages are consistently recovered in our molecular phylogenies; one with left bank Rio Negro specimens (LN), one with right bank Rio Negro specimens (RN), and a third with left bank Rio Japurá specimens (LJ). The exact relationship among these three lineages is still uncertain (as depicted in Fig. 28); however, importantly, *Cheracebus* individuals collected on the left bank of the Japurá (LJ) and the right bank of the Negro (RN) (i.e., those within the Negro-Solimões-Japurá interfluve in Brazil) never form a well-supported clade to the exclusion of *lugens* individuals collected on the left bank of the Negro (LN).

In the Bayesian mitochondrial phylogenies generated in this study (both datasets), these three *lugens* lineages form an unresolved polytomy (Fig. 28; see full trees in Suppl. File, Figs. S1 to S4). For the ML mitochondrial phylogenies, the left and right bank Negro lineages are sister for Dataset A (Fig 29), while the right bank Negro and left bank Japurá lineages are sister for Dataset B; however, bootstrap support is very low for both arrangements, and thus, the ML mitochondrial phylogenies are also unresolved (Suppl. File, Figs. S1 to S4). In the genome-wide ddRADseq data sets of Byrne (2017; chapter 4, section 4.4.2, Fig. 4.3 and Table 4.11, as well as supplementary figures), the left and right bank Rio Negro lineages (LN and RN) form a clade to the exclusion of the left bank Rio Japurá (LJ) specimen, which was significantly supported as the earliest diverging lineage within this *lugens* clade across all seven phylogenies/datasets. Divergence time estimates (Byrne 2017; chapter 4, section 4.4.2, Fig. 4.4) suggest that these three lineages diverged within a few hundred thousand years of each other around 700,000 to 900,000 years ago.

Taken together, we consider the relationships between these three *lugens* lineages as unresolved, as depicted in Figure 28. Available evidence shows little concordance with reddish versus blackish *lugens* phenotypes; the three left bank Rio Japurá specimens (CTGAM 733, 734, 753) are all dark reddish (Phenotype B); the right bank Rio Negro specimens from the MNRJ are either blackish (Phenotype A; JPB81) or mixed/intermediates, as outlined in the previous section; and the left bank Rio Negro specimens include Phenotype A and B individuals. We do not yet have molecular data for any Phenotype C individuals. In addition, it is not possible to give hypothetical geographic limits for any lineages at present because of the sparse sampling. Broader sampling from across the distribution of *lugens* (especially Colombia and Venezuela) is required to increase our understanding of the genetic diversity and diversification patterns within this clade broadly distributed north of the Solimões-Japurá-Caquetá. A comprehensive evaluation of the variation in pelage coloration across *Cheracebus lugens* populations is also much needed, besides field studies to assess the distribution of the various phenotypes. We are currently analyzing whole genome sequence data for a selection of these individuals, in addition to some samples from *C. regulus* and *C. lucifer* from distinct localities, which may shed further light on the relationship among these lineages.

Alternative putative origins for torquatus (sensu Hershkovitz 1990)

One notable alternative explanation is that Phenotype C populations (*torquatus sensu* Hershkovitz 1990) have a hybrid origin; overall the specimens share some characters with *lugens* and specimens previously classified as *purinus*. Given the locality of these specimens, there are at least two plausible scenarios that may have led to admixture: (1) dispersal by *torquatus* (formerly *purinus*) individuals across this region of the Rio Solimões (perhaps passively owing to the dynamic nature of this river, or a larger shift in river course), and subsequent hybridization with *lugens*; (2) dispersal by *lugens* from the northwest of the Negro-Solimões interfluve and admixture with a red-bellied lineage (*torquatus*, formerly *purinus*, or a distinct taxon), that had either been isolated in a subsection around Codajás and Manacapuru on the left (north) bank of the Solimões or was once more widespread and gradually displaced by *lugens*. Each of these scenarios should be testable with genomic data and thus, future molecular studies will shed further light on the affinity of Phenotype C individuals (*torquatus sensu* Hershkovitz 1990).

One character seen in many specimens is the weakly developed or diffused collar that could be described as “confused” with the surrounding ventral hairs. Some specimens are almost entirely lacking evidence of a collar, while some individuals have more defined thin collars (Fig. 7). Theoretically, collar loss or diffusion of collar hairs with the ventral coloration could be a result of admixture between two distinct lineages in which the genetic/molecular mechanisms

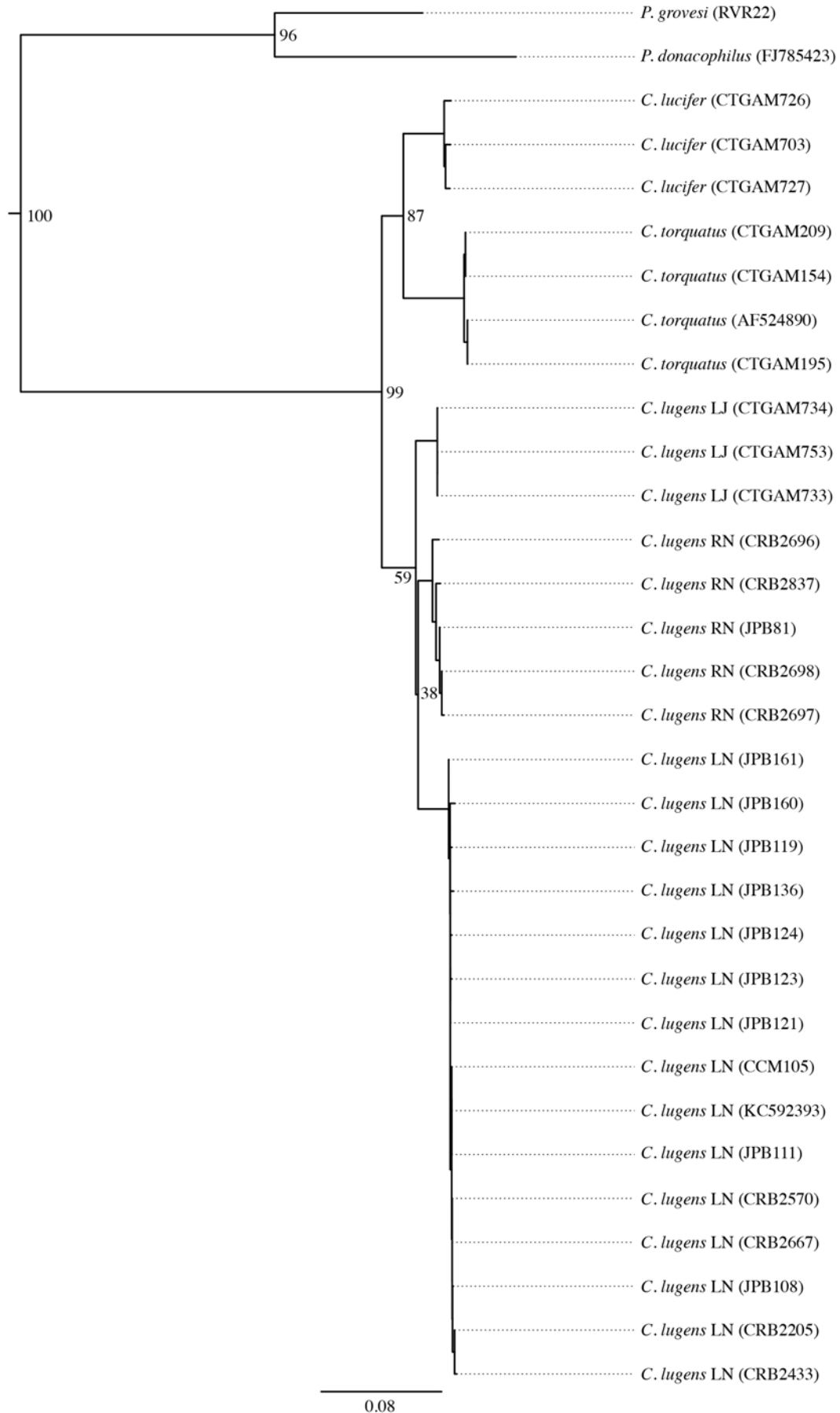


Figure 29. Maximum likelihood phylogeny for *Cheracebus* inferred with mitochondrial dataset A. See Suppl. File Figs. S1 to S4 for the full phylogenies with pitheciine outgroups.

underlying the expression of the collar are incompatible, i.e., the combination of two distinct genotypes does not produce the clearly-defined collared phenotypes of the parent lineages, even if the collars appear similar in these lineages. Notably, the other known case of diffused or weak collars is among some specimens of *medemi* from the western extreme of the Solimões-Japurá-Caquetá division in Colombia; populations of *Cheracebus* to the north of the Río Caquetá are classified as *lugens*, while *lucifer* (*sensu* Hershkovitz 1990) is found farther east along the same interfluvium as *medemi* (Caquetá–Putumayo interfluvium). The diffusion or complete loss of the collar seen in specimens of *medemi* and Phenotype C *lugens* (*torquatus sensu* Hershkovitz 1990) could be a result of admixture between individuals belonging to the putative clades north and south of the Solimões-Japurá-Caquetá (i.e., *lugens* with *lucifer* or *torquatus/purinus*, respectively), and underlying molecular differences impacting the development of the collar.

Detwiler (2019) found phenotypic and molecular evidence for hybridization between two sympatric guenons, *Cercopithecus mitis doggetti* and *C. ascanius schmidtii*, the former taxon has a distinct light grey speckled brow band while the latter has a heart-shaped white nasal spot. The most “*mitis*-like” of the hybrids showed some “*ascanius*-like” white coloration to the nose, whereas even this individual had a much more weakly defined and reduced brow band than that of non-admixed *Cercopithecus mitis* (Fig. 4 in Detwiler 2019). Although the hybridizing lineages show different features (i.e., brow band versus nasal spot), it sheds light on the effects of admixture on such contrasting chromatic fields; facial patterns in guenons may have evolved under selection to be more distinctive between sympatric species, aiding the identification of conspecifics (Allen *et al.* 2014).

Other Comments and Observations

The reddish-bellied form, ignitus Thomas, 1927

As mentioned in the section “Oldfield Thomas (1914, 1927),” the final widow monkey taxon described by Thomas was *ignitus* (1927b). This description was based on a reddish-bellied specimen (1927.8.11.4) from the “Rio Tonantins,” Brazil, which Thomas proposed was closely allied to the form he considered to be *torquatus* (i.e., here considered to be Phenotype C *lugens*). On the specimen’s label, the collection locality is somewhat confusingly specified as “Rio Tonantins, Tabatinga”—the Rio Tonantins presumably refers to the river at the Amazonian city now called Tonantins (locality 34 on Fig. 3), between the rios Putumayo and Japurá, which does not fall in the Tabatinga municipality that is to the west between the rios Içá–Putumayo and Napo. The form *ignitus* is currently considered to be a junior synonym of *lucifer* (e.g., Hershkovitz 1990).

The ventral color of the *ignitus* type is a dull reddish-brown (Fig. 30; panel A), not tipped with blackish as in most Phenotype C *lugens* (*torquatus sensu* Hershkovitz 1990) specimens, and duller/more brownish than is typical in *torquatus* (formerly *purinus*). The ventral color does not extend onto the outer thighs as it tends to in these other reddish-bellied forms. The specimen has a very thin, nearly pure-white collar. The paler color on the hands (a dull golden yellow) covers only the fingers, while the rest of the forehands are black. The forehead is black and the crown is deep reddish. As noted by Thomas (1927b), the dorsal color of the *ignitus* type is distinct from Phenotype C *lugens* (*torquatus sensu* Hershkovitz 1990) in the rich reddish chestnut tone (Fig. 31; panel A), which is achieved through dark brown to blackish and bright red banding on the distal half of the hair shaft (brown proximal/base portion) (Fig. 32; panel A). The proximal third of the tail is similar to the dorsal tone, with the rest of the tail blackish. Thomas (1927b) described the dorsal color as “deep rich rufous without any superficial darkening of the hairs,” and suggested that the reddish proximal tail and the “more brilliantly rufous general color” distinguished it from Phenotype C *lugens* (*torquatus sensu* Hershkovitz 1990) (p.287). The red-on-brown/black banding pattern is somewhat similar to that seen in the reddish Phenotype B *lugens*; however, the red bands at the tip are richer and brighter and the distinct agouti banding pattern appears more striking (Fig. 32). The specimen also differs from the reddish chestnut specimens of *torquatus* (formerly *purinus*) in the dark bands and the lack of paler bands/flecking.

Although Thomas (1927b) apparently classified another specimen (1927.8.11.7) from the same locality (“Rio Tonantins, Tabatinga”) as *lucifer*, the BMNH catalogue and Hershkovitz (1990) label this specimen along with another from Tonantins (1927.3.6.7) as *ignitus* paratypes. These two specimens are very similar to each other and, overall, they are similar to the *ignitus* holotype though less reddish in most pelage characters (more brownish/eumelanized). The ventral color is dark brownish (Fig. 30; panel B). The dorsal color is a duller reddish-brown with dark brown and lighter reddish to reddish-brown bands at the tip of the hair shaft and brown at the base (Figs. 31 and 32; panel B). The reddish color banded at the tip is less bright (brilliant) than in the *ignitus* type. They have a defined white collar of medium width that runs up the center of the throat, golden yellow hands (with a small amount of black intermixed), a thick black forehead and a deep reddish posterior crown. There are two similar specimens also at the NRM (630127, 640219) from the Rio Içá (i.e., Portuguese name for the Río Putumayo) in Brazil, one of which has a dull reddish-brown ventral color (630127) like the *ignitus* holotype (Figs. 30 and 31; panels C and D), as well as three further specimens with a similar dorsal pattern recently collected on the right bank of the Rio Japurá (CTGAM 703, 726, 727; locality 32 on Fig. 3) (Fig. 32; panels



Figure 30. Ventral view of specimens of *Cheracebus ignitus/lucifer*: A) Holotype, Rio Tonantins, BMNH (1927.8.11.4); B) Paratype, Rio Tonantins, BMNH (1927.8.11.7); C) Rio Içá, NRM (640219); D) Rio Içá, NRM (630127). Photos (panels C, D) by Daniela Kalthoff at the NRM.

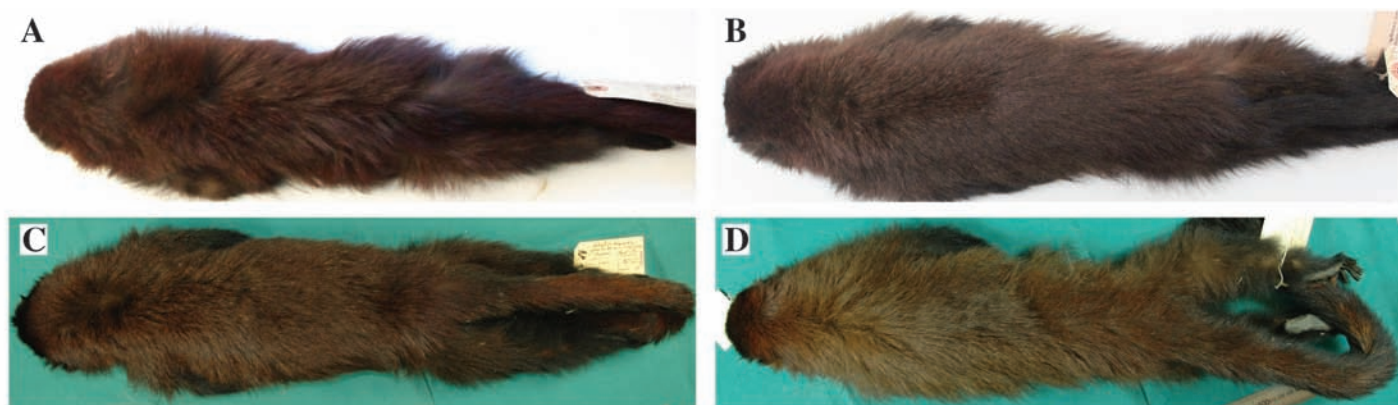


Figure 31. Dorsal view of specimens of *Cheracebus ignitus/lucifer*: A) Holotype, Rio Tonantins, BMNH (1927.8.11.4); B) Paratype, Rio Tonantins, BMNH (1927.8.11.7); C) Rio Içá, NRM (640219); D) Rio Içá, NRM (630127). Photos (panels C, D) by Daniela Kalthoff at the NRM.

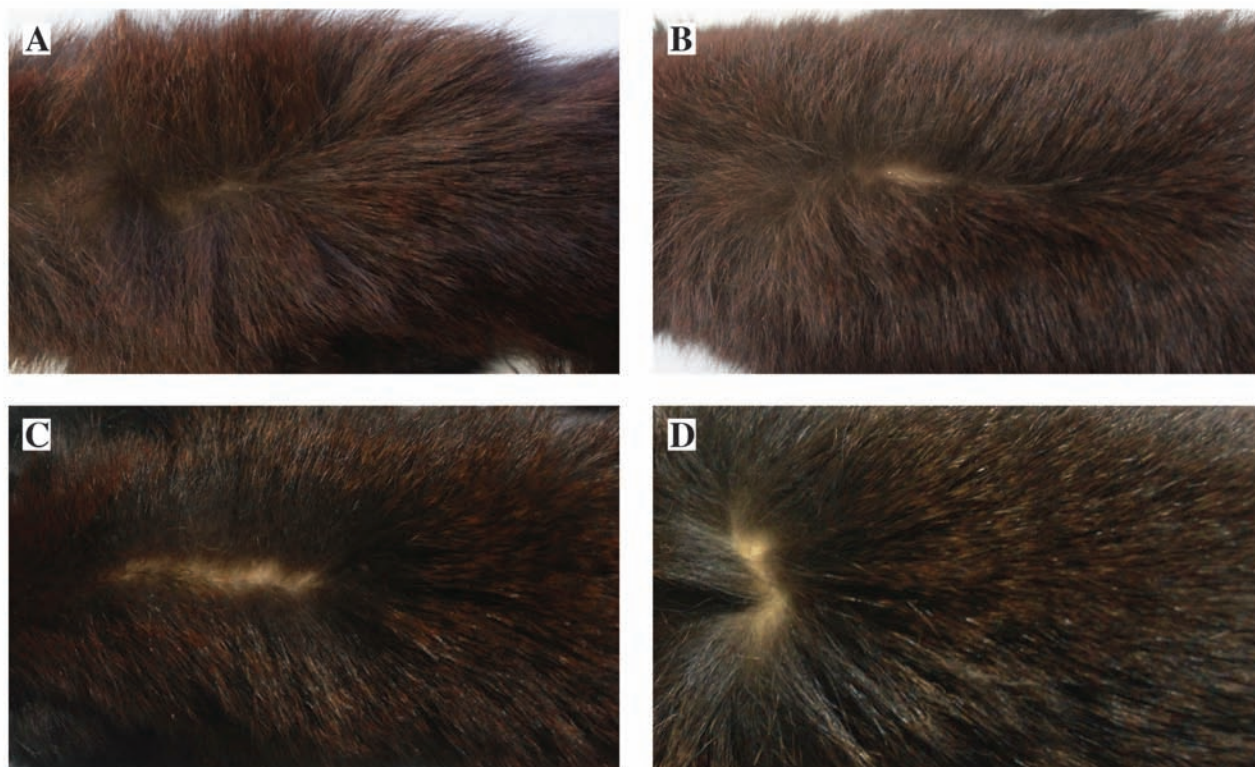


Figure 32. Coloration of the hair shaft at the shoulders of specimens of *Cheracebus ignitus/lucifer*: A) Holotype, Rio Tonantins, BMNH (1927.8.11.4); B) Paratype, Rio Tonantins, BMNH (1927.8.11.7); C) Right bank Rio Japurá, INPA (CTGAM726); D) Right bank Rio Japurá, INPA (CTGAM727).

C and D). Indeed, *ignitus* may be a valid taxon and the proper name for *Cheracebus* populations found in the interfluvium delineated by the rios Japurá-Caquetá and Içá-Putumayo (at least the eastern section). Most specimens in museum collections are typically darker bellied than the *ignitus* holotype specimen, however. They are currently classified as *lucifer*.

The extensive phenotypic variation in pelage coloration across *Cheracebus* species, as documented throughout this article, often appears to be driven by the degree of pheomelanin to eumelanin in the hair shaft. The more reddish ventral coloration in the *ignitus* type in comparison to most other specimens from this region can be explained by more pheomelanin in the ventral hairs. The brighter, more striking red bands on the distal portion of the dorsal hair of the holotype may, however, also be an age-related trait. Notably, the *ignitus* type specimen is an immature (juvenile) male and similar striking bright (brilliant) reddish bands on the tips of the dorsal hairs can be observed in skins from several other juveniles including another *ignitus*-like specimen (CTGAM726) that has a stronger reddish banding pattern in comparison to an adult (CTGAM727) collected at the same locality (Fig. 32; panels C and D, respectively). The *medemi* specimen with the brightest, most distinct red bands to the tip of the dorsal hair shaft is a juvenile (FMNH 70697), and similarly, a juvenile *lugens* (1899.9.11.1) has a bright reddish tip to dorsal hairs which are otherwise uniformly dark brown to blackish (Fig. 33; panels A and B, respectively). Age-based color changes have not been recorded in the scientific literature for widow monkeys to date, though they are well-documented for many catarrhine primates (e.g., see some examples in Table 1, Alley 1980), as well as howler monkeys (e.g., Thorington Jr. *et al.* 1984). This trend warrants further investigation as the confirmation of subtle age-based color changes in collared titis may be helpful in disentangling some of the variation seen across specimens of the same species.

Distinction between medemi and lucifer

In this article, we focused on issues related to the identity of *torquatus*, which necessitated a detailed discussion of both *purinus* and *lugens*, but not strictly of *lucifer*, *regulus*, and *medemi* (the Colombian black-handed titi). We note, however, that the validity of *medemi* Hershkovitz, 1963, is highly uncertain, at least as it is currently defined. It is restricted to the western extreme of the Caquetá and Putumayo interfluvium in Colombia (Fig. 21). The primary distinguishing feature proposed to validate and distinguish *medemi* from other *Cheracebus* are its blackish hands (Hershkovitz 1963, 1990; Groves 2001; Van Roosmalen *et al.* 2002). Hershkovitz (1990; p.80), who described *medemi*, states that *medemi* is distinguished from “*lucifer*, *regulus*, and *lugens* by upper surface of hands uniformly or dominantly blackish.” Three recently collected specimens of *lucifer* from the same locality on the right bank of the Rio Japurá in Brazil (farther east in the same interfluvium as *medemi* is found; see locality 32 on Fig. 3) indicate that blackish hands are not a geographically restricted phenotype—one of these specimens (CTGAM 703)

has blackish hands with some yellow hairs mixed on the fingers, another has yellowish mixed with black (CTGAM 727), while the third has yellowish hands (CTGAM 726) which are considered typical of *lucifer* (hence its common name “the yellow-handed titi monkey”) (Fig. 34). In addition, as discussed, the *ignitus* type specimen has yellow hairs only on its fingers, with the remainder of the forehands blackish. Furthermore, one *medemi* specimen at the FMNH (70700) has partially yellowish fingers, and entirely yellow-handed individuals are thought to co-occur with black-handed individuals even in the western extreme of this interfluvium within the supposed distribution of *medemi*. As such, the co-occurrence of yellow- and black-handed forms (as well as intermediates) seemingly throughout the Caquetá-Japurá and Putumayo interfluvium casts serious doubt on the validity of *medemi* as a distinct black-handed form restricted to the western extreme. In general, we consider hand coloration as a variable trait across widow monkeys and we are generally cautious of its use as a diagnostic character.

Like *torquatus* (formerly *purinus*) and *lugens*, *Cheracebus lucifer* is also highly phenotypically variable and its current hypothetical distribution across two major interfluves (Japurá-Caquetá to Putumayo, and Putumayo to Napo) is somewhat unusual. This is particularly notable given the most probable route of dispersal between these interfluves may be towards the western extreme across the upper Río Putumayo (or around the headwaters), which would be through the distribution of *medemi*. We plan to further investigate these peculiarities in order to adequately address the issues and uncertainty surrounding the current classification of *lucifer*, *ignitus*, and *medemi* in a future revision of the genus.

Torquatus: An Identity Crisis?

For over 70 years, from the late 1920s to 2000s, all widow monkeys were classified as subspecies of *C. torquatus*, and for much of that time, Thomas’s forms (*purinus*, *lucifer*, and *regulus*) were recognized as synonyms of the subspecies *torquatus*. Together, these forms were assigned the moniker “*torquatus* species group” by Hershkovitz (1988, 1990), and the monophyly of this group was corroborated by the morphometric analyses of Kobayashi (1995). This species group name was used to distinguish the widow monkeys or collared titis from other callicebines, and Byrne *et al.* (2016) eventually placed them into their own genus, *Cheracebus*. Thus, for nearly a century, the word *torquatus*, whether referring to a species group, a species, and even to an extent a subspecies, has been used in the taxonomic literature to refer to all or most *Cheracebus* taxa. The word *torquatus* has been recharacterized into obscurity, and has essentially become nearly synonymous with the terms “widow monkeys” or “collared titis” across much of primatology and the broader scientific community.

While often a taxonomic name has been used primarily in scientific literature because it previously represented a group of lineages that were only more recently divided into multiple



Figure 33. Dorsal view showing bright red tips to the hair shaft on juvenile specimens: A) *Cheracebus medemi* juvenile from Rio Mecaya at the FMNH (70697); B) *Cheracebus lugens* juvenile from Rio Orinoco at the BMNH (1899.9.11.1).



Figure 34. Variation in hand coloration of specimens of *Cheracebus ignitus/lucifer* from the right bank of the Rio Japurá at INPA. From left to right: CTGAM703, CTGAM727, CTGAM726.

taxa, the case with *torquatus* appears more complex. Apart from *medemi*, which was described in 1963, all currently recognized forms of widow monkeys were described by 1927, although as of then Thomas (1927a) treated them as subspecies of *C. torquatus*. It wasn't until after Hershkovitz's first appraisal in 1963 that titis began to be studied more broadly in the scientific community. At this point, *purinus*, *lucifer*, and *regulus* were treated as synonyms of the subspecies *torquatus* and some of the pioneering works on titis were based on this arrangement—Warren Kinzey's early studies on pitheciid behavioral ecology, for example (Kinzey 1982). Following Hershkovitz (1963), Kinzey referred to the titi at his study site, the Estación Biológica Callicebus (EBC) to the south of the Río Nanay in northeastern Peru, as *C. torquatus torquatus* (for example, Kinzey 1977; Kinzey *et al.* 1977; Kinzey and Gentry 1979; Kinzey and Wright 1982; Kinzey and Robinson 1983; Easley and Kinzey 1986; also Starin 1978; Lawler *et al.* 2006). The identity of this lineage is still unknown and it is possibly a new taxon (labeled as *Cheracebus* cf. *lucifer* in Fig. 21), differing from the neighboring taxa (*lucifer* and *regulus*) most notably in the tie-like collar that does not extend to the ears (Aquino *et al.* 2008). Two specimens from this region are in the Field Museum collection (FMNH 86978, 86979; locality 27 on Fig. 3) and were subsequently classified by Hershkovitz (1990) as *lucifer*. Kinzey's works were among the earliest comprehensive studies of the ecology and behavior of Neotropical primates in their natural habitats, and are still central to our understanding of the little-studied widow monkeys today.

Despite the subsequent resurrection of *purinus*, *lucifer*, and *regulus* as subspecies, most studies on *Cheracebus* taxa identified them just to species-level based on Hershkovitz (1990), and thus, widow monkeys were nearly ubiquitously referred to as *C. torquatus* across the scientific literature in the following years. Several key articles on the ecology of *Cheracebus* identified them to species-level based on Hershkovitz (1990). Defler (1994) and Peres (1997) referred to the widow monkey populations observed in their field studies across Colombia and around the Río Juruá, respectively, solely as *C. torquatus*. Based on the hypothetical distributions for *Cheracebus* taxa, Defler's (1994) field studies possibly included observations of *lugens*, *lucifer*, and *medemi*, while those of Peres (1997) possibly included *torquatus* (which, at this time, was classified as *purinus*) and *regulus*—notably, every lineage apart from *torquatus* as recognized at the time by Hershkovitz (1990) (i.e., left bank Río Solimões populations). Other important studies include Benirschke and Bogart (1976) and Barros *et al.* (2000) on the karyotype of widow titis referred to as *torquatus* (specimen origin unknown in both, different karyotypes $2n = 20$ and $2n = 22$).

Thus, by the 2000s, *torquatus* refers to a subspecies, a polytypic species, and a species group, and the name *C. torquatus* has been used across much of the literature underlying what we know of *Cheracebus* taxa. It has been the primary name employed across non-taxonomic literature on widow monkeys and collared titis, however, there are few

known recent examples of it being used to directly identify *torquatus* (*sensu* Hershkovitz 1990) (for example, based on a WebOfScience search on 08/May/2018; titi+torquatus, Callicebus+torquatus, or Cheracebus+torquatus), except studies dealing with taxonomy or classification and one brief mention in Casado *et al.* (2007). Bonvicino *et al.* (2003) mention *lugens* and *purinus* but refer to *regulus* as *torquatus*. Across scientific literature, the general synonymous use of the name *torquatus* for all widow titi taxa, or for varying taxa in different studies without explanation, has been detrimental to understanding the diversity of *Cheracebus* taxa and the true identity of *torquatus* (*sensu* Hoffmannsegg 1807).

We hope that the detailed, explicit and chronological account of the taxonomic history of *torquatus* (*sensu* Hoffmannsegg 1807) provided here has helped to clarify the often confounding information found across the taxonomic literature on this group, and provides a baseline for future research into the diversity of these enigmatic, under-studied primates.

Conclusion

We, therefore, currently consider the genus *Cheracebus* to comprise five described species, as follows; *torquatus* (formerly *purinus*) between the rios Purus and Juruá in Brazil; *regulus* between the rios Juruá and Javari in Brazil; *medemi* between the upper Río Caquetá and Río Putumayo in Colombia; *lucifer* between the rios Napo, Solimões and Caquetá-Japurá (excluding the distribution of *medemi*) in Brazil, Colombia, Peru and Ecuador; and *lugens* broadly distributed north of the rios Caquetá-Japurá-Solimões in Brazil, Colombia and Venezuela (Figs. 21 and 35). Given the lack of research on the diversity and taxonomy of widow monkeys, the extensive phenotypic diversity, the aforementioned issues with the classification of *lucifer/ignitus/medemi*, and the recovery of diverse lineages in the molecular phylogenies generated to date, further changes to the taxonomy of *Cheracebus* are likely, including the description of unnamed taxa that deserve recognition, for example, the distinct *Cheracebus* populations south of the Río Napo between the rios Nanay and Tigre in Peru (Heymann *et al.* 2002; Aquino *et al.* 2008).

Acknowledgments

We sincerely thank all of the staff at the museums that made this work possible either through receiving HB in person or by providing images of specimens in their collections, in particular; Lauren Smith and Bruce Patterson at the FMNH; Roberto Portela Miguez and Paula Jenkins at the BMNH; Maria Nazareth Silva at INPA; Christiane Funk and Frieder Mayer at the MNB; Daniela Kalthoff at the NRM; João Oliveira at the MNRJ; Jacques Cuisin at the MNHN; and Kristen Quarles, Kate Sherwood and Darrin Lunde at USNM. We thank Felipe Ennes Silva, Laura K. Marsh, Ivan Batista da Silva and Houseboat Amazon/Global Conservation Institute for images from the field of the specimen from the Río

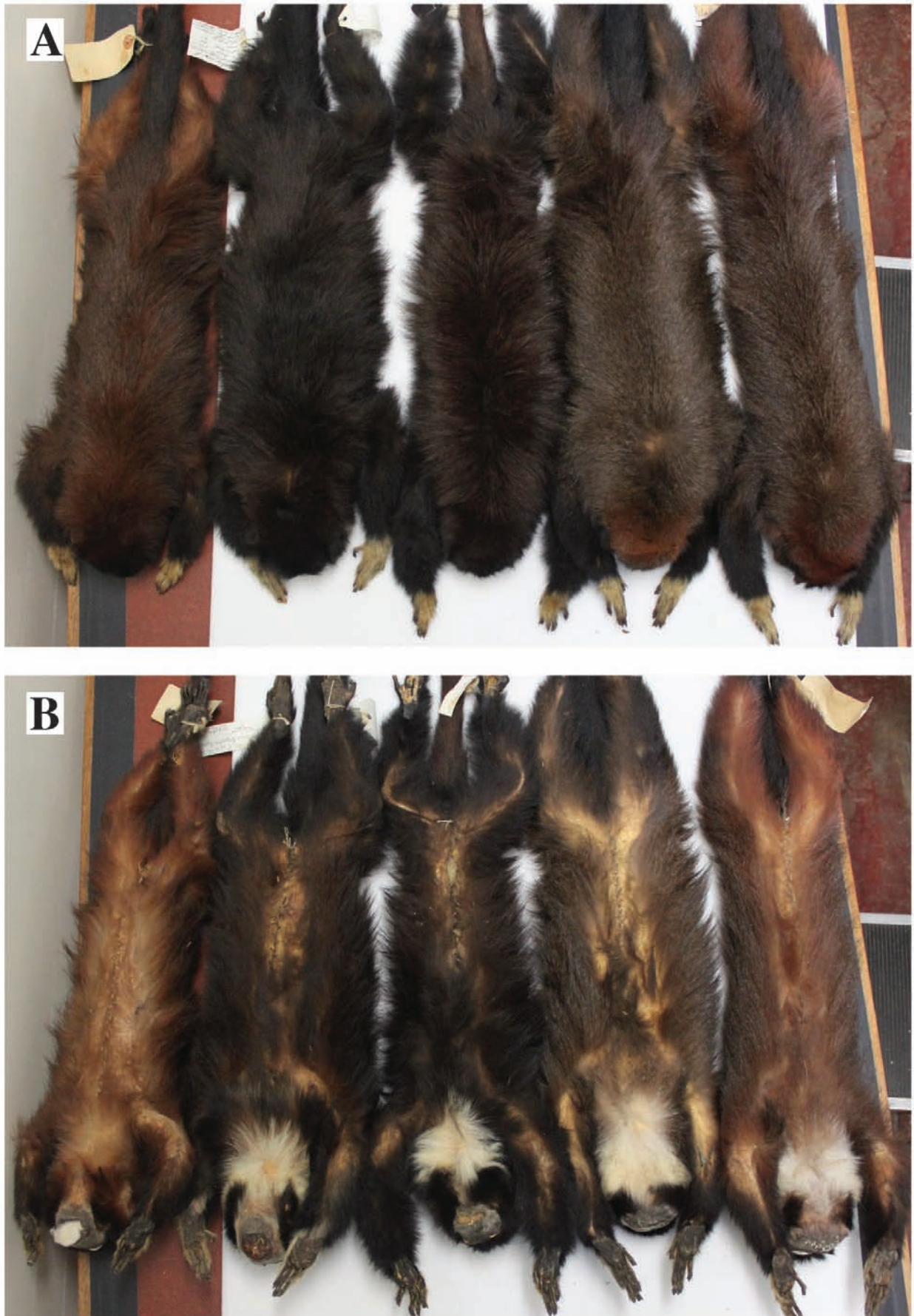


Figure 35. Dorsal (A) and ventral (B) view of *Cheracebus* specimens housed at the BMNH. From left to right: cf. *lugens* (phenotype C, i.e., *torquatus sensu* Hershkovitz 1990; 1925.12.11.8), *lugens* (1951.714), *lucifer* (holotype; 1914.3.1.2), *regulus* (holotype; 1927.3.6.8), *torquatus* (formerly *purinus* [*purinus* holotype specimen], 1926.5.5.21).

Tarauacá, and Michelle Mercês for photographing a specimen at the AMNH. We thank John Patrick Quinn and Anne Schulz for their assistance with the translation of German texts. We thank, most sincerely, the excellent insights, comments and suggestions of two reviewers. They were very much appreciated and a great help.

Online Resources

This published work has been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix <<http://www.zoobank.org/>>. The LSID for this publication is: urn:lsid:zoobank.org:pub:41620505-935B-4E43-9FF4-CD7776E2EF06. We have also deposited the published version of this article and supplementary file on the open access repository Zenodo.

Supplementary Material

An explanation of the molecular dataset and phylogenetic analyses in the Supplementary File; Table S1 - Detailed information on all museum specimens assessed for this study, including taxon assignments and collection locality; Table S2 - List of the Genbank accession numbers for all sequences; Figure S1 - Phylogenetic trees inferred from the mitochondrial Dataset A based on Bayesian methods; Figure S2 - Phylogenetic trees inferred from the mitochondrial Dataset B based on Bayesian methods; Figure S3 - Phylogenetic trees inferred from the mitochondrial Dataset A based on maximum likelihood methods; and Figure S4 - Phylogenetic trees inferred from the mitochondrial Dataset B based on maximum likelihood methods. Available at <http://www.primates-g.org/storage/pdf/PC34_Suppl_Mat_Byrne_et_al_C_torquatus_2020.pdf>.

Literature Cited

- Allen, W. L., M. Stevens and J. P. Higham. 2014. Character displacement of Cercopithecini primate visual signals. *Nature Commun.* 5(1): 1–10.
- Alley, T. R. 1980. Infantile coloration as an elicitor of caretaking behaviour in Old World primates. *Primates* 21(3): 416–429.
- Aquino, R., W. Terrones, F. Cornejo and E. W. Heymann. 2008. Geographic distribution and possible taxonomic distinction of *Callicebus torquatus* populations (Pitheciidae: Primates) in Peruvian Amazonia. *Am. J. Primatol.* 70(12): 1181–1186.
- Barros, R. M., J. C. Pieczarka, M. D. C. O. Brigido, J. A. P. Muniz, L. R. Rodrigues and C. Y. Nagamachi. 2000. A new karyotype in *Callicebus torquatus* (Cebidae, Primates). *Hereditas* 133(1): 55–58.
- Benirschke, K. and M. H. Bogart. 1976. Chromosomes of the tan-handed titi (*Callicebus torquatus* Hoffmannsegg, 1807). *Folia Primatol.* 25: 25–34
- Bonvicino, C. R., V. Penna-Firme, F. F. do Nascimento, B. Lemos, R. Stanyon and H. N. Seuánez. 2003. The lowest diploid number (2n = 16) yet found in any primate: *Callicebus lugens* (Humboldt, 1811). *Folia Primatol.* 74(3): 141–149.
- Boubli, J. P., M. V. Amado and I. Farias. 2005. Platyrrhines of the upper Rio Negro, Amazonas, Brazil: *Callicebus lugens*. In: *Abstracts, III Congresso Brasileiro de Mastozoologia*. Poster presentation. Abstract 232. SESC Praia Formosa, Aracruz, ES. 12–16 October, 2005.
- Byrne, H. 2017. Evolutionary History and Taxonomy of the Titi Monkeys. PhD thesis, University of Salford, Manchester, UK.
- Byrne, H., A. B. Rylands, J. Carneiro, J. W. Lynch-Alfaro, F. Bertuol, M. N. F. da Silva, M. Messias, C. P. Groves, R. A. Mittermeier, I. Farias, I., T. Hrbek, H. Schneider, I. Sampaio and J. P. Boubli. 2016. Phylogenetic relationships of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy based on molecular evidence. *Front. Zool.* 13: 10. DOI 10.1186/s12983-016-0142-4.
- Byrne, H., J. W. Lynch Alfaro, I. Sampaio, I. Farias, H. Schneider, T. Hrbek and J. P. Boubli. 2018. Titi monkey biogeography: parallel Pleistocene spread by *Plecturocebus* and *Cheracebus* into a post-Pebas western Amazon. *Zool. Scripta* 47: 499–517.
- Cabrera, A. 1957. Catalogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 4(1): 1–307.
- Casado, F., C. R. Bonvicino and H. N. Seuánez. 2007. Phylogeographic analyses of *Callicebus lugens* (Platyrrhini, Primates). *J. Hered.* 98(1): 88–92.
- Cruz Lima, E. da. 1945. *Mammals of Amazônia, Vol. I. General Introduction and Primates*. Contribuições do Museu Paraense Emílio Goeldi de História Natural e Etnografia, Belém do Pará.
- Defler, T. R. 1994. *Callicebus torquatus* is not a white-sand specialist. *Am. J. Primatol.* 33: 149–154.
- Defler T. R. 2012. Studying primates in eastern Colombia: thirty-five years of a primatological life. *Rev. Acad. Colomb. Cienc.* 36(140): 421–434.
- Detwiler, K. M. 2019. Mitochondrial DNA analyses of *Cercopithecus* monkeys reveal a localized hybrid origin for *C. mitis doggetti* in Gombe National Park, Tanzania. *Int. J. Primatol.* 40: 28–52.
- Easley, S. P. and W. G. Kinzey. 1986. Territorial shift in the yellow-handed titi monkey (*Callicebus torquatus*). *Am. J. Primatol.* 11(4): 307–318.
- Elliot, D. G. 1913. *A Review of Primates*. Monograph Series. American Museum of Natural History, New York.
- Groves, C. P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.

- Groves, C. P. 2005. Order Primates. In: *Mammal Species of the World: A Taxonomic and Geographic Reference, 3rd Edition, Volume 1*, D. E. Wilson and D. M. Reeder (eds.), p.111–184. Johns Hopkins University Press, Baltimore, MD.
- Haugaasen, T. and C. A. Peres. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. *Am. J. Primatol.* 67(2): 243–258.
- Hershkovitz, P. 1963. A systematic and zoogeographic account of the monkeys of the genus *Callicebus* (Cebidae) of the Amazonas and Orinoco River basins. *Mammalia* 27(1): 1–80.
- Hershkovitz, P. 1988. Origin, speciation, and distribution of South American titi monkeys, genus *Callicebus* (Family Cebidae, Platyrrhini). *Proc. Acad. Nat. Sci. Philadelphia* 140(1): 240–272.
- Hershkovitz, P. 1990. Titis, New World monkeys of the genus *Callicebus* (Cebidae, Platyrrhini): a preliminary taxonomic review. *Fieldiana, Zoology*, n.s. (55): 1–109.
- Heymann, E. W., F. Encarnación and P. Soini. 2002. On the diagnostic characters and geographic distribution of the “yellow-handed” titi monkeys, *Callicebus lucifer*, in Peru. *Neotrop. Primates* 10: 124–126.
- Hill, W. C. O. 1960. *Primates. Comparative Anatomy and Taxonomy IV. Cebidae Part A*. Edinburgh University Press, Edinburgh.
- Hoffmannsegg, G. von. 1807. Beschreibung Vier affenartiger Thiere aus Brasilian. *Magazin Gesellschaft Naturforschungen Freunde, Berlin* 1: 83–104.
- Humboldt, A. von. 1811. Sur les singes qui habitent les Rives de l’Orénoque du Cassiquiare et du Rio Negro. La Viudita. In: *Recueil d’observations de zoologie et d’anatomie comparée faites dans l’Ocean Atlantique, dans l’interior du nouveau continent et dans la Mer du Sud pendant les années 1799, 1800, 1801, 1802 et 1803, Premier Volume*, A. von Humboldt and A. Bonpland (eds.), p.319–321. F. Schoell, Paris.
- Humboldt, A. von. 1852. *Personal Narrative of Travels to the Equinoctial Regions of America during the years 1799–1804*. Henry Bohn, London.
- Kinzey, W. G. 1977. Positional behavior and ecology in *Callicebus torquatus*. *Yearb. Phys. Anthropol.* 20: 468–480.
- Kinzey, W. G. 1982. Distribution of primates and forest refuges. In: *Biological Diversification in the Tropics*, G. T. Prance (ed.), pp.455–482. Columbia University Press, New York.
- Kinzey, W. G. and A. H. Gentry. 1979. Habitat utilization in two species of *Callicebus*. In: *Primate Ecology: Problem-Oriented Field Studies*, R. W. Sussman (ed.), p.89–100. John Wiley and Sons, New York.
- Kinzey, W. G. and J. G. Robinson. 1983. Intergroup loud calls, range size, and spacing in *Callicebus torquatus*. *Am. J. Phys. Anthropol.* 60(4): 539–544.
- Kinzey, W. G. and P. C. Wright. 1982. Grooming behavior in the titi monkey (*Callicebus torquatus*). *Am. J. Primatol.* 3: 267–275.
- Kinzey, W. G., A. L. Rosenberger, P. S. Heisler, D. L. Prowse and J. S. Trilling. 1977. A preliminary field investigation of the yellow handed titi monkey, *Callicebus torquatus*, in northern Peru. *Primates* 18(1): 159–181.
- Kobayashi, S. 1995. A phylogenetic study of titi monkeys, genus *Callicebus*, based on cranial measurements: I. Phyletic groups of *Callicebus*. *Primates* 36(1): 101–120.
- Lawler, R. R., S. M. Ford, P. C. Wright and S. P. Easley. 2006. The locomotor behavior of *Callicebus brunneus* and *Callicebus torquatus*. *Folia Primatol.* 77(3): 228–239.
- Lönnberg, E. 1939. Notes on some members of the genus *Callicebus*. *Ark. f. Zool., Stockholm* 31A(13): 1–18, pl. 1.
- Olson, J. S. 1991. *Historical Dictionary of European Imperialism*. Greenwood Press, New York.
- Peres, C. A. 1997. Primate community structure at twenty western Amazonian flooded and unflooded forests. *J. Trop. Ecol.* 13(3): 381–405.
- Ridgway, R. 1912. *Color Standards and Color Nomenclature*. The author, Washington, DC.
- Röhe, F. 2012. Monitoring the Impacts of the Reopening of the BR-319 Highway on Local Mammal Community Structure and Abundances in the Madeira-Purus Interfluvium, Amazonas, Brazil: Baseline Study. Report. Wildlife Conservation Society, Manaus, Amazonas.
- Schlegel, H. 1876. *Muséum d’Histoire Naturelle des Pays-Bas. Revue méthodique et critique des collections déposées dans cet établissement. Tome 7. Monographie 40: Simiae*. E. J. Brill, Leiden.
- Starin, E. D. 1978. Food transfer by wild titi monkeys (*Callicebus torquatus torquatus*). *Folia Primatol.* 30(2): 145–151.
- Thomas, O. 1903. Notes on South American monkeys, bats, carnivores, and rodents, with descriptions of new species. *Ann. Mag. Nat. Hist.*, series 7, 12: 455–464.
- Thomas, O. 1914. On various South-American mammals. *Ann. Mag. Nat. Hist.*, series 8, 13: 345–363.
- Thomas, O. 1927a. On the titi monkeys of the *Callicebus torquatus* group. *Ann. Mag. Nat. Hist.*, series 9, 19: 509–511.
- Thomas, O. 1927b. On further monkeys of the *Callicebus torquatus* group. *Ann. Mag. Nat. Hist.*, series 9, 20: 287.
- Thorington Jr, R. W., J. C. Ruiz and J. F. Eisenberg. 1984. A study of a black howling monkey (*Alouatta caraya*) population in northern Argentina. *Am. J. Primatol.* 6(4): 357–366.
- Van Roosmalen, M. G. M. 2003. New species from Amazonia. Website: <<http://amazonnewspecies.com/callicebus.htm>>, 16 August 2003, updated 20 September 2003. Accessed 26 September 2003. URL no longer active.
- Van Roosmalen, M. G. M. 2020. *Man’s Territorial Primate Factor: Evolutionary Roots of Tribalism and Human Societies*. LAP Lambert Academic Publishing, Mauritius.

- Van Roosmalen, M. G. M., T. van Roosmalen and R. A. Mittermeier. 2002. A taxonomic review of the titi monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. *Neotrop. Primates* 10(suppl.): 1–52.
- Wagner, J. A. 1855. *Schreber's Die Säugethiere*. Suppl. Vol. 5. Weigel, Leipzig.

Authors' addresses

Hazel Byrne, Department of Anthropology, University of Utah, UT 84112, USA; **Anthony B. Rylands**, Global Wildlife Conservation, P.O. Box 129, Austin, TX, USA; **Stephen D. Nash**, Department of Anatomical Sciences, Health Sciences Center, State University of New York, Stony Brook, NY 11794-8081, USA; and **Jean Philippe Boubli**, School of Science, Engineering and the Environment, University of Salford, Manchester, UK. *Corresponding author*: Hazel Byrne, e-mail: <byrne.hazell@gmail.com>.

Received for publication: 3 June 2020

Revised: 21 July 2020