A New Species of Titi Monkey, *Plecturocebus* Byrne *et al.*, 2016 (Primates, Pitheciidae), from Southwestern Amazonia, Brazil

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Abstract: In 2011, a distinct but unnamed form of titi, *Plecturocebus*, was re-discovered in the Chapada dos Parecis, a plateau in the southern extreme of the Brazilian state of Rondônia. Here we describe it as a new species based on an analysis of morphological and molecular traits. It can be distinguished from all other species of the genus *Plecturocebus* by its generally grayish agouti pelage. The limbs are grayish agouti on the outer surface, and grayish white on the inner surface; the breast, throat, and sideburns are also grayish white; the dorsum is reddish chestnut, and the tail is gray, paler to white at the tip. A phylogenetic analysis of the new species revealed a monophyletic clade with the four geographically closest species, and four scenarios of species delimitation indicated that speciation was recent. The geographic distribution of the new species is still poorly defined. Most of the recorded localities coincide with areas of higher elevation in the transition zone between the Amazon forest and the Cerrado savanna, in southern Rondônia and western Mato Grosso, including part of the Chapada dos Parecis (Parecis Plateau), and extending into the Aripuanã/Juruena and Aripuanã/Roosevelt interfluves. The range of the new species is in the area of the Amazon's "Arc of Deforestation", where enormous tracts of forest are being destroyed for timber, colonization and industrial agriculture. It occurs in the Juruena National Park and a few Indigenous protected areas. Based on the categories and criteria of the IUCN Red List, this new titi should be considered Near Threatened.

Key words: Pitheciidae, Chapada dos Parecis, geographic distribution, morphology, genetics

Introduction

The genus *Plecturocebus* was proposed by Byrne *et al.* (2016) to accommodate an essentially Amazonian group of titi monkeys, previously assigned to the genus *Callicebus*. *Plecturocebus* includes all the taxa from the *Callicebus moloch*,

Callicebus cupreus, *Callicebus donacophilus*, and *Callicebus modestus* species groups recognized by Hershkovitz (1990), Kobayashi (1995), Van Roosmalen *et al.* (2002), and subsequent authors. Byrne *et al.* (2016), however, recognized just two species groups: a redefined *moloch* group, with 16 species, and the *donacophilus* group, with six species.

Rylands et al. (2012) predicted that the taxonomy of *Plecturocebus* (then still *Callicebus*) would undergo further changes through the discovery and identification of new forms. Eight of the 22 Plecturocebus species recognized by Byrne et al. (2016) have been described over the last 15 years-Plecturocebus stephennashi (van Roosmalen et al., 2002), Plecturocebus bernhardi (van Roosmalen et al., 2002), Plecturocebus caquetensis (Defler et al., 2010), Plecturocebus aureipalatii (Wallace et al., 2006), Plecturocebus vieirai (Gualda-Barros et al., 2012), Plecturocebus miltoni (Dalponte et al., 2014), Plecturocebus urubambensis (Vermeer and Tello-Alvarado, 2016), and, just recently, Plecturocebus grovesi Boubli et al., 2019. Vermeer and Tello-Alvarado (2016) also revalidated Plecturocebus toppini (Thomas, 1914) as distinct from Plecturocebus cupreus. These recent discoveries make *Plecturocebus* the most species-rich of the platyrrhine genera.

In 1914, a distinct form of Plecturocebus was discovered in the Chapada dos Parecis, a plateau in the southern extreme of the Brazilian state of Rondônia. The coloration of the pelage clearly differentiated it from that of other Amazonian titis. The first report on the occurrence of titis in the Parecis region was published by Miranda-Ribeiro (1914). It was recorded during the Rondon Telegraph Commission expeditions to the Brazilian states of Mato Grosso and Amazonas and the then territory (now state) of Rondônia. This titi was then identified as *Plecturocebus cinerascens* (Spix, 1823). It was known by the Parecis, the local indigenous people, as the "otôhô" (Miranda-Ribeiro 1914). Here we describe it as a distinct species based on the morphological and molecular analyses of a series of specimens collected in the region of the Chapada dos Parecis, complemented by new field data, in particular, on the geographic distribution of the new taxon in the Brazilian states of Rondônia and Mato Grosso, in the southwestern Amazon basin.

Methods

The type series consists of four specimens (Appendix), which were prepared at the Mammalogy Laboratory of the Federal University of Rondônia (UNIR) in Porto Velho and deposited in the UNIR Rondônia Mammalian Reference Collection (CRMRO). Specimens of the phylogenetically closest species of the *moloch* group (*sensu* Byrne *et al.* 2016) were examined for comparative analyses.

The external morphology of the specimens was described based on the standard parameters established in the recent studies of *Plecturocebus* (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 2016; Boubli *et al.* 2019). Following Gualda-Barros *et al.* (2012), Dalponte *et al.* (2014), and Boubli *et al.* (2019), we compared pelage color and the coloration patterns of the: 1) crown; 2) forehead; 3) pre-auricular region; 4) dorsum; 5) flanks; 6) throat, thorax, and abdomen; 7) hands and feet; 8) limbs (external surface); 9) limbs (internal surface); and 10) tail. Our comparisons focused on the species of the *moloch* group (*P. cinerascens*, *P. bernhardi*, *P. miltoni*, *P. moloch* and *P. vieirai*), which Carneiro *et al.* (2016) identified as the taxa related most closely to the new species. Specimens of other *Plecturocebus* species were included in the complementary analyses.

The cranial measurements used for our comparative analysis were as follows: 1 - Extension of the nasal bone; 2 - Distance between the nasal bone and the frontal process; 3- Distance between the glabella and upper maxilla; 4 – Width of the lacrimal bone; 5 - Width of the frontal bone; 6 - Extension of the upper maxilla; 7 -Width of the frontal process of the zygomatic bone; 8 - Width of the maxilla; 9 - Cranium width; 10 - Distance between the temporal process and the zygomatic bone; 11 – Width of the temporal suture; 12 – Width of the parietal bones; 13 – Distance between the frontal process of the maxilla and the bregma; 14 – Distance between the bregma and the glabella; 15 - Distance between the bregma and the lambda; 16 - Distance between the lambda and the upper maxilla; 17 – Distance between the bregma and the external occipital protuberance; 18 - Width of the maxilla; 19 - Distance between condylar processes; 20 - Distance between the coronoid processes; 21 - Distance between the condylar process and the alveolar; 22 – Width of the mandible (between the mental foramina); and 23 – Distance between the angle and coronoid process.

The molecular analyses were based on 26 samples of blood and muscle tissue preserved in alcohol, including two *P. bernhardi*, two *P. brunneus*, seven *P. cinerascens*, one *P. cupreus*, two *P. hoffmannsi*, two *P. miltoni*, six *P. moloch*, two *P. vieirai*, one *Cheracebus lugens*, and one *Callicebus melanochir*. The samples were provided by the Federal University of Pará, Belém, the Rio de Janeiro Primatology Center (CPRJ), Rio de Janeiro, and the Goeldi Museum, Belém. The specimens were identified from their morphological characteristics, based on the identification keys and diagnostic traits described in the literature, i.e., Hershkovitz (1990), Van Roosmalen *et al.* (2002), Gualda-Barros *et al.* (2012), Dalponte *et al.* (2014), and Boubli *et al.* (2019).

The total DNA was extracted from the samples using a Wizard Genomic kit (Promega Corporation, Madison, WI, USA), following the maker's instructions. The markers were amplified by Polymerase Chain Reaction (PCR), based on the following protocol: initial denaturation at 95°C for five minutes, followed by 35 cycles of three steps, (i) denaturation at 94°C for 30 s, (ii) hybridization of the primers for 45 s, and (iii) extension at 72°C for 45 s, with a final extension of 5 minutes at 72°C. The final volume of the PCR was 15 µl, containing approximately 50 ng of the genomic DNA, 2.4 µl of dNTPs (1.25 mM), 1.5 µl of 10 x buffer solution (200 mM Tris-HCl, 500 mM KCl), 1 µl of MgCl2 (25 mM), 1 µl of each primer (0.2 µM), and 1 U of Taq DNA polymerase. The PCR products were purified using polyethylene glycol 8000 and ethanol (Paithankar and Prasad 1991). The sequencing reactions were run in a Big Dye sequencing kit v.3.1 (Life Technologies, Carlsbad, CA, USA), and the product was injected

into an ABI 3500XL automatic sequencer for sequencing (Life Technologies, Carlsbad, CA, USA).

We sequenced eight molecular markers, including four mitochondrial genes (12S rRNA, 16S rRNA, Cytochrome Oxidase I and Cytochrome b) and four nuclear loci (Alu Pitheciidae2, Alu Pith_Alu1D_26, Alu Pith_Alu1D_27, and Alu Pith_Alu1D_84). The sequences were aligned in the online version of the Mafft program (Katoh *et al.* 2019), run in auto mode. Following alignment, the sequences were edited in BioEdit v.7.2.5 (Hall 1999).

The most appropriate partitioning scheme and evolutionary models for the sequences were inferred using Partition-Finder v.1.1.0 (Lanfear *et al.* 2012). In this analysis, the position of the bases in the codons was taken into consideration for the fragments of the protein-codifying genes, i.e., COI and Cytb. The search was run using the Greedy algorithm, based on the Bayesian Information Criterion (BIC). An initial scheme with five partitions was selected by PartitionFinder, and was found to be the most appropriate for the database acquired during the present study. Genetic distances were estimated in MEGA v.6.0 (Tamura *et al.* 2013), using the Kimura 2-parameter model (Kimura 1980).

Phylogenetic analysis was based on Bayesian Inference (BI), run in MrBayes v.3.2.1 (Ronquist and Huelsenbeck, 2003) with two independent runs of four Markov Monte Carlo chains (MCMC), one cold and three hot, with one million generations and trees being sampled every 10,000 generations, with 25% of each run being discarded as burn-in. The convergence of the runs was verified in Tracer v.1.6 (Rambaut *et al.* 2014), and Effective Sample Sizes (ESSs) of greater than 200 were considered to be satisfactory.

The species were delimited in Bayesian Phylogenetics and Phylogeography (BPP) v.3.3a (Yang 2003; Yang and Rannala 2010), and the guide tree used in the BPP to test the hypothesis that a new *Plecturocebus* species exists was selected based on the topology of the BI phylogenetic tree. The BPP program is sensitive to the priors of population size (θ) and divergence time, τ (Zhang *et al.* 2011). Given this, the four possible scenarios for these two parameters were tested, i.e., (i) large θ and ancient τ ; (ii) large θ and recent τ ; (iii) small θ and ancient τ ; and (iv) small θ and recent τ . The gamma priors $\alpha = 1$ and $\beta = 10$ were used to represent large θ and ancient τ , respectively, while $\alpha = 2$ and $\beta = 2000$ were applied for small θ and recent τ . The Dirichlet $\alpha=1$ was used in all the τ values, and the runs had 300,000 generations, being sampled every 30 generations, with a burn-in of 25%. We also estimated the θ and τ values for the most recent common ancestor between P. cinerascens and the new species.

The investigation of the geographic distribution of the new species included a review of the data on the type series, the field data, and published records (Miranda-Ribeiro 1914; Alencar 2011; Sampaio *et al.* 2012; Gusmão and Costa 2014). During fieldwork, playbacks of titi vocalizations (initially using recordings of the vocalization of *Callicebus coimbrai*, and subsequently, of the new species itself) were used to facilitate the detection of the animals in the forest. Fieldwork

was conducted in the municipalities of Vilhena in the state of Rondônia, and Comodoro, Juina, and Aripuanã in the state of Mato Grosso.

Information on the behavioral ecology of the new species was obtained from the type locality, where a group of five individuals (an adult pair, a female juvenile, a young male, and an infant), was monitored on 50 complete days between June 2010 and January 2011, resulting in a total of 491 hours of observation (Alencar 2011). Quantitative behavioral records were collected using a standard scan-sampling technique, with a five-minute interval (Ferrari and Rylands 1994), complemented by *ad libitum* observations (Altmann, 1974), behavioral sampling (Martin and Bateson 1993) and focal-tree sampling (Strier 1989).

Plecturocebus parecis sp. nov.

Holotype: UFROM 354; skin, cranium, and complete skeleton, adult male, collected by M. R. Messias at the type locality, on 4 February 2011 (Fig. 1).

Paratypes: Three. UFROM 195: skin, cranium, and complete skeleton, adult male, collected by M. R. Messias at the type locality, on 30 January 2011. UFROM 352: skin, cranium, and complete skeleton, adult female, collected by M. R. Messias at the type locality, on 2 August 2011. UFROM 355: skin, cranium, and complete skeleton, juvenile male, collected by M. R. Messias at the type locality, on 4 April 2011.

Synonyms: Callicebus cinerascens (Spix, 1823) (in part). Miranda Ribeiro, A. de. 1914. *Hist. Nat. Zool.* Publ. 84. Annexo n. 5, p.19. Commissão de Linhas Telegraphicas Estratégicas de Matto-Grosso ao Amazonas, Rio de Janeiro; Hershkovitz, P. 1990. *Fieldiana, Zool.* n.s. (55); Van Roosmalen *et al.* 2002. *Neotrop. Primates* (10 suppl.); *Callicebus moloch* (Hoffmannsegg, 1807) (in part). Hershkovitz, P. 1990. *Fieldiana, Zool.* n.s. (55). *Callicebus brunneus* (Wagner, 1842) (in part). Hershkovitz, P. 1990. *Fieldiana, Zool.* n.s. (55).

Type locality: The Rondon II hydroelectric dam on the middle Rio Comemoração, a tributary of the left margin of the Rio Ji-Paraná, municipality of Pimenta Bueno, Rondônia, Brazil.

Molecular analysis

The molecular markers amplified in the present study produced a concatenated sequence of 4930 base pairs (bps). In the BI topology (Fig. 2), *Cheracebus lugens*, the only species of this genus included in the analysis, was recovered as the sister species of all the other taxa, while *Callicebus melanochir* was the sister species of the genus *Plecturocebus*. Within the *Plecturocebus* clade, *P. hoffmannsi* was the sister species of all other taxa. The *Plecturocebus* clade has three subclades, one containing two species, *P. brunneus* and *P. cupreus*, the



Figure 1. Holotype of *Plecturocebus parecis* sp. nov.

second with three species, *P. moloch, P. vieirai*, and *P. bernhardi*, and the third containing *P. miltoni*, *P. cinerascens*, and *Plecturocebus parecis* sp. nov. It was not possible to include the very recently-described *P. grovesi* in this analysis, but as this species aligned clearly with *P. moloch*, *P. vieirai*, and *P. bernhardi* in the molecular analysis of Boubli *et al.* (2019), it seems reasonable to conclude that it is part of a separate clade from that of *Plecturocebus parecis* sp. nov.

Genetic distances between the pairs of *Plecturocebus* species ranged from 0.5% to 2.7%. Considering the mitochondrial and nuclear markers separately, the distances recorded for the former were, as expected, greater than those of the latter. In all cases, the smallest distances were recorded between *P. cinerascens* and *Plecturocebus parecis* sp. nov. (Table S1).

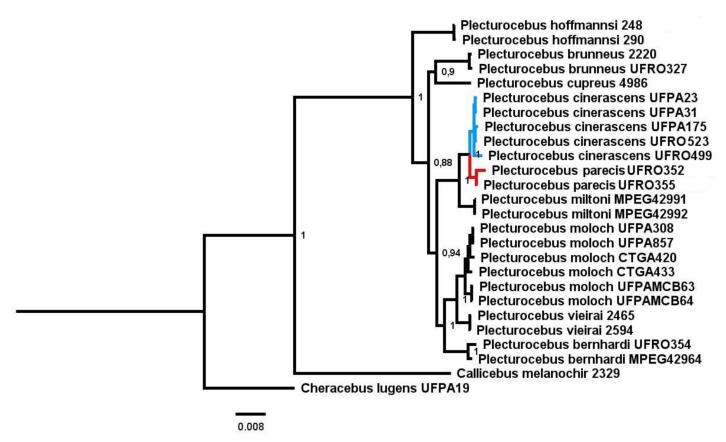


Figure 2. Phylogenetic tree of Bayesian Inference of species of the genus *Plecturocebus*, *Callicebus* and *Cheracebus* included in the present study. Posterior probability values are shown near nodes.

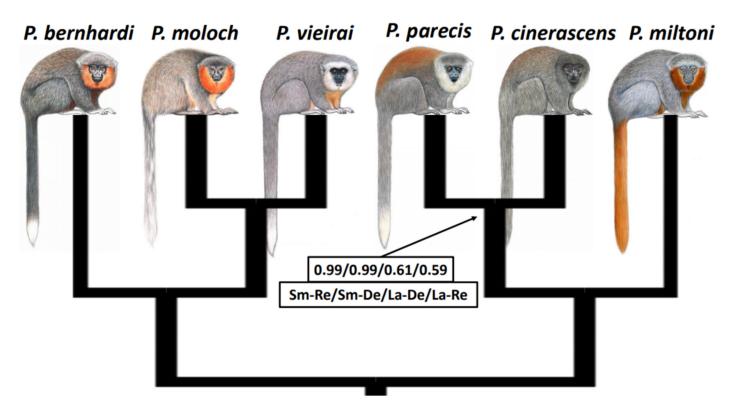


Figure 3. Results of the species delimitation analysis.

Species delimitation analyses were run to verify whether the new species proposed here was recovered in each of the four possible scenarios of population size and divergence time. These analyses included P. moloch, P. bernhardi, P. vieirai, P. miltoni, P. cinerascens, and Plecturocebus parecis sp. nov., which formed a monophyletic group. Two of the scenarios – (i) small population size and recent divergence, and (ii) small population and ancient divergence - indicated that Plecturocebus parecis sp. nov. should be considered a valid species. However, the two other scenarios (large population/recent divergence and large population/ancient divergence) indicated that Plecturocebus parecis sp. nov. is a population of P. cinerascens (Fig. 3). Given this contrast in the potential scenarios, we estimated the θ and τ values for the most recent common ancestor of P. cinerascens and Plecturo*cebus parecis* sp. nov., which were $\theta = 0.00098$ (95% HPD 0.000034 - 0.002385) and $\tau = 0.000035$ (95% HPD 0.000001 -0.000112). These values correspond to scenario (i), that is, small population size and recent divergence time, which supports the recognition of *Plecturocebus paresis* sp. nov. with a probability of 99% (Fig. 3).

While we consider the taxon to be a valid species, it should be noted that the samples used in the molecular study all come from the southwestern extreme of the geographic distribution of the species, and that further samples are needed to expand our understanding of *Plecturocebus parecis* sp. nov. at the molecular level.

Geographic distribution

The geographic distribution of *Plecturocebus parecis* sp. nov. (Fig. 4; Table 1) is still poorly defined. The recorded localities largely coincide with areas of higher elevation in the transition zone between the Amazon Forest and the Cerrado savanna, in southern Rondônia, western Mato Grosso, including part of the Chapada dos Parecis (Parecis Plateau), and the Aripuanã/Juruena and Aripuanã/Roosevelt interfluves. The one exception is the record from Juruena National Park, which is in a relatively low-lying area. This region had previously been considered (Miranda-Ribeiro 1914; Sampaio et al. 2012) to form part of the geographic ranges of P. cinerascens and P. miltoni (see Dalponte et al. 2014). To the northwest, the new species is also found in part of the basin of the Rio Comemoração, where it is replaced by P. bernhardi near the headwaters of the Rio Ji-Paraná. As the ranges of these two species are not separated by a river, it seems likely that the distribution of *Plecturocebus parecis* sp. nov. is limited by ecological factors determined, at least in part, by climatic and ecological variables. A similar situation is found in the western extreme of the range of Plecturocebus parecis sp. nov., where it is substituted by a second species, *Plecturocebus* sp., in the region between the Rio Mequéns Indigenous Lands and the western margin of the upper Rio Pimenta Bueno, which does not encompass any major physical barrier. The cluster of localities west of the Rio Aripuanã (Fig. 4; 10-13) is close to the type locality of the distinct P. miltoni (Dalponte et al.

2014). It is possible that the Rio Branco, a left bank tributary of the Aripuanã (9°45'38.17"S, 59°23'52.64"W) delimits the ranges of the two species there.

Plecturocebus parecis sp. nov. has been observed to the east of the upper Rio Roosevelt, at the Sítio Sírio Libanês, in an area of transition between the Amazon forest and the Cerrado savanna, in the municipality of Vilhena (Rondônia). The northernmost record of the new species is from Juruena National Park, in the Brazilian state of Mato Grosso. The eastern limit of the distribution of Plecturocebus parecis sp. nov. is still unclear, although it seems likely that the species occurs throughout the high plateau of the municipality of Comodoro, in the Brazilian state of Mato Grosso. The limits of the distribution of the new species in relation to that of P. cinerascens also appear to be determined by ecological factors. Sampaio et al. (2012) and Gusmão and Costa (2015) recorded P. cinerascens in the basin of the Rio Guaporé, in the municipality of Pontes e Lacerda, Mato Grosso. In this case, the southern limit of the new species would likely coincide with that of the Parecis Plateau.

Description of the holotype

General pelage coloration of the holotype is grayish agouti, with the dorsal region distinctly reddish chestnut; hands and feet with short whitish gray hairs; ears grayish agouti, lightly hirsute; chin, throat and venter grayish white, darkening to grayish agouti towards the hindlimbs; internal surface of forelimbs grayish white, contiguous with the throat and chin; hair of the forehead light gray, hair tips darkening to gray; tail gray from proximal to median portion, lightening to grayish white in distal portion.

Description of the paratypes

The three paratypes are similar to the holotype in the majority of their morphological traits. They have a generally grayish agouti pelage coloration, with a distinctly reddishchestnut dorsal region; hands and feet lightly covered with short whitish gray hairs; ears grayish agouti, lightly hirsute; chin, throat and venter grayish white, darkening to grayish agouti towards the hindlimbs; internal surface of forelimbs grayish white, contiguous with throat and chin; hair on forehead light gray, hair tips darkening to gray; tail gray from proximal to median portion, lightening to grayish white in distal portion.

Diagnosis

The beard, sideburns, thorax, and anterior portion of the anterior members of *Plecturocebus parecis* sp. nov. are gray-ish-white, as are the hands, feet, and distal portion of the tail (Fig. 5). The general coloration of the new species is dark grayish agouti, in particular on the flanks and external surface of the members (Fig. 1), with a distinctly reddish chestnut-colored dorsal region (Fig. 4). This combination of external

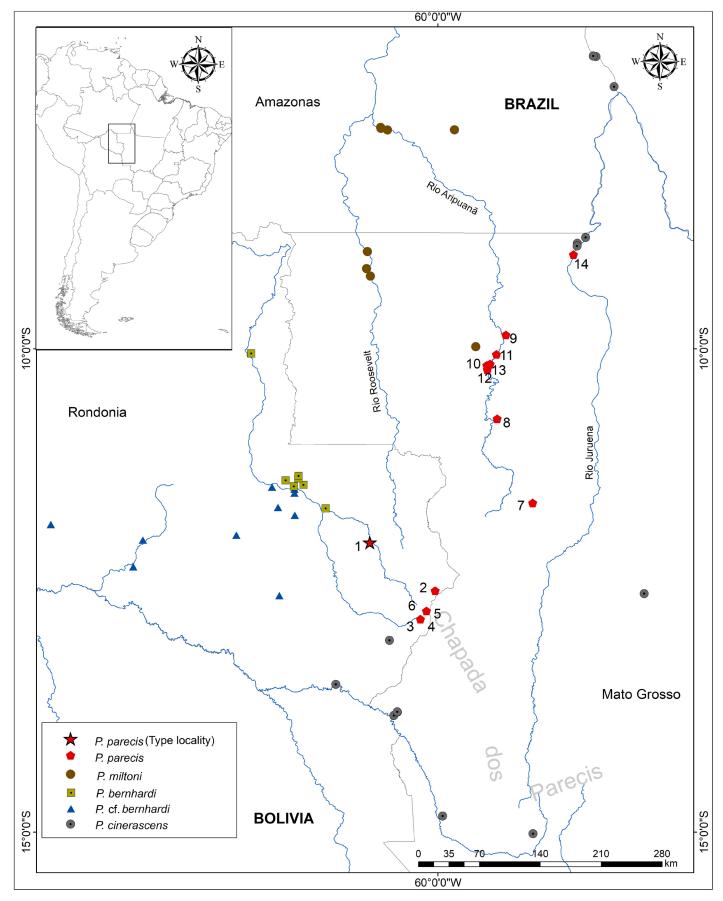


Figure 4. Localities of the occurrence of *Plecturocebus parecis* sp. nov. in southwestern Brazilian Amazonia, numbered as in Table 1 and nearby species.

Table 1. Sampling localities of Plecturocebus parecis sp. nov. in southwestern Brazilian Amazonia, numbered as in Fig. 1.

Site	State ¹	Locality	Latitude	Longitude	Habitat	Observer	Number of individuals (group)	Type of record	
1	RO	Area of influence of UHE Rondon II	12°0.4'41.9"S	60°37'0.34"W	Terra firma forest	TBA	2 adults 1 juvenile 1 infant	Col./Obs.	
2	RO	Sítio Sirio Libanes, Vilhena	12°30'10.09"S	60°1'39.94"W	Terra firma forest	ACG	8 adults 2 juveniles (2)	Obs.	
3	RO	Chacará do Miguel, Setor Chacareiro, Vilhena	12°47'46.46"S	60°10'48.37"W	Gallery forest	ACG	3 adults (1)	Obs.	
4	RO	Urban forest fragment, Vilhena	12°42'41.75"S	60°7'3.68"W	Terra firma secondary forest	ACG	4 adults (1)	Obs.	
5	RO	BR-174, 117 km southeast of Juína	12°05'16.38"S	59°36'45.24"W	Terra firma forest	JCD	3 adults (1)	Obs.	
6	RO	BR 174, 13 km north of Vilhena	12°36'56.7"S	60°08'10.2"W	Terra firma forest	JCD	3 adults (1)	Obs.	
7	MT	BR 174, 9,7 km north of Juína	11°19'55.71"S	58°48'47.97"W	Terra firma forest	JCD	1 adult	Obs.	
8	MT	60 km south of Aripuanã	10°43'28.62"S	59°23'10.01"W	Terra firma forest	JCD	6 adults (2)	Obs.	
9	MT	Fazenda Primavera, 37 km downstream of Aripuanã	9°51'26.17"S	59°17'46.39"W	Terra firma forest	JCD	5 adults (2)	Obs.	
10	MT	Left bank the Rio Aripuanã, downstream of the mouth of the Rio Loreto	10°03'27.18"S	59°23'40.18"W	Terra firma forest	JCD	1 adult	Obs.	
11	MT	Left bank of the Rio Aripuanã, opposite the town of Aripuanã	10°10'18.28"S	59°29'36.34"W	Terra firma forest	JCD	1 adult	Obs.	
12	MT	Left bank of the Rio Aripuană, opposite the town of Aripuană, just SW of the Cachoeira de Dardanelos	10°13'0.1"W	59°29'22.7"W	Terra firma secondary forest	ABR	Numerous groups, adults and juveniles	Obs	
13	MT	Left bank of the Rio Aripuanã, opposite the town of Aripuanã	10°9'27.59"S	59°27'35.63"W	Terra firma forest	ABR	-	Obs.	
14	MT	Parque Nacional do Juruena	09°1'33.56"S	58°36'55.29"W	Terra firma forest	RBA	-	Obs.	

AM = Amazonas; MT = Mato Grosso; RO = Rondônia

²Record type: Col.= Specimen collected; Obs = Observation

morphological traits confers the new species with a unique appearance when compared with all other *Plecturocebus* species.

Comparisons with other species (Table 2)

Plecturocebus parecis sp. nov. can be distinguished from *P. cinerascens* by having the beard, sideburns, throat, breast, and hands grayish-white rather than dark gray. The tail of *Plecturocebus parecis* sp. nov. is also gray with a light gray extremity, in contrast with uniformly dark gray in *P. cinerascens* (Fig. 6).

Plecturocebus parecis sp. nov. can be distinguished from *P. bernhardi* by its general grayish-agouti coloration, and the distinct reddish-chestnut dorsal region in comparison with the uniformly grayish coloration of *P. bernhardi*. The beard, sideburns, throat, breast, and interior surface of the forelimbs of *Plecturocebus parecis* sp. nov. are also grayish white, in comparison with the dark ochre coloration of *P. bernhardi*. The tail of the new species is also light gray rather than black, with a distinct white tip.

The reddish chestnut dorsal portion of the pelage of *Plecturocebus parecis* sp. nov. is also distinct from *P. miltoni*, which has a general gray coloration. The beard, sideburns, throat, breast, and interior surface of the forelimbs of the new species are grayish white, in comparison with orangish chestnut in *P. miltoni*, and the tail of the new species is gray with a white tip, rather than uniformly orangish.

The general grayish agouti coloration of the body of *Plecturocebus parecis* sp. nov. also contrasts with the brownish agouti body of *P. moloch*, and the beard, sideburns, throat, breast, and interior surface of the forelimbs of this species are orangish, rather than grayish white, as in the new species. The tail is similar in the two species, although in *P. moloch*, the distal two-thirds, rather than only the tip, are light gray.

In *P. hoffmannsi*, the beard, sideburns, throat, breast, and interior surface of the forelimbs are yellowish, rather than grayish white, as in *Plecturocebus parecis* sp. nov., and the tail of this species is blackish, rather than gray, with a pale tip.

Plecturocebus parecis sp. nov. can be distinguished from *P. baptista* by its grayish white beard, sideburns, throat, breast, and interior surface of the forelimbs, which are reddish brown

Table 2. Pigmentation patterns of the pelage of 10 species of the genus Plecturocebus.

Character/species		<i>Plecturocebus parecis</i> sp. nov.	P. moloch	P. miltoni	P. cinerascens	P. bernhardi		
1	Crown	wn Grayish agouti		Dark grayish agouti	Dark grayish agouti	Dark grayish agouti		
2	Forehead	Light grayish agouti	Grayish agouti	Dark grayish agouti, with white band contrasting with the crown	te band contrasting			
3	Sideburns	Whitish gray	Light ochre (orange)	Dark ochre	Grayish agouti	Dark red to brown		
4	Dorsum	Reddish brown	Light brownish gray	Dark gray Bownish agouti red		Dark grayish agouti		
5.	Flank	Grayish agouti	Gray to chestnut agouti	Dark gray	Grayish agouti	Dark grayish agouti		
6	Neck, breast, and belly	Whitish gray	Light ochre (orange)	Neck orangish chestnut, breast and belly, orange	Grayish agouti	Dark reddish chestnut		
7	Hands and feet	Whitish gray	Light gray	Grayish-white agouti, contrasting with the members	Grayish agouti	Dark grayish agouti		
8	Limbs (outside	Grayish agouti	Brownish gray	Dark grayish agouti	Grayish agouti	Dark grayish agouti		
9	Limbs (inside)	Whitish gray	tish gray Light ochre (orange) Light ochre (orange) Grayish agouti		Grayish agouti	Dark reddish chestnut		
10	Tail 2/3 grayish agouti, tip whitish gray		Agouti gray base, blackish middle, suede tip	Light ochre (orange)	Grayish agouti	Agouti. Base gray, middle black, tip chamois		
Cha	aracter/species	P. baptista	P. brunneus	P. hoffmannsi	C. vieirai	P. grovesi		
1	Crown	Dark agouti	Yellowish chestnut	Grayish agouti	Light grayish-agouti	Uniform gray agouti		
n	Farahaad	Plack acouti	Dark brown	Gravish agouti	Whistish acouti	Earshead with this black		

1	Crown	Dark agouti	Yellowish chestnut	Grayish agouti	Light grayish-agouti	Uniform gray agouti
2	Forehead	Black agouti	Dark brown	Grayish agouti	Whistish agouti	Forehead with thin black narrow stripe contrasting with gray agouti crown
3	Sideburns	Grayish agouti	Reddish brown	Yellowish agouti	White	Bright red-brown contrasting with light yellow cheek hairs
4	Dorsum	Black agouti	Reddish- or brownish agouti	Grayish agouti	Brownish-gray agouti or chestnut agouti	Bright red-brown contrasting with light yellow cheek hairs
5	Flank	Black agouti	Dark brownish agouti or dark reddish agouti	Grayish agouti	Light chestnut-agouti	Gray agouti, slightly contrasting with external parts of the limbs
6	Neck, breast, and belly	Dark reddish chestnut	Dark brown	Yellowish agouti	Light yellowish to light orange-agouti	Bright red-brown
7	Hands and feet	Black agouti	Darkened	Grayish agouti	Whitish agouti	Dirty white
8	Limbs (outside)	Black agouti	Dark chestnut agouti or dark reddish agouti	Grayish agouti	Light grayish agouti	Gray agouti (lighter than dorsum)
9	Limbs (inside	Dark reddish chestnut	Black to brown or red agouti	Yellowish agouti	Light yellowish agouti	Bright red-brown
10	Tail	Black agouti	Dark reddish agouti, tip light brown	Black agouti	Agouti, base gray; middle black; tip whitish	Black tail, with evident gray-white at the tip

in the latter species. The tail of *P. baptista* is also blackish, rather than light gray.

In *P. grovesi*, the beard, sideburns, throat, breast, and interior surface of the forelimbs are bright reddish brown, rather than rather than grayish white, as in *Plecturocebus parecis* sp. nov., and the tail of this species is blackish, rather than gray. The general grayish agouti coloration of *Plecturocebus parecis* sp. nov., and the grayish white coloration of the beard, sideburns, throat, breast, and interior surface of the forelimbs form a set of traits that distinguish the new species from all the other taxa of the moloch group (*P. aureipalatii*, *P. brunneus*, *P. caligatus*, *P. caquetensis*, *P. cupreus*, *P. discolor*, *P.*



Figure 5. *Plectrocebus parecis* from the forest reserve of the UHE Rondon II hydroelectric plant. Photograph A by Alberto Caldeiras; photographs B, C and D by Manoel Pinheiro, and photographs E and F by Fabiano Mattos.

ornatus, *P. stephennashi*, and *P. toppini*), which all have a dark brown to reddish brown general coloration (Van Roosmalen *et al.* 2002).

Craniometry

The dimensions of the cranium of the new species (Table 3) are broadly similar to those of the other *Plecturocebus* species, although the sample was too small for any systematic statistical comparisons.

Natural history

Plecturocebus parecis sp. nov. has been the subject of two ecological studies at the type locality (Alencar 2011; Mattos 2016). They have shown that the behavior and ecology of the new species are typical of other titis of the genus *Plecturocebus* (see Bicca-Marques and Heymann 2013).

The group studied by Alencar (2011) was formed of a breeding pair and their immature offspring, which engaged in typical territorial behaviors, in particular the characteristic vocal duet at the beginning of the daily activity period. Infants were carried almost exclusively by the breeding male. The study group occupied a small home range, of only 5.5 ha, and had a predominantly frugivorous diet (70% fruit, 20% leaf, 8% insects, and 2% flowers; n = 4060 scan sample records), with the consumption of fruit declining during the dry season, when other items increased in importance.

Mattos (2016) recorded *Plecturocebus parecis* sp. nov. groups of up to six individuals, with a modal size of four. This study also emphasized the importance of ripe fruit pulp, seeds, and arils in the diet of the species, which is typical of *Plecturocebus*.

Conservation

The geographic distribution of *Plecturocebus parecis* sp. nov. coincides with the agricultural frontier known as the "Arc of Deforestation" of southern Brazilian Amazonia (Song *et al.* 2018), which has suffered extensive impacts, in particular from cattle ranching, and soybean and corn plantations (Song *et al.* 2018). The remaining tracts of native forest are also frequently impacted by wildfires, mostly during the dry season, between June and November (Brazil, MCT and MMA 2013). The loss of forest cover in the region has been further promoted by the construction of hydroelectric dams, in particular the UHE Rondon II plant, which has flooded an area of 75 km² (Alencar 2011).

The rural settlements established along the agricultural frontier by agrarian reform projects or by squatters have further contributed to the environmental degradation found throughout the region. Deforestation is especially intense around urban centers in the municipality of Vilhena, where at least three major highways contribute to the modification of the local landscape. These highways also constitute a threat to local wildlife, due to frequent roadkill (Turci and Bernarde

Table 3. Craniometric measurements of *Plecturocebus parecis* sp. nov.Measurements in mm.

Mana	Holotype	Para			
Measure	UFROM 354	UFROM 195	UFROM 352	Mean	
1	0.9	0.8	0.9	0.8	
2	11	11	11	10	
3	20	20	20	19	
4	0.7	0.5	0.5	0.6	
5	32	33	32	32	
6	29	26	26	27	
7	15	13	13	14	
8	13	13	13	14	
9	38	32	32	35	
10	39	38	37	38	
11	31	31	31	37	
12	34	34	33	33	
13	49	45	45	47	
14	33	27	27	30	
15	28	30	30	29	
16	65	62	63	64	
17	31	30	30	32	
18	31	31	31	32	
19	36	34	34	35	
20	40	36	36	37	
21	43	40	41	42	
22	13	12	12	12	
23	40	34	34	35	

2009). Throughout the Brazilian Amazon region, highways contribute to the advance of deforestation and the occurrence of wildfires. Based on the categories and criteria of the IUCN Red List, *Plecturocebus parecis* sp. nov. should be considered Near Threatened because of ongoing habitat loss and fragmentation throughout its range.

There are few protected areas within the known distribution of *Plecturocebus parecis* sp. nov. To the north, the new species may be found in the Apuí (751,295 ha) and Sucunduri state forests (492,905 ha), and it has been observed in the Juruena National Park (1,958,014 ha). Local indigenous reservations, known as Indigenous Lands (Terras Indígenas or TIs), including the Enawenê Nawê (1,603,250 ha) and Roosevelt TIs (230,826 ha), and probably also the Nambikara TI



Figure 6. Plectrocebus parecis sp. nov. and its geographically adjacent species to the east, P. cinerascens, provided by Stephen D. Nash.

(1,012,000 ha), may also play an important role in the conservation of the new species. However, all but the national park are protected areas allowing for sustainable use, and reliable protection of *Plecturocebus parecis* sp. nov. populations will only be possible through the establishment of new, strictly-protected areas for its remaining forests.

Etymology

The species' epithet is a reference to the Chapada dos Parecis, or the Parecis Plateau, where the new species, *Plecturocebus parecis* sp. nov., was found.

Vernacular names

Miranda-Ribeiro (1914) reported that the Parecis people refer to the new species as "otôhô". The non-indigenous residents of the region refer to the new species as "zogue-zogue", the name given to titi monkeys throughout the Brazilian Amazon basin. We recommend the Parecis titi.

Conclusions

The genetic, morphological, and zoogeographic evidence presented here are sufficient to denominate *Plecturocebus parecis* sp. nov., a taxon distinct from *P. cinerascens*, with which it had been synonymized historically (Miranda-Ribeiro, 1914). The findings of the present study indicate a recent speciation process, with *P. cinerascens* as the sister group. Following the recognition of this new taxon, the genus *Plecturocebus* is now composed of 24 species.

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genetic samples, sequenced the material, and ran the statistical procedures. SDN provided the illustrations. ACG, SFF, ABR, JCD, AAB wrote and revised the manuscript; other authors provided editorial advice.

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Appendix – Supplementary material

	Taxa	1	2	3	4	5	6	7	8	9	10
1	P. sp. nova										
2	P. bernhardi	2.1									
3	P. brunneus	2.4	2.3								
4	P. cinerascens	0.5	2.0	2.3							
5	P. cupreus	2.3	2.4	2.1	2.4						
6	P. hoffmannsi	2.9	2.7	2.5	2.7	2.7					
7	C. lugens	8.0	8.0	8.5	8.1	8.2	8.0				
8	C. melanochir	8.1	8.1	8.6	8.1	7.9	8.3	9.1			
9	P. miltoni	1.0	1.9	2.2	0.9	2.2	2.7	8.0	8.0		
10	P. moloch	2.1	1.5	2.2	2.0	2.3	2.5	7.8	8.2	1.9	
11	P. vieirai	2.0	1.5	2.4	2.0	2.2	2.7	7.7	8.3	1.9	0.8

Table S1. Percentages of genetic distances between species examined in the present study.

Material examined at the Mammalogy Laboratory of the Federal University of Rondônia (CRMRO – UNIR), Porto Velho and the Goeldi Museum (Museu Paraense Emílio Goeldi: MPEG), Belém, Brazil.

Plecturocebus parecis sp. nov. RONDÔNIA: UHE Rondon II, municipality of Pimenta Bueno, UFROM 195, 354, 355, 352.

Plecturocebus cinerascens: AMAZONAS: Juruena National Park: MPEG 41235, RONDÔNIA; UFROM 499, 523, Cabixi region (Rio Cabixi, a tributary of the Rio Guaporé).

Plecturocebus miltoni: MATO GROSSO: Curva do Cotovelo, RESEX Guariba-Roosevelt, municipality of Colniza (type locality): MPEG 42654 (holotype); AMAZONAS: Interfluvial region, near the confluence of the rios Guariba and Aripuanã (left bank of the Aripuanã and right bank of the Guariba), Novo Aripuanã: MPEG-42810, 42811, 42812; Left bank of the Rio Aripuanã, mouth of the Igarapé Jatuarana, Novo Aripuanã: MPEG-42991, 42992, 42993.

Plecturocebus bernhardi: AMAZONAS: BR-230 (Humaitá-Itaituba), Km, 17: MPEG 22000; Fazenda Vista Alegre, BR-230, Km 150 (Humaitá-Apuí), right bank of the Rio Marmelos: MPEG 22996; BR-230, Km 164 (Humaitá-Apuí), right bank of the Marmelos: MPEG 22997; RONDÔ-NIA: Calama, right bank of the Rio Ji-Paraná: MPEG 22007.

Plecturocebus baptista: PARÁ: Vila Braga, Rio Tapajós: MPEG 251.

Plecturocebus brunneus: RONDÔNIA: Fazenda Rio Candeias, BR-364, km 28, Porto Velho: MPEG 10941, 10942; Cachoeira Nazaré, Rio Ji-Paraná: MPEG 21353, 21355-56; Samuel Hydroelectric Dam, Rio Jamari, right-bank tributary of the Rio Madeira: MPEG 21686-23035, 35306.

Plecturocebus hoffmannsi: AMAZONAS: Near Parintins: MPEG 250, 690; PARÁ: Rio Arapiuns: MPEG 587; Vila Maripá: MPEG 21444.

Plecturocebus moloch: PARÁ: Serra do Cachimbo: MPEG 38332; Forest of the Igarapé Refuge, Curionópolis: MPEG 38491; São João, Rio Araguaia: MPEG 245; Santarém: MPEG 2396; BR 165 (Santarém-Cuiabá highway): MPEG 12627; BR 165 (Santarém-Cuiabá highway), km 212: MPEG 8122, 8123; Igarapé João Ribeiro, left bank of the Rio Iriri: MPEG 21837; Tucuruí, Sítio Calandrinho, above the dam, left bank of the Rio Tocantins: MPEG 8873, 8874; Luzilândia, near Itaipava, left bank of the Rio Araguaia: MPEG 10932; Luzilândia, Xinguara, left bank of the Rio Araguaia: MPEG 10933, 10939; Marabá, Serra Norte, Carajás, N1, Iron ore mining region: MPEG 10943, 10944, 11843; Marabá, Serra dos Carajás, N2, Manganese ore mining region: MPEG 11832; Saúde, 170 km South of Tucuruí, left bank of the Rio Tocantins: MPEG 12175; Tucuruí, left bank of the Rio Tocantins: MPEG 12311, 12176, 22014-18; Altamira-Marabá highway, Km 18: MPEG 14966, 21442; Itaituba, Igarapé do Patoá, left-bank tributary of the Rio Aruri: MPEG 21972; 54 km S and 150 km W from Altamira, Gleba 61, Lote 02: MPEG 20181; MATO GROSSO: Alta Floresta: MPEG 24590, 24591; RONDÔNIA: Alvorada D'Oeste, BR-429, line 64, Km 87: MPEG 19709-19713.

Plecturocebus vieirai: PARÁ: Upper Iriri-Xingu basin: MPEG 246; Igarapé Mundo Novo, right bank of the middle Rio Iriri: MPEG 21836.

Plecturocebus grovesi: MATO GROSSO: Alta Floresta.