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Original paper

A new species of titi monkey, genus *Cheracebus* Byrne et al., 2016 (Primates: Pitheciidae), from Peruvian Amazonia

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Abstract. The subfamily Callicebinae is composed of 35 recognized living species that are grouped into the genera, *Callicebus*, *Plecturocebus*, and *Cheracebus*. In this study we assess the taxonomic status of the population of *Cheracebus* from the Nanay-Tigre interfluvium in Peruvian Amazonia, based on morphological (cranial and pelage) and molecular (mitochondrial DNA) evidence. Following the integrated assessment of the evidence, we conclude that specimens from the Nanay-Tigre interfluvium comprise a distinct lineage at the species level. It is easily distinguished from the other species of the genus, including *C. lucifer* to which the new species was considered to belong so far, by, among other characters, overall Reddish-brown pelage; crown intense reddish brown; Cream-colored collar, like a bow tie, with a band that does not extend laterally. The description of a new species of *Cheracebus* is not unexpected since other new species of titi monkeys have been described in recent years and there are several candidate species awaiting validation of their distinction. As such, we anticipate that in the next few years several taxonomic changes will be proposed in order to reveal a classification that mirrors the real species diversity of the subfamily Callicebinae.

Key words: Aquino's titi monkey, Peru, Platyrrhini, taxonomy.

The taxonomy of the titi monkeys (Pitheciidae, Callicebinae) has been considerably revised in the last two decades with the description of ten new species (e.g., van Roosmalen et al. 2002; Wallace et al. 2006; Defler et al. 2010; Gualda-Barros et al. 2012; Dalponte et al. 2014; Vermeer and Tello-Alvarado 2015; Boubli et al. 2019; Gusmão et al. 2019), the reinstatement of *Callicebus toppini* Thomas, 1914, by Vermeer and Tello-Alvarado (2015), the reevaluation of the taxonomic status of some species (e.g., Byrne et al. 2020), and the first broad molecular-based phylogenetic study that included 15 of the 30 species recognized by then (Byrne et al. 2016). The phylogenetic and divergence time analyses of Byrne et al. (2016) resulted in the recommendation placing the titi monkeys into three genera, of which two were new, as follows: (1) *Cheracebus* Byrne et al. 2016 for the collared titi monkeys from the Amazon and Orinoco basins (the *torquatus* group of Hershkovitz 1990); (2) *Plecturocebus* Byrne et al. 2016, for the remaining species of the Amazon basin and the Chaco (the *modestus*, *donacophilus* and *moloch* groups, excepting *C. personatus*, of Hershkovitz 1990); and (3) *Callicebus* Thomas 1903, for the titis of the Atlantic forest and Caatinga of Brazil (the *personatus* group). This division has been largely

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accepted (e.g., Carneiro et al. 2018; Souza-Alves et al. 2019; Mammal Diversity Database 2022), although some authors have argued the use of subgenera rather than genera (e.g., Gutiérrez and Marinho-Filho 2017; Teta 2018).

Recent studies of Peruvian callicebines have focused mostly on aspects of ecology and conservation (e.g., Lawrence 2007; Nadjafzadeh and Heymann 2008; Bóveda-Penalba et al. 2009; DeLuycker 2012; Shanee et al. 2013; DeLuycker 2014; Kulp and Heymann 2015; van Kuijk et al. 2015; Huashuayo-Llamocca and Heymann 2017; Dolotovskaya et al. 2019; Dolotovskaya and Heymann 2020; Aquino et al. 2021), while fewer studies have addressed taxonomic issues (Heymann et al. 2002; Vermeer 2009; Vermeer and Tello-Alvarado 2015). Despite recent advances, information gaps still exist, including aspects regarding the number and identity of the species of titi monkeys present in large areas of Peru.

Studies of the primates from the Nanay-Tigre interfluvium, in northwestern Peruvian Amazonia, have been conducted since the decade of 1970. First, in a series of studies Kinzey (1976, 1977, 1979, 1981) focused on the behavior and ecology of titi monkeys (referred as *C. torquatus*) from nearby the village of Mishana, on the right (south) bank of the Rio Nanay. Despite these studies, Hershkovitz (1990) wrongly established the north bank of the Nanay as the southern limit of *C. t. lucifer* (see also the map in Hershkovitz 1988). Then, Heymann et al. (2002), by noting some phenotypical particularities, were the first authors suggesting that the titi monkeys from south of the Rio Nanay, considered to be *C. lucifer*, may represent a different species. As from 2004, Rolando Aquino initiated a series of surveys to assess the mammal communities south of the Nanay (e.g., Aquino et al. 2007, 2012; Rengifo and Aquino 2012; Rengifo et al. 2013; Aquino et al. 2014; Aquino et al. 2015b; Charpentier et al. 2015, Aquino et al. 2021). From those surveys, Aquino et al. (2008) reported phenotypic differences between the southern Nanay population and the one from north of the Rio Napo/Rio Amazonas (referring both populations to *C. torquatus* and not *C. lucifer*), suggesting that both populations might represent distinct species. Given these antecedents, in this study we examine the morphology, pelage color and patterns, and variation of mtDNA sequences of the cytochrome-b gene of the Nanay-Tigre collared titi monkeys. We frame our interpretations and conclusions in the General Lineage Species Concept of de Queiroz (1998, 2007). We conclude that the Nanay-Tigre interfluvium population represents an undescribed species of titi monkey for which no name is available; as such, we described it as a new species herein.

Materials and methods

Morphological analysis

A total of 40 specimens of *Cheracebus* were examined (see details in Appendix 1). These specimens are housed at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú (MUSM); Field Museum of Natural History, Chicago, USA (FMNH); American Museum of Natural History, New York, USA (AMNH); British Museum (Natural History), London, United kingdom (NHMUK); Mammal Collection of Instituto Alexander von Humboldt, Cartagena, Colombia (IAvH-M); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); and Museu Nacional do Rio de Janeiro, Brazil (MNRJ). All specimens were examined in person, except for those housed at NHMUK and Humboldt IAvH-M that were assessed only by photos.

We assessed external traits, including coloration of the venter, dorsum, head, limbs, and tail. Likewise, cranial traits, in particular in the frontal, interorbital, occipital, and palatal regions, were visually examined following the nomenclature of Hershkovitz (1990). In addition, 17 cranial and dental measurements of adult specimens, using a digital caliper (to the nearest 0.01 mm), following the definitions of Gualda-Barros et al. (2012): greatest length of skull (GLS), condylobasal length (CBL), greatest breadth of braincase (GBB), zygomatic breadth (ZB), orbital breadth (OB), postorbital breadth (POB), palatal length (PL), breadth of foramen magnum (FOM), bullar length (BL), rostral breadth across the upper canines (RC), maxillary toothrow length (MTR), mandible length (MBL), infradental-gnatio distance (IDG), coronoid process height (CPH), lower postcanine toothrow (LTR), breadth across lower molars (M1B), and breadth across lower canines (LCB). A ratio diagram (Musser et al. 1998) was constructed to show proportional relationships between samples. For each measurement listed above, the absolute value was log-converted (base 10). An arbitrary value near the midpoint of the observed range among samples was chosen as the standard. For each dimension, the difference between the log value of the standard and each of the other samples was calculated and plotted; measurements larger than the standard are thus represented by positive values, while those smaller by negative values.

Genetic and phylogenetic analyses

The first 801 base pairs of the mitochondrial cytochrome-b gene (hereafter *cyt-b*) were used as evidence for the genetic comparison and phylogenetic analyses. We gathered sequences from four specimens, two (MUSM 46904 and MUSM 46905) from the Nanay-Tigre interfluvium and two (MUSM 46903 and MUSM 46902) of *C. lucifer*. These sequences were obtained from muscle tissue following the protocol outlined in Hurtado and D'Elía (2019). The Wizard® SV Genomic DNA Purification System Kit (Promega Corp.) was used, following the indications of the manufacturer, to purify total genomic DNA. Primers MVZ05 and MVZ16 were used to amplify the first 801 of the *cyt-b* gene. Amplifications were performed in 50 μL reactions with Platinum® Taq Polymerase (InvitrogenTM). Amplification conditions were as follows: an initial denaturation phase at 94°C for 3 min; 35 cycles at 94°C for 45 s, 45°C for 30 s, and extension at 72°C for 90 s, followed by a final extension at 72°C during 10 min. The external sequencing service Macrogen, Inc. (Korea) was used to sequence the amplified products. CodonCode (CodonCode, Dedham, MA, USA) was used to edit the new sequences and to check for the existence of internal stop codons and reading frame shifts. Sequences newly acquired here were deposited in GenBank (MH638353-MH638356). We integrated the newly generated sequences to a matrix with other 31 *cyt-b* sequences of four (*C. lucifer*, *C. lugens*, *C. regulus*, and *C. torquatus*) of the five currently recognized species of *Cheracebus* obtained from Genbank; our sampling lacks representative of *C. medemi*. We followed the species adjustments advanced by Byrne et al. (2020). Additionally, sequences of the titi monkey species *C. personatus* (accession number AF289988) and *Plecturocebus moloch* (KU694295), together with sequences of the other pitheciid genera, *Cacajao* (FJ531644), *Chiropotes* (FJ531667), and *Pithecia* (FJ531668), also downloaded from Genbank, were used as outgroup. Clustal X (Thompson et al. 1997) was used, employing default parameter values, to align the sequences. Alignment was straightforward and no correction was needed; the matrix has no gap. Bayesian inference (BI; Rannala and Yang 1996) and Maximum Likelihood (ML; Felsenstein 1981) analyses were used to infer a gene tree. The substitution model, HKI+G, which was selected using jModelTest (Darriba et al. 2012), was implemented in both phylogenetic analyses. The BI analysis was performed using MrBayes 3.1 (Ronquist and Huelsenbeck 2003) by means of two independent runs with five heated and one cold Markov chains each that were run for 10 million generations; trees sampled every 1000 generations. The parameters of the model were estimated in MrBayes; a Dirichlet process prior was assumed for the parameters of base composition and the HKY model; meanwhile, uniform interval priors were implemented for all other parameters. Convergence on stable log-likelihood values was checked by plotting log-likelihood values against generation time. The first 25% of the trees sampled were discarded as burn-in. The remaining trees, all sampled from the convergence zone of both runs, were used to compute a 50% majority rule consensus tree with posterior probability (PP) values. IQ-TREE (Nguyen et al. 2014) was used to carry out the ML analysis; it was implemented setting perturbation strength and number of unsuccessful iterations to 0.5 and 100, respectively; 1000 ultrafast Bootstrap replicates (UFB; Minh et al. 2013) were used to evaluate the support of each clade. MEGA 6 (Tamura et al. 2013) was used to calculate observed percentage of sequence divergence (*p*-distances) ignoring sites with missing data.

Ethical note

We developed this study following the principles for ethical treatment of nonhuman primates by the American Society of Primatologists (2001). No animal was euthanized during this research. Specimen MUSM 50736 was recovered from local subsistence hunters on June 18th 2019 by Gabriel Garcia and Edgardo Rengifo under collection permit RDG 107-2017-SERFOR-DGGSPFFS.

Nomenclatural statement

This published work and the nomenclatural act it contains have been registered in ZooBank. The Life Science Identifiers (LSID) for this publication is: urn:lsid:zoobank.org:pub:BBC94729-BC9E-4D4F-B3DD-2D864E7E3D5E. The online version of this work, with fixed content and layout, will be archived and available at BioOne.

Result

Morphological evidence

On the basis of pelage and cranial features we identified two distinct morphotypes (Figs. 1–4). Specimens

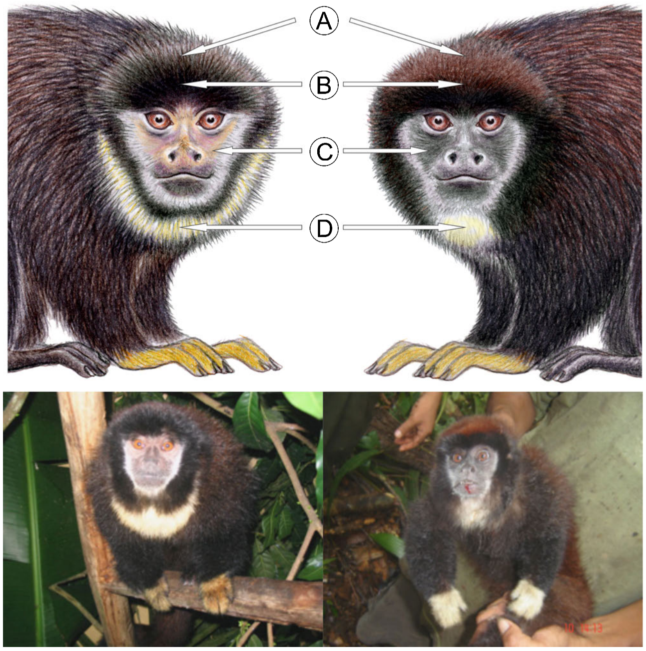

Fig. 1. External features of *Cheracebus lucifer* (left) – Photo: Fanny Cornejo, and *C. aquinoi* n. sp. (Nanay-Tigre morph; right) – Photo: Wagner Terrones. Arrow indicates the differences in A) the crown, B) the frontal band, C) the face, and D) the throat.

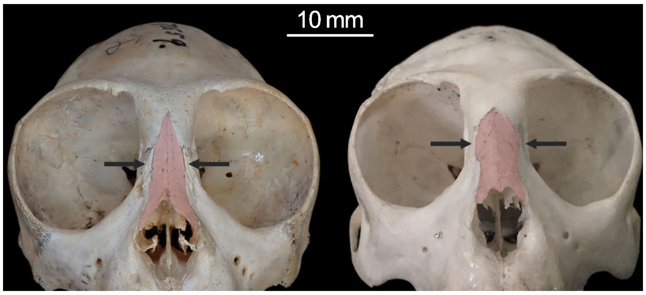

Fig. 2. View of the nasal bone –colored in light gray (light red in online version)– of *Cheracebus lucifer* (left: AMNH 73559) with a lanceolate shape, and of *C. aquinoi* n. sp. (Nanay-Tigre morph; right: MUSM 46905) with a lyrate shape.

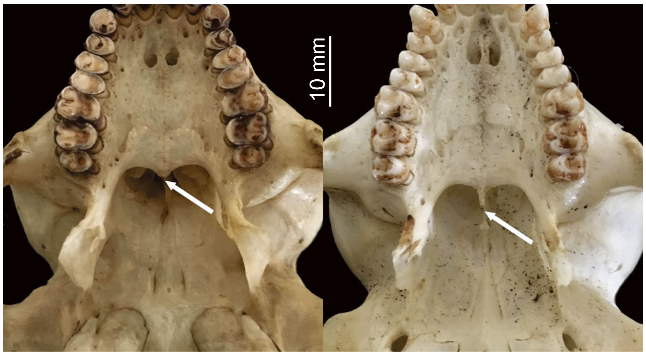

Fig. 3. The medial process of the palate (indicated by arrows) in *Cheracebus lucifer* (left: MUSM 46903) is reduced, while in *C. aquinoi* n. sp. (Nanay-Tigre morph; right: MUSM 46905) it is larger.

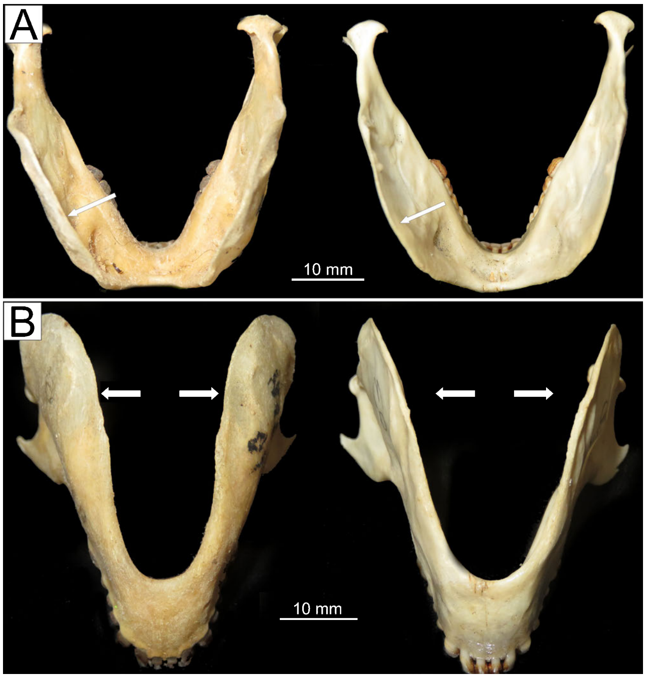

Fig. 4. Posterior and ventral view of angular process of the Jaw. A) Arrow indicates the margin, in *Callicebus lucifer* is curved (left), whereas in Nanay-Tigre morph is straight (right); B) arrow indicates the separation of the angular process, *Callicebus lucifer* show U-shape (left), while the Nanay-Tigre morph V-shape (right).

from the Caquetá, Amazonas, and Napo rivers represent one morph that we consider to be *Cheracebus lucifer* (*sensu* Byrne 2020). Specimens from the Nanay-Tigre interfluvium represent the second morph, which is here referred as the Nanay-Tigre morph. *Cheracebus lucifer* has a brownish dorsal pelage, while the Nanay-Tigre morph is dark reddish brown. Three contrasting traits between both morphs are found on the head; i) the crown of *C. lucifer* is brownish with a tinge of red, whereas in the Nanay-Tigre morph it is reddish brown; ii) the frontal band on the forehead is broad in *C. lucifer*, but narrow in the Nanay-Tigre morph; and iii) the face in *C. lucifer* is covered with abundant fine white hairs giving it a whitish appearance, while in the Nanay-Tigre morph the face has dispersed white hairs making for a greyish appearance. The throat of *C. lucifer* shows a very visible band of creamy-white hair extending laterally to the base of the ears, whereas in the Nanay-Tigre morph the band is reduced and does not extend laterally. The tail in *C. lucifer* is brownish and does not contrast with the body coloration whereas in the Nanay-Tigre morph the tail is blackish contrasting with the dark reddish-brown body.

The two titi morphs also differ in skull morphology.

Table 1. Selected cranial measurement of *Cheracebus aquinoi* n. sp. (Nanay-Tigre morph) and *Cheracebus lucifer*

Variable	*Cheracebus aquinoi*			*Cheracebus lucifer*		
	MUSM 460904	MUSM 460905	FMNH 86978	Mean ± *SE*	Range	*n*
GLS	69.90	68.90	69.33	66.4 ± 1.83	63.26–68.22	8
CBL	59.10	58.70	58.43	54.24 ± 2.02	50.65–57.37	8
GBB	38.70	39.10	37.90	36.99 ± 0.68	36.06–38.17	7
ZB	45.00	44.30	44.20	42.26 ± 1.42	39.24–43.49	8
OB	40.70	41.00	41.00	40.06 ± 1.52	37.44–41.67	8
POB	32.99	33.40	33.16	33.03 ± 0.93	31.54–33.85	8
PL	23.10	23.40	23.16	21.57 ± 1.62	19.33–23.50	7
FOM	10.10	9.90	9.10	9.62 ± 0.77	8.64–10.66	8
BL	15.43	15.16	15.95	17.1 ± 0.6	16.18–18.20	8
RC	15.40	15.61	15.94	15.72 ± 0.67	14.72–16.64	8
MTR	16.43	16.68	15.90	16.05 ± 0.73	14.73–17.04	8
MBL	44.97	45.23	44.42	43.71 ± 2.71	38.44–46.52	8
IDG	13.20	12.90	12.45	12.32 ± 0.95	10.54–13.40	8
CPH	36.67	35.40	35.57	37.03 ± 1.45	34.87–39.13	8
LTR	18.80	19.20	18.79	18.27 ± 0.59	17.07–19.04	8
M1B	18.51	18.97	18.26	18.55 ± 0.49	18.08–19.58	8
LCB	11.84	11.07	12.07	11.89 ± 0.49	11.22–12.55	8

Measurements (in mm) are given for three specimens of *C. aquinoi* n. sp. and from eight specimens of *C. lucifer* (see Appendix 1). *SE* = standard error. *n* = sample size. See Materials and methods for abbreviations.

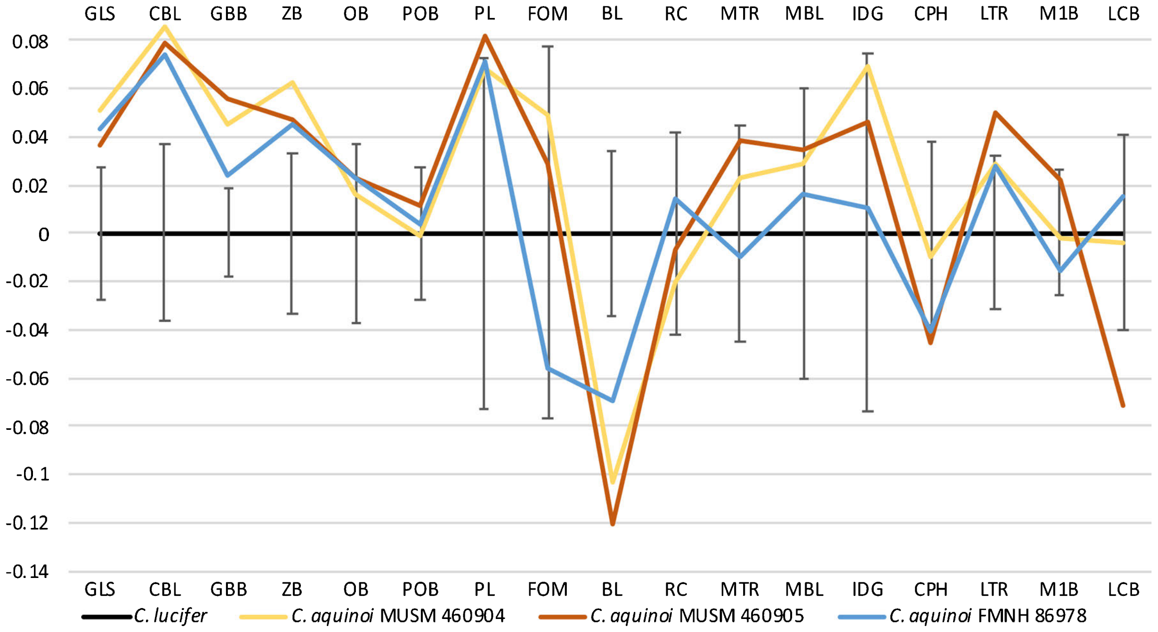

Fig. 5. Ratio diagram comparing mean logarithmic values for the cranial dimension of *Cheracebus lucifer* and *C. aquinoi* n. sp. Error bars indicate standard deviation (*SD*). See Materials and methods for abbreviations.

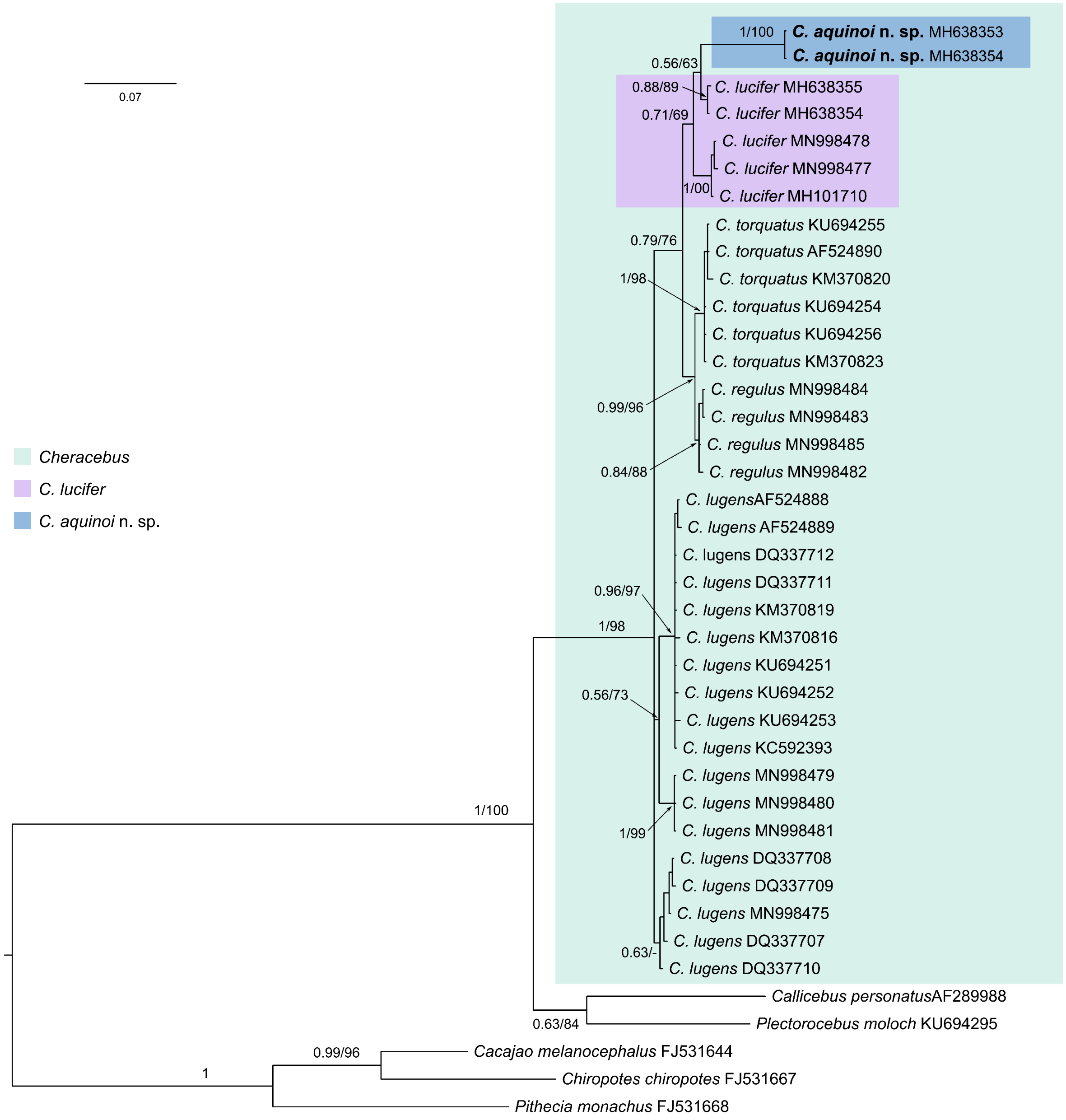

Fig. 6. Majority rule consensus tree obtained from the Bayesian analysis of cytochrome-b gene sequences of specimens of Pitheciidae with emphasis on the genus *Cheracebus*. Numbers indicate posterior probability (left) and ultrafast bootstrap (right) values of adjacent nodes (for simplicity intra-specific values are not shown). Terminal designations correspond to the taxonomic identification and accession numbers as adjusted by Byrne et al. (2020).

The middle portion of the nasal bone in *C. lucifer* is slightly narrower, giving a lanceolate shape to the nasal bone; meanwhile in the Nanay-Tigre morph the middle portion of the nasal is wider, giving a lyrate shape to the nasal bone (Fig. 2). The medial process of the palatal bone is reduced in *C. lucifer*, whereas in the Nanay-Tigre morph it is large (Fig. 3). There are also differences in the jaw. From a posterior view, the angular process of *C. lucifer* is curved, whereas in the Nanay-Tigre morph it is straight (Fig. 4A); in ventral view the angular processes appears close in *C. lucifer* giving the jaws a U-shape and more separate in the Nanay-Tigre morph giving the jaws a V-shape (Fig. 4B). Both *C. lucifer* and the Nanay-Tigre morph also differ morphometrically (Table 1); in general, the Nanay-Tigre morph is slightly larger than *C. lucifer*. The Nanay-Tigre morph has proportionally larger GLS, CBL, GBB, ZB, and PL than *C. lucifer*, and a BL proportionally shorter (Fig. 5).

Table 2. Percentage of average genetic variation (*p*-distances), based on cytochrome-b sequence data, observed within and between pairs of taxa of *Cheracebus*

	intra	*C. aquinoi* n. sp.	*C. lucifer*	*C. lugens*	*C. regulus*
C. aquinoi n. sp. (2)	0.000				
C. lucifer (5)	0.011	0.052			
C. lugens (18)	0.012	0.059	0.038		
C. regulus (4)	0.002	0.049	0.025	0.033	
C. torquatus (6)	0.002	0.056	0.027	0.036	0.010

Sample sizes are given between parentheses.

Phylogenetic and genetic analyses

In both BI and ML gene trees (Fig. 6), the subfamily Callicebinae and the genus *Cheracebus* were found to be monophyletic with high support (PP = 1; UFB = 100 and PP = 1; UFB = 98, respectively). Haplotypes assigned to *C. lugens* fall into three main clades. There is a strongly supported clade formed by haplotypes of specimens collected on the north (left) bank of the Japurá River; then, a second clade (PP = 0.96; UFB = 97) is formed by haplotypes recovered from specimens collected on the north (left) bank of the Negro River; finally, another clade, recovered only in the BI analysis and with no significant support (PP = 0.63), is formed by haplotypes of specimens of *C. lugens* collected on the south (right) bank of the Negro River. *Cheracebus torquatus* (PP = 1; UFB = 98) and *C. regulus* (PP = 0.84; UFB = 88) form a clade (PP = 0.99; UFB = 96). Haplotypes of the specimens of Nanay-Tigre morph form a clade (PP = 1; UFB = 100). Haplotypes of three specimens of *C. lucifer* s.s. collected on the right bank of the Japurá river in Brazil, form a strongly supported clade (PP = 1; UFB = 100); similarly, haplotypes of specimens of *C. lucifer* s.s. from the Napo basin in the Peruvian Amazonian form a clade (PP = 0.88; UFB = 89). The clade of *C. lucifer* s.s. from the Napo basin appears to be a sister to the clade of the Nanay-Tigre morph, although this relationship lacks significant support (PP = 0.56; UFB = 63). Therefore, haplotypes of *C. lucifer* s.s. form a paraphyletic group with respect to the clade formed by the haplotypes of the Nanay-Tigre morph. The clade formed by haplotypes of *C. lucifer* s.s. and the Nanay-Tigre morph has low support (PP = 0.71; UFB = 69). Observed average *p*-distance among haplotypes of Brazilian and Peruvian *C. lucifer* with those of the titi monkeys from the Nanay-Tigre morph is 5.5 % and 4.8%, respectively, while the observed value between Brazilian and Peruvian *C. lucifer* is 1.7%. Observed genetic divergence values between all species pairs are shown in Table 2.

Taxonomy

The specimens of *Cheracebus* from the Peruvian Nanay-Tigre interfluvium (i.e., the Nanay-Tigre morph) are morphologically distinct (see also below) from those of all other species of the genus, including the nearby distributed and phylogenetically close species *C. lucifer*. Similarly, the Nanay-Tigre morph is genetically well differentiated from the species level lineages of *Cheracebus*, including that of *C. lucifer* s.s. The latter appears paraphyletic with respect to the Nanay-Tigre morph, even when the genetic distance between both lineages, *C. lucifer* s.s. and the Nanay-Tigre morph, is similar to that observed between titi monkey species pairs. As such, we consider that the paraphyly of *C. lucifer* s.s. at the mitochondrial genome of the Nanay-Tigre morph represents a case where the gene tree departs from the species tree. The cause of this pattern is unclear, but a likely and simple explanation is that not enough time has passed since the speciation event, for the geographically broadly distributed *C. lucifer* s.s. to have reached the monophyly at the mitochondrial genome (Funk and Omland 2003). In other words, reciprocal monophyly at the mitochondrial genome is an emergent property that has yet to be reached by the species pair of *C. lucifer* s.s. and the Nanay-Tigre morph (see de Queiroz 2007). As such, based on the morphological and molecular evidence presented here, we conclude that specimens from the Nanay-Tigre interfluvium comprise a distinct lineage of species for which there is no name available. As such, we named and described it as follows.

Cheracebus aquinoi new species
Aquino's titi monkey
(Figs. 7 and 8)

urn:lsid:zoobank.org:act:25D61FBA-9C11-4D79-BF3C-1A267CE6A70B
Callicebus lucifer Thomas 1914: 345, part.

Fig. 7. Dorsal, ventral, and lateral views of the cranium and mandible of *Cheracebus aquinoi* n. sp. (Nanay-Tigre morph: MUSM 46905).

Fig. 8. Dorsal and ventral views of the skin of *Cheracebus aquinoi* n. sp. (Nanay-Tigre morph: MUSM 50735), preserved skin an adult male collected in the Quebrada Yanayacu, Distrito de San Juan, provincia de Maynas, Departamento de Loreto, Perú. Coordinates: 4°13'3"S; 73°42'33"W.

C[*allicebus*] *t*[*orquatus*] *lucifer* Thomas 1927, name combination.

Callicebus torquatus torquatus Hershkovitz 1963: 54 name combination.

C[*allicebus*] *torquatus* Kinzey 1982: 474 name combination.

C[*allicebus*] *t*[*orquatus*] *lucifer* Hershkovitz 1988 242; name combination.

Callicebus torquatus lucifer Hershkovitz 1990: 82; name combination.

Callicebus lucifer van Roosmalen et al. 2002: 33, part.

Callicebus lucifer Heymann et al. 2002: 125, part.

Callicebus torquatus Aquino et al. 2008: 1183, part.

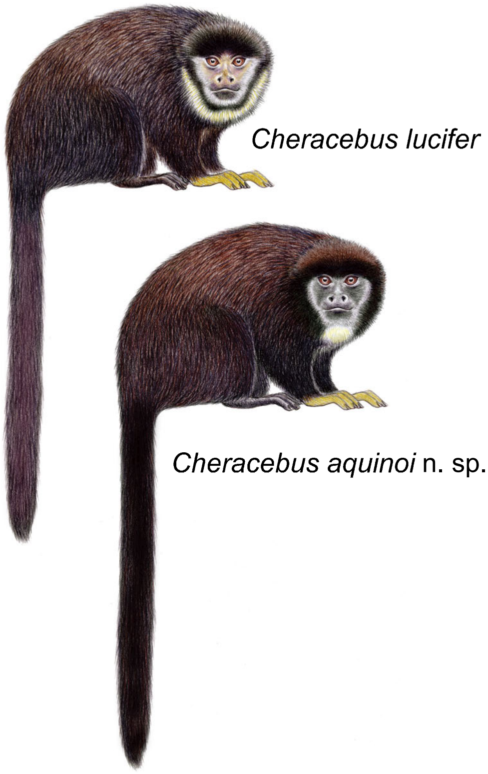

Fig. 9. *Cheracebus lucifer* and *Cheracebus aquinoi* n. sp. (Nanay-Tigre morph). Courtesy Stephen D. Nash.

Holotype: MUSM 59736, an adult female preserved as a carcass, skin, and skull obtained from local subsistence hunters on June 18th 2019 and recovered by Gabriel Garcia and Edgardo Rengifo.

Type locality: 2.5 km NE Villa Belén, San Juan Bautista, Maynas, Loreto, Peru (4°15'45"S; 73°42'00"W).

Diagnosis: *Cheracebus aquinoi* n. sp. can be easily distinguished from all other *Cheracebus* by the following combination of characters: overall reddish-brown pelage; crown intense reddish brown; face with a slightly whitish appearance due to dispersed white hairs; narrow black band between face and crown hairs; cream-colored collar, like a bow tie, with a band that does not extend laterally; creamy-white dorsal hand coloration; blackish tail that contrasts with the body (Fig. 9); thin middle portion of the nasal bone; large medial process of the palatal bone; straight angular process of the jaw in posterior view; and more separated right and left angular processes in ventral view.

Distribution: *Cheracebus aquinoi* n. sp. is known from only a small area in the Peruvian department of Loreto,

Table 3. List of the known localities of *Cheracebus aquinoi* n. sp.

	Locality	Cordinates	Reference
1	Peru: Loreto, Mishana (Estación Biológica Callicebus)	3°54'56"S; 73°29'59"W	Kinzey (1977)
2	Peru: Loreto; Mishana (Rio Nanay)	3°52'0"S; 73°29'0"W	Heymann et al. (2002)
3	Peru: Loreto, Quebrada Aleman	2°41'45"S; 75°2'9"W	Aquino et al. (2000)
4	Peru: Loreto, Quebrada Seis Unidos	4°12'27"S; 73°49'50"W	Aquino et al. (2008)
5	Peru: Loreto, Quebrada Agua Blanca I	4°11'33"S; 73°52'47"W	Aquino et al. (2008)
6	Peru: Loreto, Quebrada Yanayacu	4°13'3"S; 73°42'33"W	Aquino et al. (2008)
7	Peru: Loreto, Quebrada Nauta I (Left bank)	4°15'10"W; 73°54'21"W	Aquino et al. (2008)
8	Peru: Loreto, Quebrada Nauta II (right bank)	4°17'42"S; 73°54'18"W	Aquino et al. (2008)
9	Peru: Loreto, Quebrada Miraflores	4°20'46"W; 73°44'41"W	Aquino et al. (2008)
10	Peru: Loreto, Quebrada Agua Blanca II	4°7'27"S; 73°35'8"W	Aquino et al. (2008)
11	Peru: Loreto, Quebrada Pension	4°20'19"W; 73°36'32"W	Aquino et al. (2014)
12	Peru: Loreto, KM 51 carretera Iquitos Nauta	4°10'59"S; 73°27'24"W	Aquino et al. (2014)
13	Peru: Loreto, Santa Lucia	3°19'59"S; 74°34'59"W	Hershkovitz (1990)
14	Peru: Loreto, Alto Itaya - Botin	4°8'14"S; 73°57'20"W	This study
15	Peru: Loreto, 2.5 km NE Villa Belén	4°15'45"S; 73°42'00"W	This study

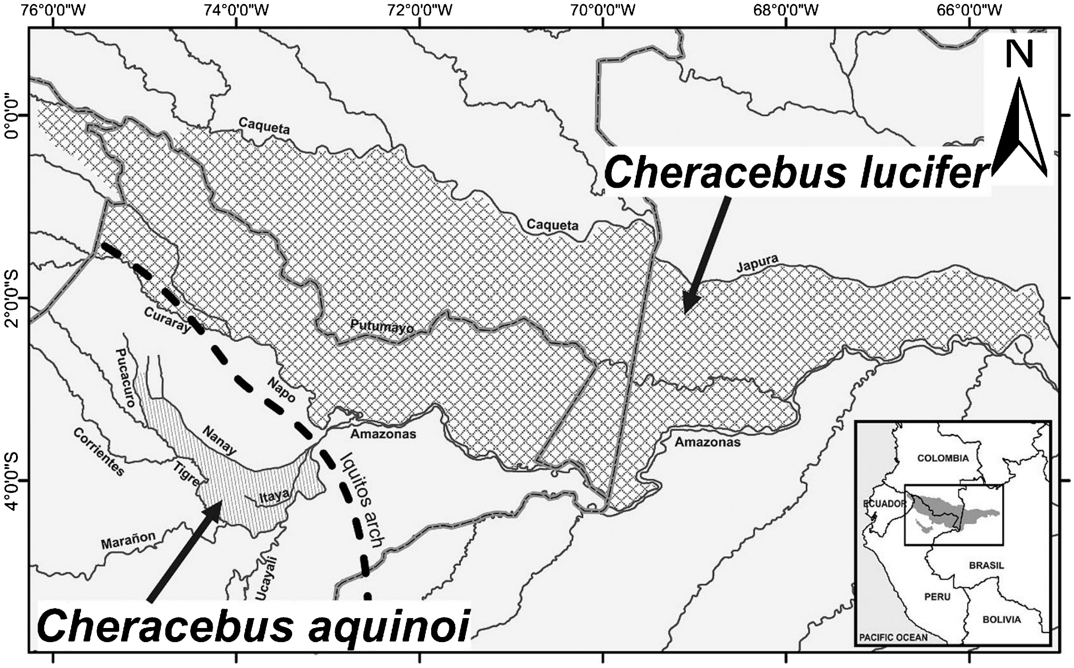

Fig. 10. The geographic distribution of *Cheracebus lucifer* and *Cheracebus aquinoi* n. sp. The dashed line indicates the Iquitos arch.

between the Nanay and Tigre rivers. To the northwest the species distribution is unclear, but it may be limited by the confluence of the Quebrada Alemán and the Pucacuro River, a right bank tributary of the Tigre River. Localities are listed in Table 3 (see also Fig. 10).

Etymology: The species epithet, *aquinoi*, refers to Rolando Aquino, an eminent Peruvian primatologist (Fig. 11). In addition to his extensive research on the distribution, ecology, and conservation of Peruvian primates, Rolando Aquino has encouraged, mentored, and

Fig. 11. Rolando Aquino working in his office at the Instituto Veterinario de Investigaciones Tropicales y de Altura (IVITA), Iquitos, Peru.

trained numerous Peruvian mammalogists. The species name is a patronym in the genitive singular.

Description: Aquino's titi monkey is characterized by an intense reddish-brown pelage. Dorsal and lateral body to neck, forelimbs to elbow, and hind-limbs to knee are brownish or reddish-brown; forearm to wrist is dark brownish; dorsal coloration of hands is creamy-white sometimes with a yellow-orangish tonality; leg with reddish-brown hairs, thigh is whitish; foot with black hairs. Ventral body is reddish chestnut. The throat has a bow tie-like tuft of creamy-white hair that does not extend laterally. The crow has very reddish-brown hairs. The facial skin is blackish and sparsely covered with short white hair. The tail is mostly dark in appearance; the proximal portion (one-third) of the tail is blackish chestnut, and the distal two-thirds and terminal portion of tail are black.

The skull of *C. aquinoi* n. sp. resembles those of other species of the genus. The rostrum is very short. The nasal has a lyrate shape, and its nasal aperture is of a broad fleur-de-lys form; in lateral view the nasal angle is slightly acute. The premaxillaries project anteriorly to the level of the anterior margin of the nasals. The malar is broad with two distinguishable infraorbital foramens. The zygomatic bone presents a noticeable malar foramen and a small zygomatic-orbital foramen. The squamous portion of the zygomatic arch is gracile, with parallel sides that slightly converge anteriorly; the postglenoid process is moderately large. The posterior side of the roots of the squamosal of the zygomatic arch is aligned and the anterior side is deep. The interorbital region is broad; the nasion is slightly swollen. The orbital region is wide with a pronounced orbital ridge or crest, the inferior orbital fissure is small, the superior orbital suture is oval, and the optic foramen is rounded; the lacrimal fossa is evident. The frontal bone is flat with a soft metopion; the coronal suture converges posteriorly but does not form a "V". The parietal presents a clear superior temporal line; the interparietal suture is smooth and it does not build a sagittal crest. The opisthocranium coincides with the inion of the occipital bone, the occipital angle is ca. 45 degrees; a delicate occipital crest is present. The occipital foramen is rounded; the occipital condyles project ventrally and the hypoglossal canal is large; the basioccipital is wide with a trapezoid-shape and lacks a medial spine. The basisphenoid is thin and long with the anterior margin like an arrowhead. The auditory region is moderately large with a large tympanic bulla. The stapedial process is developed but does not reach the parapterygoid process. The mastoid process is small. The palatal region is wide and slightly short. The transverse contour of the palatal vault is slightly arched. The incisive foramen is oval-shaped; the greater palatine foramen is small and placed at the level of the first molars; the lesser posterior palatine foramen is very small and placed posteriorly of the plane of third molars. The mesopterygoid fossa is wide with a distinguishable medial process.

The jaw is high and broad, the coronoid process is more strongly developed than the condyle; the superior mandibular notch is short and slightly deep. The gonion is barely posterior to the condyle; the superior masseteric ridge is noticeable; the masseteric fossa is slightly deep. The mental foramen is small and placed at the level of the first premolar. From a posterior view the angular process is straight; from a ventral view the right and left angular processes have a V-shape.

The dental formula is 2.1.3.3/2.1.3.3.

Comparisons: *Cheracebus aquinoi* n. sp. can be distinguished from all other species of *Cheracebus* (see Table 4).

The overall pelage coloration of *C. aquinoi* n. sp. is dark reddish brown, being something similar to *C. lucifer* that is brownish, *C. regulus* that presents a chestnut brownish, and *C. torquatus* that exhibits a light brownish coloration. Meanwhile *C. lugens* and *C. medemi* exhibit overall a darker pelage than that of

Table 4. Differences of the external features among *Cheracebus aquinoi* n. sp., *C. lucifer*, *C. lugens*, *C. medemi*, *C. torquatus*, and *C. regulus*

Characters/Species	*C. aquinoi*	*C. lucifer*	*C. lugens*	*C. medemi*	*C. torquatus*	*C. regulus*
Appearance	Dark reddish brown	Brownish	Dark brown/ brownish	Chestnut blackish	Light brownish	Brownish
Dorsum	Dark reddish brown	Chestnut brown	Dark brownish	Chestnut blackish	Light brownish	Chestnut brownish
Crown	Reddish brown	Brownish	Brownish	Blackish	Ochraceous	Ochraceous
Forehead	Blackish	Blackish	Blackish	Blackish	Blackish	Brownish
Forehead (frontal band)	Distinguishable	Teneusly distinguishable	Teneusly distinguishable	Indistinguishable	Distinguishable	Distinguishable
Face	Scarce hairs	Covered by hairs	Scarce hairs	Covered by hairs	Scarce hairs	Scarce hairs
Throat collar	Bow tie-like, small	Extending laterally to the base of the ears	Extending laterally to the base of the ears	Extending laterally to the base of the ears	Extending laterally to the base of the ears	Extending laterally to the base of the ears
Sideburns	Dark brown and broad	Dark brown and narrow	Blackish and narrow	Blackish and broad	Reddish brown and narrow	Reddish brown and broad
Flanks	Reddish	Brownish	Blackish	Blackish	Reddish	Chestnut
Arm	Brownish	Brownish	Blackish	Chestnut blackish	Brownish	Brownish
Hand	Creamy/ yellow-orangey	Yellow-orangey	Yellow-orangey	Dark	Whitish / Creamy	Yellow-orangey
Feet	Chestnut blackish	Chestnut blackish	Blackish	Chestnut blackish	Blackish	Chestnut blackish
Limbs (outer face)	Brownish	Brownish	Blackish	Chestnut blackish	Brownish	Brownish
Tail	Blackish	Brownish	Blackish	Blackish	Blackish	Blackish

C. aquinoi n. sp., being dark brown/brownish and chestnut blackish, respectively.

The crown of *C. aquinoi* n. sp. is dark reddish brown, slightly different from that of *C. lucifer and C. lugens*, that show a brownish coloration, while it is clearly distinct from that of *C. torquatus* and *C. regulus* that show an orange like coloration and that of *C. medemi* that is blackish. Aquino's titi monkey has scarce hairs on the face; this feature is also seen in most of species of the *Cheracebus*; although, *C. lucifer* and *C. medemi* show a face covered by hairs. The frontal band above the eyebrow of *C. aquinoi* n. sp. is very distinct and contrasts with the colour of the crown; the same pattern is observed in *C. torquatus* and *C. regulus*, while the frontal band is barely visible in *C. lucifer* and *C. lugens*; additionally, a contrasting frontal band is not evident in *C. medemi*. One of the traits present only in *C. aquinoi* n. sp. is the bow tie-like collar; that does not extend beyond of the central part of the neck; the other species have a more or less distinct collar that, in some cases, extends from ear to ear. *Cheracebus aquinoi* n. sp., like *C. torquatus*, *C. lucifer*, *C. lugens*, and *C. regulus* yellow-orangey hands, but in some creamy; *C. regulus*; *C. medemi* has dark hands, while *C. torquatus* has white or creamy-colored hands. The tail in *C. aquinoi* n. sp. is blackish like that of *C. lugens*, *C. medemi*, *C. torquatus*, and *C. regulus*, while in *C. lucifer* and *C. torquatus* the tail is brownish.

Cheracebus aquinoi n. sp. co-occurs with the titi monkey *Plecturecebus discolor*; both species are very distinct; among all of their differences, the most clear-cut are that *P. discolor* has sideburns, side of neck, lower arms, legs, chest, and belly reddish that are in sharp contrast with the agouti of the crown, back, body sides, and tail; whereas *C. aquinoi* n. sp. exhibits a reddish brown in overall pelage coloration; in addition, *P. discolor* has a forehead with a whitish transverse band, which in *C. aquinoi* n. sp. is blackish; the anterior portion of the crown is agouti in *P. discolor* and reddish brown in *C. aquinoi* n. sp. The tail in *P. discolor* is mixed brownish and agouti and often with a dominantly buffy penciled tip, which differs from the generally black tail of *C. aquinoi* n. sp.

Natural History: Aquino's titi monkey is a diurnal species that lives in family groups with mean sizes ranging between 2.9 and 3.5 individuals (Aquino et al. 2008). The home range in groups studied by Kinzey (1977), Kinzey et al. (1977), and Easley and Kinzey (1986) was 20 ha.

Population density varies from 0.3 to 4.8 individuals/km^2 (Freese 1975; Aquino et al. 2015a, 2021). *Cheracebus aquinoi* n. sp. prefers the higher strata of the forest between 15 and 25 m (Kinzey 1976). Aquino et al. (2008) mentioned that *C. aquinoi* n. sp. is restricted to "varillales," a type of forest with thin-stemmed trees that grows on sandy soils (Encarnación 1985); however, Freese (1975) and Kinzey (1976) observed this species also in gallery forests, flooded forests, and palm-dominant forests. *Callicebus aquinoi* n. sp. feeds on buds, flowers, fruit pulp, insects, leaves, and seeds (Kinzey 1976, 1977; Kinzey and Gentry 1979; Kinzey 1981; Easley 1982). *Cheracebus aquinoi* n. sp. can be found in temporary associations with *Plectorocebus discolor*, *Pithecia aequatorialis*, and *Leontocebus lagonotus* (Terrones 2006).

Discussion

The subfamily Callicebinae of titi monkeys encompasses the most complex and diverse group of South American primates, which inhabit most of the humid and xeric forest of South America (Hershkovitz 1990). Currently, ca. 35 living species of callicebine are recognized (van Roosmalen et al. 2002; Byrne et al. 2018; Boubli et al. 2019, Gusmão et al. 2019; this study), which in the current classification (e.g., Mammal Diversity Database 2022) are allocated into three genera (i.e., *Callicebus*, *Cheracebus*, and *Plecturocebus*; Byrne et al. 2016). *Cheracebus* includes the species *C. torquatus*, *C. lugens*, *C. lucifer*, *C. regulus*, *C. medemi*, and *C. aquinoi* n. sp. (this study).

The description of a new species of *Cheracebus*, Aquino's titi monkey, is not unexpected because it was earlier suggested that it might represent a distinct species (Heymann et al. 2002; Aquino et al. 2008) and since in recent years the known species diversity of Callicebinae has increased with the description of numerous new species (e.g., Defler et al. 2010; Vermeer and Tello-Alvarado 2015; Boubli et al. 2019; Gusmão et al. 2019). In fact, 124 new primate species have been described since 1990, of which 32 are from the Neotropics (Mittermeier and Rylands 2022). In this regard, it is interesting to note that the current concept of *C. lugens* includes three divergent lineages (Boubli et al. 2015; Byrne et al. 2016); further evaluation of the distinction of those two genetic units is needed. In spite of the results of such assessment, we anticipate that in the next few years several taxonomic changes will be proposed in order to reflect the real species diversity of Callicebinae.

Based on specimens collected by C. Kalinowski, Hershkovitz (1963, 1988), extended the geographic distribution of *C. lucifer* west towards the headwater of the Nanay River in eastern Peruvian Amazonia. Here we examined these specimens (FMNH 86978, 86979), assigning them to *C. aquinoi* n. sp. The two species are allopatric and there is an area between the Nanay and Napo Rivers where neither have been recorded. Vriesendorp et al. (2007), who explored this area, noticed the absence of *Cheracebus* suggesting that it may be due to the absence of the habitat called "varillales."

When mapping the geographic distribution of *C. aquinoi* n. sp. and *C. lucifer* on the biogeographic ecoregions of Dinerstein et al. (2017), it emerges that *C. lucifer* occurs in the Solimões-Japurá moist forest ecoregion, while *C. aquinoi* n. sp. occurs in the biodiversity rich Napo moist forest ecoregion (Olson and Dinerstein 1998). In addition, the distribution of *C. aquinoi* n. sp. almost perfectly matches the geological formation "Formación Nauta" as delineated in the "Mapa Geológico del Perú" (Geological map of Peru; INGEMMET). Similarly, the distribution of *C. lucifer* and *C. aquinoi* n. sp. are separated by the Iquitos arch (Fig. 10), a geologic accident that has shaped the differentiation of several small mammals (Patton et al. 2000) and that could have played an important role in the diversification of these primate species. As a hypothesis to be tested in future studies, we note that the phylogenetic pattern of a paraphyletic species (*C. lucifer*) with respect to another (*C. aquinoi* n. sp.) is expected if the latter differentiated from the former as a small peripheral isolate, either by peripatric speciation or through a founder event (Funk and Omland 2003; see examples of this phylogenetic pattern due to peripatric speciation in Kruckenhauser et al. 2014). The analysis of nuclear genes is much needed to test this hypothesis. More in general, a robust phylogenetic hypothesis with a complete taxonomic and a broad geographic and character sampling is needed in order to advance a biogeographic hypothesis for the genus. The phylogenetic trees by Byrne et al. (2018) and Carneiro et al. (2020) provide promising foundation.

The understanding of the diversity of Peruvian primates has slowly but steadily increased in recent decades; known species have grown from 32 at the end of last century (Aquino and Encarnación 1994) to currently 48 (Aquino et al. 2015b and including this new species). Despite these advances, several relevant information gaps still persist; this scenario is mostly due to the nonexistence of good specimen series in museum collections. We note that the specimens that are the base of some of the species recently reported or described from Peru (Matauschek et al. 2011; Marsh 2014; Botero et al. 2015; Di Fiore et al. 2015) were either collected several decades ago (by, among others, the Olalla brothers, P. Hershkovitz, J. M. Schunke, E. Heller, C. Sanborn, C. Kalinowski; see Velazco and Cornejo 2014), or obtained in recent years from the activities of local hunters and later deposited in museum collections (e.g., Vermeer and Tello-Alvarado 2015). Taking advantage, as was done in this study, of specimen remains gathered from the activities of subsistence hunters has proved to be useful for scientific and conservation purposes, as specimen samples are still much needed in order to gain an adequate understanding of basic aspects of primate species diversity, distribution, and natural history. To gain such knowledge is critical to get a better basis to control primate illegal traffic and to design sound conservation strategies.

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Appendix 1.

Collection number and locality information of the specimens of titi monkeys morphologically assessed in this study. Collection numbers in bold indicate measured specimens; collection numbers in italics and underlined indicate specimens assessed only by photos. Sex is indicated as m for male, f for female, and n for not known. Asterisks indicate remains obtained from local subsistence hunters, which were recovered in diverse expeditions (2004–2019) with research permit RDG 107-2017-SERFOR-DGGSPFFS. Examined specimens are housed at the following collections: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú (MUSM); Field Museum of Natural History, Chicago, USA (FMNH); American Museum of Natural History, New York, USA (AMNH); British Museum (Natural History), London, United kingdom (NHMUK); Mammal Collection of Instituto Alexander von Humboldt, Cartagena, Colombia (IAvH-M); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); and Museu Nacional do Rio de Janeiro. Rio de Janeiro, Brazil (MNRJ).

Cheracebus aquinoi (*n* = 6):
PERU: Loreto: Maynas: Rio Nanay, Santa Luisa (FMNH **86978**m, 86979f); San Juan Bautista, Campamento Botin (MUSM **46904m*, 46905f***); San Juan Bautista, Quebrada Yanayacu (MUSM 50735m); San Juan Bautista, 2.5 km NE Villa Belén (MUSM 50736f* Holotype)
Cheracebus lucifer (*n* = 14):
COLOMBIA: Amazonas, En selva Entre Puerto Arara y la Carretera Leticia-Tarapacá (IAvH-M-<u>*00366*</u>f); Caqueta, Rio Caquetá, El chorro de La Libertad (IAvH-M-<u>*01795*</u>f); PERU: Loreto: Maynas, Napo, 13 km oeste del rio algodón (MUSM 46902m*, 46903f*); Maynas, R. Apayacu (AMNH **74383m, 74384m, 74385f, 74386m**); Maynas, Curaray River mouth (AMNH **72164f, 72166m, 72167m, 73559m**); Pebas, Yahuas Territory (NHMUK <u>*1914.3.1.2*</u>m -Holotype)
Cheracebus lugens (*n* = 7):
COLOMBIA: Guaviare, Rio Guaviare, "la Maria" nr Laguna Grande (FMNH 88246f), Guaviare, Upper Cano Grande (FMNH 88248m), Guaviare, Laguna de Espejo, Lagos El Dorado (FMNH 89479f); BRASIL; Romaina, Lago da Cobra dir. Rio Mucajaí (MZUSP 9689n), Amazonas, Pq. Nac. Pico da Neblina (MNRJ 59657n).
BRAZIL: Amazonas: Manaus (FMNH 35076n) Amazonas, Upper R Amazonas, R Negro (FMNH 35144n)
Cheracebus torquatus (*n* = 2):
BRASIL: Amazonas, Rio Purus, west bank, Lago Aiapua (FMNH 38885m), Amazonas, Amazon River, Mouth of Tefe Lake (AMNH 78961f)
Cheracebus medemi (*n* = 11):
COLOMBIA: Caqueta, La Tagua, Tres Troncos (FMNH 70691f); Putumayo, San Antonio, Rio Mecaya (FMNH 70692f, 70693f, 70694f, 70695f, 70696f, 70697f, 70698m, 70699f, 70700f); Putumayo, San Antonio, Puerto Umbria (FMNH 84551f)
Plectorocebus discolor (*n* = 5):
PERU: Loreto, Loreto: Rio Tigre, 1 km above Rio Tigrillo (FMNH 122783m, 122784f, 122785m, 122786m, 122787f)