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In search of a meaningful classification for Amazonian marmosets: should dwarf marmosets be considered *Mico* congenerics?

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The criteria to classify the diversity of Neotropical Primates have recently taken the discussion boards due to the reappraisal on the phylogenetic relationship of some groups. Such controversial and arbitrary decisions, however, can hamper conservation actions in as much as it becomes difficult to prioritise and set meaningful targets. It is the case for dwarf marmosets from Central Amazonia. Today, the classification of dwarf marmosets in *Mico* or *Callibella* genus has not been satisfactorily settled. Aiming to contribute to the taxonomic and conservation assessment of dwarf marmosets, we conducted new data collection during 3-year fieldwork in the Aripuanã River, where the species was discovered. We present the first phylogenomic analysis of the evolutionary relationships between marmosets, new data from mitochondrial DNA and morphology, as well new records to clarify geographic distribution. With this new evidence, we support dwarf marmosets as the genus *Callibella*. We further discuss the implications for the conservation of this marmoset.

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Introduction

Since the last two main proposals for the classification of Neotropical primates (Groves 2001; Rylands *et al*. 2000), several new classification schemes at the genus level have been presented for some groups (Byrne *et al*. 2016; Lynch-Alfaro *et al*. 2012a; Rylands *et al*. 2016; Schneider *et al*. 2012). The reason for such debate is primarily rooted in the field of molecular phylogenetics, which, in addition to often unveiling a much greater diversity of lineages than initially suspected, provides a timescale on which this diversification occurred. Consequently, divergence time has been widely adopted as an argument to support the classification of lineages of Neotropical primates, following the proposal of Goodman *et al*. (1998).

However, the use of the divergence time as a key criterion for taxonomic classification in the genus level of Neotropical Primates has been discussed in recent publications (Garbino 2015; Gutiérrez & Marinho-Filho 2017). These authors argue that divergence time, as well as geographic distribution, is not a diagnostic character and should not be used as the sole criterion in the taxonomic classification.

The recent taxonomic reclassifications at the genus level in Neotropical Primates, however, are based on a robust molecular phylogeny that synthesize a number of ecological, morphological and biogeographic parameters previously identified in the studied groups (*see* Alfaro *et al*. 2012, ByrneBuchanan-Smith & Hardie 1997; Hardie & Buchanan-Smith 1997; Heymann 1990, Kobayashi 1995). The most recent proposals were put forward by Byrne *et al.* (2016) for the titi monkeys (formerly the genus *Callicebus*, currently the genera *Callicebus*, *Cheracebus* and *Plecturocebus*), and by Buckner *et al*. (2015) and Rylands *et al.* (2016) for the tamarins (formerly the genus *Saguinus*, currently the genera *Saguinus* and *Leontocebus*).

Byrne *et al.* (2016) reconstructed the phylogenetic relationships of the titi monkeys and proposed a new genus for the *torquatus* species group (*Cheracebus*) and for the *donacophilus* and *moloch* species groups (*Plecturocebus*), retaining only the group *personatus* in the genus *Callicebus* Thomas, 1903. In the same way, Buckner *et al.* (2015) presented a phylogenetic and biogeographical analysis that support the splitting of the large and small-bodied tamarin lineages, proposing the use of a distinct generic name, *Leontocebus* Wagner, 1839, for the *nigricollis* group. Rylands *et al.* (2016) reviewed the taxonomy of the tamarins and supported previous molecular and biogeographic analyses (Buckner *et al*. 2015; Matauschek *et al*. 2011), classifying the small-bodied species (*nigricollis* group) in the genus *Leontocebus* Wagner, 1839 and retaining the large-bodied species in the genus *Saguinus* Hoffmannsegg, 1807.

Although these authors follow an age-driven classification scheme, other parameters were agued to support those proposals such as the differences in morphology and ecology. For example, the widespread sympatry of species of the *nigricollis* and *mystax* groups (Buckner *et al*. 2015; Rylands *et al*. 2016), with members of the two species groups commonly forming mixed groups and using different forest strata to forage (Buchanan-Smith & Hardie 1997; Hardie & Buchanan-Smith 1997; Heymann 1990). In addition, Byrne *et al*. 2016 argue that the morphology—especially cranial morphology, body size and pelage (Hershkovitz 1977; Kobayashi 1995)—and the sympatric distribution of the *torquatus* and *moloch* groups – explained by its ecological differences – also support their classification in distinct genera (Byrne *et al.* 2016).

The taxonomic classification of robust and gracile capuchins is another controversial debate. The variation in size and shape of the body and crania of capuchins supported a taxonomic classification of robust and gracile species in two subgenera (Silva-Jr. 2001), a rank defended by Gutiérrez & Marinho-Filho (2017). Differences in group size, home range, densities and habitat use were identified where gracile (*Cebus*) and robust (*Sapajus*) capuchins are sympatric (Lynch-Alfaro *et al.* 2012a). These morphological and ecological differences of robust and gracile capuchins monkeys (Lynch-Alfaro *et al*. 2012a) agree with the biogeographical analyses presented in Lynch-Alfaro *et al*. (2012b) to advocate placing species of these two groups into the genera *Sapajus* and *Cebus*, respectively. This taxonomic classification was largely adopted thereafter (e.g. Bezerra *et al*. 2014; Martins *et al*. 2015; Robinson *et al*. 2016; Young & Heard-Booth 2016; Fedigan 2017. The divergence time between the *Sapajus* and *Cebus* clades was estimated at 6.2 Ma (Lynch-Alfaro *et al*., 2012b) and the widespread sympatry was explained by a rapid diversification during the Pliocene followed by expansion and invasion by the Atlantic Forest *Sapajus* of the Amazon basin, where currently species of the two genera occur in sympatry (Lynch-Alfaro *et al.*, 2012b).

The Amazon marmosets (*Mico*, *Cebuella* and *Callibella*) remain among phylogenetically least studied Neotropical Primates and the classification of this clade is controversial. In the early 1990s, all marmosets (Atlantic Forest + Amazon) were included in the genus *Callithrix*. However, the first molecular studies of Neotropical primates revealed the pygmy marmoset (*Cebuella*, Gray, 1870) more closely related to the Amazon marmosets (Canavez *et al*. 1999; Chaves *et al*. 1999; Tagliaro *et al*. 1997), than to Atlantic forest marmosets *Callithrix* Erxleben, 1777. Thereafter, (Rylands *et al*. 2000) proposed a classification scheme for Amazon marmosets where *Cebuella* was maintained as a valid monophyletic genus and the genus *Mico* Lesson, 1840, was revalidated for the Amazonian marmosets of the "*argentata* group". The Atlantic marmosets, the "*jacchus* group", were maintained in the genus *Callithrix*.

van Roosmalen *et al*. (1998) described a "new and distinctive" dwarf marmoset (*Callithrix humilis*) based on the external morphology of an adult male kept as a pet. Since the description of van Roosmalen *et al.* (1998), the classification of this diminutive marmoset is under debate. The first change in classification came about from the proposal of Rylands *et al.* (2000) with the species reclassified as *Mico humilis*. Three years later, van Roosmalen & van Roosmalen (2003) analysed two additional individuals, and for the first time assessed the phylogenetic relationship of *M. humilis* to other Amazonian marmosets using the mitochondrial control region. The authors concluded that these three dwarf marmosets were distinct enough from *Mico* and *Cebuella* to justify placing them in their own genus: *Callibella*. In the meantime, Aguiar & Lacher (2003) presented a craniometric analysis to reinforce the distinctiveness of dwarf marmosets and to support the classification of *M. humilis* in the genus *Callibella*.

Groves (2001, 2005) adopted an age-related molecular classification based on Goodman *et al.* (1998) and included *Mico*, *Cebuella* and *Callithrix* and *Callibella* as subgenera of *Callithrix*. Rylands *et al*. (2009) kept *Callibella* as a genus, following the criteria proposed by Rylands *et al.* (2000) where *Cebuella* and *Mico* were recognised as distinct genera. Recently, Schneider *et al*. (2012) combined the mitochondrial control region with four nuclear regions containing *Alu* elements and argued that dwarf marmosets are *Mico* congenerics. Garbino (2015a) also supported the classification of dwarf marmosets as *M. humilis* based on an phylogenetic analysis of a morphological data set.

In fact, the genus-level classification of *Callibella humilis* was based on little material available for analysis and little information from the field. Almost two decades after its description, the classification of dwarf marmosets remains controversial. Here, we presented the first phylogenomic assessment of evolutionary relationship among Amazonian marmosets' genera and a reappraisal of the classification of dwarf marmoset arguing for the use of the genus *Callibella*. We included an entirely new dataset obtained thorough fieldwork, and present the following information in our analysis: (1) skull morphology, (2) body-size, (3) updated geographic distribution and the overlap to *Mico marcai*. In addition, we provided an important start point for its conservation assessment based on threats and phylogeny by calculating its EDGE score (Isaac *et al.* 2007).

Material and Methods

Surveys

In this study, we conducted five field expeditions between January 2012 and February 2015 in the Marmelos–Aripuanã interfluve (Fig. 1). Data collections were carried out using existing trails. We recorded the number of individuals sighted, and if the dwarf marmosets were associated with other primates. In 2015, we opened 10 transects in upland forests with an average length of 3.07 ± 0.63 km and 1 m width keeping a minimum distance of 2 km between adjacent transects. We placed the transects randomly in the study areas, totalling an effort of 271.6 km surveyed. The transects were travelled twice a day by two observers moving at a speed of 1.5 km/h, during the early morning from 7 to 11hs, and the afternoon from 14 to 17hs. We defined an interval of two paused days after travelling each transect to reduce the impact of the observers' presence on the primates' behaviour. When a group of marmosets was detected, we counted the number of individuals to estimate the encounter rate. We present new records of dwarf marmosets (*C. humilis*) and compare the sighting rate with the sympatric Marca's marmoset (*Mico marcai*). Finally, we estimate the extent of occurrence based on the new data collected in this study.

Morphometrics

We examined 104 specimens (skins and skulls) from scientific collections, including 16 specimens recently collected in a broad study of the taxonomy, biogeography and conservation of marmosets from Aripuanã River basin (Silva *et al.* 2013) (permit SISBIO numbers 13507 and 6493-1). For each collected specimen, we recorded sex, age category, body mass and standard mammalian measurements (head-body length, tail, foot and ear) in the field. The specimens were stored in the mammalian collection of the Museu Paraense Emílio Goeldi (MPEG), Belém, Brazil.

Only adult specimens, determined by the complete erupted dentition and by the complete fusion of the spheno-occiptal and spheno-ethmoidal sutures, were used for craniometrics. We used digital callipers (precision 0.01 mm) to obtain craniometric variables following (Hershkovitz 1977). We analysed the data using a Principal Component Analysis in R 3.3.3 (R Core Development Team 2017). This analysis captures the multidimensionality of the cranium measurements and reduces it into few principal components, i.e., axis. Here we used the first two axes to represent the cranium metrics of specimens in two dimensions to test if there are discrete morphological groups that correspond to the different marmosets genera. Additionally, we present an anatomical description of the skull of *C. humilis* and compared with its sympatric Marca's marmoset (*M. marcai*).

Molecular analyses

For molecular phylogenetic analyses, we extracted whole genomic DNA from tissue samples using standard phenol-chloroform extraction protocol of Sambrook *et al.* (1989). We amplified the complete mitochondrial cytochrome b gene by polymerase chain reaction (PCR) with the primers MonkeyGluF1 (5'-

CCATGACTAATGATATGAAAARCC-3') and MonkeyProR1 (5'-AGAATSTCAGCTTTGGGTGTTG-3') (Boubli *et al.* submitted). PCR products were purified using ExoSap (Werle *et al*. 1994) and subjected to fluorescent dye-terminator (ddNTP) sequencing following the manufacturer's recommended protocol for BigDye sequencing chemistry (Applied Biosystems) and using the primers MonkeyCytbF2 (5'-GGATCAARYAAYCCRTCAGG-3'), MonkeyCytbR1 (5'-GCBCCTCAGAADGATATTTG-3') and MonkeyCytbR2 (5'-CGTAGRATTGCRTATGCRAA-3') (Boubli *et al.* submitted). Subsequent to the cycle sequencing reaction, the products were precipitated with 100% Ethanol / 125 mM EDTA solution, resuspended in Hi-Di formamide, and resolved on an ABI 3130xl automatic sequencer (Applied Biosystems). Sequences were assembled, edited, aligned and trimmed using the software Geneious v8.1.8; alignment was done using MUSCLE (Edgar 2004) plugin and conferred visually.

We also performed a partial representational genome sequencing using the double digest RAD sequencing protocol (ddRAD) (Peterson *et al*. 2012). The standard protocol was adapted to allow simultaneous digestion and adaptor ligation, and for use on the IonTorrent PGM (https://github.com/legalLab). Briefly, 200 ng of genomic DNA of each individual was digested with SdaI and Csp6I restriction enzymes (Fermentas) and the IonTorrent P and A adapters were linked to the digested fragments, all in one step. The fragments were enriched via PCR. The A adaptor is a "Y divergent" (Coyne *et al.* 2004), resulting in the enrichment of only those ddRAD fragments with one P1 and one A adaptor. Furthermore, the A adaptor contains a unique molecular barcode for identification of individuals. Following the PCR enrichment, we selected fragments in the range of 320 to 400 bp using the Pippin Prep (Sage Science). Based on the analysis of *complete* primate genomes deposited in Genbank, we expected to observe ~ 12,000 ddRAD fragments in the range of 320 to 400 bp. This information was then used to optimise the number of individuals to be analysed in each run of the IonTorrent PGM. The complete ddRAD protocol, scripts for estimating the number of ddRAD fragments in a given size range, and scripts for extracting ddRAD fragments from published genomes are available on GitHub (https://github.com/legalLab).

To construct our phylogenetic trees we included fresh or dried tissues from *C.*

humilis (n=2 [5]), *Cebuella* cf. *niveiventris* (n=1), *Cebuella* aff. *pygmaea* (n=1), *Mico argentatus* (n=1), *M. humeralifer* (n=1), *M. intermedius* (n=1), *M. marcai* (n=1), *M. mauesi* (n=1) and *Callithrix jacchus* (n=1); *Callimico goeldii* (n=1) and *Saguinus bicolor* (n=1) were included as outgroups. For mitochondrial DNA analyses, we collected 1140 bp of the cytochrome *b* gene. For phylogenomic analyses, we analysed 340,593 nucleotides representing 1063 loci. Bayesian time tree was estimated in the program BEAST v2.4.2 (Drummond *et al*. 2012) via constraining the divergence of *Saguinus bicolor* from the callithrichid clade at 14.89 mya, and *Callimico goeldii* from other callithrichids at 10.68 mya. We assumed normally distributed secondary calibrations, with means and standard deviations of divergence times obtained from (Perelman *et al.* 2011). We also estimated phylogenetic relationships within the maximum likelihood framework implemented in RAxML (Stamatakis 2014), and the Bayesian framework implemented in ExaBayes (Aberer *et al*. 2014).

EDGE analyses

Evolutionary Distinct, Globally Endangered (EDGE) analyses (Isaac *et al.*, 2007) were carried out using a custom script written in the statistical language R (R Core Development Team 2017). We calculated the evolutionary distinctness (ED) score using the ecol.distinct function in the package picante (Kembel *et al*. 2010) with the ddRADseq phylogeny estimated in BEAST as input. EDGE scores for each taxon were then calculated using formula (1) of Isaac *et al.* (2007) and the current Red List extinction risk category of each taxon.

Results

Surveys

We detected nine groups of *C. humilis* with a total of 18 individuals (mean=2.0 indviduals/group, sd=1.12). The number of individuals sighted per group ranged from 1 to 5 and the estimated encounter rate was 0.033 groups/km and 0.066 individuals/km.

Comparatively, the number of sighted individuals per group of the sympatric *Mico marcai* ranged from 1 to 11 (mean=4.56 individual/group, sd=2.42, N=41), in an encounter rate of 0.11 groups/km and 0.50 individuals/km. Both species were found travelling together on two situations; however, it is unclear if the they forage in mixed groups. We had three other occasional records of *Callibella humilis* in this area. The localities where we found the dwarf marmosets represent a range extension of its distribution (Fig. 1). On the left bank of Aripuanã River, we recorded the species close to the mouth of Roosevelt River (see Garbino *et al*. 2013) in a secondary forest limited by cassava crops. On this occasion, FES was looking for evidence of *Mico marcai* using a recording of long calls of *Mico emiliae.* An adult male of *C. humilis* came straight toward the researcher, while issuing long calls. The other sightings in this region were in a secondary forest between the lower Roosevelt River and the BR-230 Transamazonica highway. We also recorded *C. humilis* on the both banks of the lower Manicoré River (Fig. 1). Our records thus, extend the range of *C. humilis* to the left bank of Manicoré River, but further surveys will clarify its presence throughout the interfluve Manicoré-Marmelos. We have no records of the species south of the Campos Amazônicos National Park, but further surveys in the south of this region will clarify if, in fact, the savanna vegetation of this region delimits the southern occurrence of this species (see Garbino *et al.* 2013). The extent of occurrence was estimated in 29,164km^2.

Morphological analyses

Principal Component Analysis of the 11 craniometric characters clearly differentiates the three genera of Amazon marmosets – *Cebuella*, *Callibella*, and *Mico* – from each other (Fig. 2, Table S1). The first two components explained 96.5% of the total variation of the data, with most of this variation explained by the first axis (95.4%). Each cluster contains only allopatric species. The sympatric *Callibella* and *Mico* are clearly discriminated along the first principal axis of the morphospace, while less differentiation is evident between the allopatric *Callibella* and *Cebuella* along both the first and second principal components (Fig. 2, Table S2). The species of the genus *Mico* broadly overlap in morphospace (Fig. 2), therefore, the majority of variance in shape and size is partitioned between the genera *Callibella* and *Mico* rather than among species within the genus *Mico*. Comparison of specific features of skull anatomy of *Callibella humilis* and *Mico marcai*, two sympatric marmosets, therefore reflects differences in anatomical features of the supraspecific taxa *Callibella* and *Mico* (Fig. S1).

The surface of the parietal bone of *M. marcai* has a lower convexity, especially in the areas of the occipital and frontal angles, giving a flatter appearance (Fig. S1). In *Callibella*, a muscular line clearly delimited the middle third of the surface of the parietal bone. This line is positioned in a caudal-rostral direction, being continuous and rougher in the frontal bones (Fig. S1). In both species, a temporal line reaches the super ciliary arch marking the point of insertion of the temporalis muscle (Fig. S1). This muscle is smaller in *Callibella*, cover approximately 2/3 of the parietal bone and a small portion of the lateral surface of the frontal bone. In *Mico marcai*, the same muscle occupies virtually the entire parietal bone and nearly half the lateral-dorsal surface of the frontal bone. The external occipital protuberance, positioned in the middle third of the occipital bone, is wider and prominent in *M. marcai* and more longilineus laterally in *Callibella* (Fig. S1).

Molecular analyses

In the time tree phylogenomic analyses, *Callibella* and *Mico* were sister taxa with 100% posterior probability and an estimated 2.37 mya divergence; the age of the root of *Mico* was estimated at 1.30 mya (Fig. 3). Similarly, in the analyses of the mitochondrial cytochrome b gene, *Callibella* and *Mico* were sister taxa with 100% posterior probability and an estimated 2.33 mya divergence; the age of the root of *Mico* was estimated at 1.05 mya (Fig. S2). The same set of highly supported relationships were observed in the maximum likelihood (RAxML) and Bayesian inference (ExaBayes) analyses. The cytochrome b and ddRADseq analyses differed in the relationships of species of the genus *Mico*, however, the sister taxon relationship of the discordant individual–*M. intermedius* FES09–to the clade comprising *M. humeralifer* and *M. mauesi* is poorly supported.

EDGE analyses

The Evolutionary Distinct, Globally Endangered (EDGE) score (Isaac *et al.*, 2007) for *Callibella humilis* was 3.30, while EDGE scores for species of the sister genus *Mico* varied from 0.80 to 1.05. Only *Callimico goeldi* had a greater EDGE score at 4.70.

Discussion

The criteria for the classification of Amazon marmosets

The divergence times estimated for the three Amazon marmosets clades is smaller than the majority of intergeneric divergences in Neotropical primates (Goodman *et al.*, 1998; Lynch-Alfaro *et al.*, 2012a; Byrne *et al.*, 2016; Rylands *et al.*, 2016). *Callibella* diverged from *Mico* approximately 2.3 Mya, while the main in-group diversification of the extant *Mico* species was estimated in 1.3 Mya. However, the estimated 1 million years separating the divergence of *Callibella* and *Mico* ancestors, and the beginning of diversification of *Mico*, together with morphological differences between them—both in size and shape—reinforce the distinctness of *Callibella*.

Callibella humilis has a much smaller and lighter body than in *Mico* species and only slightly larger and heavier than *Cebuella pygmaea*, the smallest Neotropical Primate (see Table S2). In addition, *Callibella humilis* also live in smaller social groups and apparently has a lower densities when compared with its sympatric *Mico marcai*. In primates, differences in morphology are associated with differences in resource use, i.e. morphology reflects niche use (ecomorphology) (Rosenberger 1992; Bicca-Marques 1999; Meloro *et al*. 2013). While niche occupation of *C. humilis* and *M. marcai* remains largely uncharacterized—both species are widely sympatric—their sympatry must be made possible by minimal realised niche overlap. Similarly to other Neotropical Primates currently classified as different genera (e.g. *Leontocebus* and *Saguinus*; *Cheracebus* and *Plecturocebus*), character displacement minimising realised niche overlap, and thus interspecific competition, would be a process that reinforces the divergence between *Callibella* and *Mico*.

Since the late 1990's, the classification of marmosets has been in flux, in part due to lack of or conflicting phylogenetic hypotheses, and in part due to differing philosophical approaches to classification. In 1998, *C. humilis* was described as a species of the genus *Callithrix*. This was prior to the proposal by Rylands *et al.* (2000) that the generic name *Mico* is used for Amazonian marmosets found east of the Madeira River, and that the pygmy marmosets found west of the Madeira River be placed in the genus *Cebuella* (Tagliaro *et al.* 1997; Canavez *et al.* 1999; Chaves *et al.* 1999). In 2003, van Roosmalen and colleagues reanalysed the data of Tagliaro *et al.* (1997) including sequence data of "*Callithrix*" *humilis*. "*Callithrix*" *humilis* was found to be the sister taxon to the genera *Cebuella*+*Mico*, thus the authors reclassified "*Callithrix*" *humilis* in the genus *Callibella*. The primatological community largely did not follow this new classification, culminating with an analysis of mitochondrial and nuclear DNA data by Schneider and colleagues in 2012. Schneider *et al.* (2012) then argue for the inclusion of *C. humilis* in the genus *Mico*, to which it was sister, based on an estimated time of divergence of slightly less than 2.5 my between *C. humilis* and other species of the genus *Mico*, which is more recent than the age of the root of diversification of the genera *Callithrix*, or *Saguinus*. This argument effectively follows the proposal of Goodman *et al.* (1998), who suggest that taxa sharing a last common ancestor less than 4 mya should be classified as members of the same genus.

However, strict divergence time-based criteria, such as that proposed by Goodman *et al.* (1998), do not convey any other information besides divergence time. We are of the opinion that the genus can and should convey other evolutionary information such as morphological and/or ecological divergence/distinctness, and as such become the first identifiable entities in biodiversity studies (Dubois 1988; Vences *et al.* 2013). Vences *et al.* (2013) pointed out that the attempts to fit inherent biological meaning for taxa of the same supraspecific Linnaean ranks are unrealistic; instead, only species can be considered equivalent to each other because they correspond to the same level of biological organisation. The authors then suggest that an adopted classification scheme should also bring the information that will facilitate the communication between scientists and between those and the lay public.

The generic name is an irreplaceable part of the Latin binomial attributed to all species in the Linnaean binomial, being the first identifiable entity (Dubois 1988; Vences *et al*. 2013). The few publications on the genus concept (Lemen & Freeman 1984; Dubois 1988; Garbino 2015b; Talavera *et al*. 2013) in contrast to the vast body of literature focusing on species and species concepts indicate how imperative is the discussion of a classification system that best conveys the evolutionary history of a higher-level taxon.

Thus while the *Callibella* and *Mico* lineages began to diverge at approximately 2.3 mya (Fig. 3), which is less than the minimal 4 my divergence suggested for the diverge of genera by Goodman *et al.* (1998), the *Callibella* and *Mico* lineages are morphological and ecologically distinct and divergent. The molecular phylogeny in line with the morphological and ecological distinctions supported the classification in different genera of previously congeneric species occurring in sympatry (Byrne *et al.* 2016; Lynch-Alfaro *et al*. 2012a; Rylands *et al.* 2016). In Neotropical primates, sympatry occurs between species belonging to different genera, where species of the different genera are characterised by different morphologies and different ecological requirement (Rylands 1989; Ferrari & Martins 1992). Our morphological analyses support the findings of Aguiar & Lacher (2003, 2009) in that *C. humilis* is divergent and distinct from species of the genus *Mico*. As such, the sympatric distribution between *C. humilis* and *M. marcai* is probably possible due to differences in their realised niche, as found in other Neotropical Primates recently classified in different genera (Byrne *et al.* 2016; Lynch-Alfaro *et al*. 2012a; Rylands *et al.* 2016). However, several issues should be investigated to clarify this assumption, such as feeding ecology, home range, use of the forest strata and formation of mixed-species group. Considering this evidence, and adhering to the school of though that genus should convey information on the evolutionary history in the higher-level taxon, we propose the following classification for the marmosets:

1 – *Callibella* van Roosmalen and van Roosmalen, 2003: as a monotypic genus occurring east of the Madeira River in the Marmelos-Aripuanã interfluve, its area of occurrence apparently being entirely within the distribution area of *Mico marcai*.

2 – *Mico* Lesson, 1840: with 13 valid species occurring east of the Madeira River in the Madeira-Tocantins interfluve, with *M. melanurus* also occurring in the Bolivian basin (headwaters of the Madeira River).

3 – *Cebuella* Gray, 1823: a monotypic genus occurring west of the Madeira River. *Cebuella pygmaea* is morphologically similar to *C. humilis* (Fig. 2) and is sister to the *Callibella*+*Mico* clade having diverged from the ancestor of this clade at approximately 4.3 mya (Fig. 3).

4 – *Callithrix* Erxleben, 1777: with six valid species, all occurring the Atlantic Rainforest. Species of *Callithrix* are morphologically similar to those of *Mico* (Fig. 2). *Callithrix* is the sister taxon to the clade comprising the three Amazonian genera (*Callibella*, *Mico* and *Cebuella*), and diverged from them approximately 4.9 mya (Fig. 3).

The Conservation of dwarf marmosets (<u>Callibella humilis</u>)

Our field surveys revealed that dwarf marmosets are not restricted to a tiny area between the mouths of Aripuanã and Manicoré Rivers as argued by van Roosmalen *et al.* 2003). These primates can be found further west, on the left bank of the Manicoré River, and further south, on the left margin of lower Roosevelt River. Our surveys point to a complete overlap of the distribution of *C. humilis* and *M. marcai* (Silva *et al.* in prep.), with an extent of occurrence at least ten times as large as the area suggested by van Roosmalen & van Roosmalen (2003).

Callibella humilis was confirmed in only two legally protected areas: Juma Reserve of Sustainable Development and Campos Amazônicos National Park. The first has 590,000 ha, delimiting an area on both banks of the Aripuanã River; however, the species is presented only in the sector of the left bank of Aripuanã River. The second protected area in Aripuanã-Marmelos interfluve is the Campos Amazônicos National Park, but just a small northern portion of this park encompassed the dwarf marmoset's distribution. Most of the vegetation in that region is composed of open Cerrado patches with *Campinaranas*—a dense low canopy forest grown over weathered sandy soils. It is unlikely that *C. humilis* will occur in this habitat, thus the northern portion of the

Campos Amazônicos National Park most likely represents the southern distributional limit for *C. humilis*.

Assessing the conservation status of *C. humilis* is a challenge, although an imperative matter that urges at least two stages: systematic surveys and threat assessment. The only indirect inference of its population was provided by van Roosmalen and van Roosmalen (2003) based on the home range size and group size. However, in our surveys, the difficulty to sighting the species in the dense forest because of its diminutive size and cryptic behaviour resulted in the low encounter rate of *C. humilis* (0.066 individuals/km). We suggest, therefore, the use of combined methods, especially linear transects and playbacks, to increase the number of sightings of dwarf marmosets in the wild (Plumptre *et al*. 2013; Gestich *et al*. 2016) to get a reliable estimate of its abundance and density.

In the last IUCN assessment (2015, http://dx.doi.org/10.2305/IUCN.UK.2015-1.RLTS.T41584A70616233.en), *Callibella humilis*—listed as *Mico humilis* apud Schneider *et al.* (2012)—was evaluated as Vulnerable D2. The Conservation status of *Callibella humilis* was considered as Least Concern in the national assessment under the justification that there is no evidence of any major threats (Röhe 2015). In our opinion, the arguments for listing *C. humilis* as Least Concern does not reflect the real conservation status of the species, or are, at least, premature. We defend a careful categorization based on further population and occurrence data. Considering the current IUCN category for *Callibella humilis*, its EDGE score (3.30) is the second highest ranked for Amazonian primate after *Callimico goeldii*, with only 18% of all other mammals having higher EDGE score. *Callibella humilis* is a unique taxon as manifested by its phylogenetic uniqueness and its morphological distinctness. As such, the species and its habitat are worthy of focused conservation efforts.

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Figure and Tables legends

Fig. 1 The records of *Callibella humilis* in the literature and in this study. The dark grey area is the estimated geographical range of the species considered in the last assessment of the conservation status.

Fig. 2 Plots of scores for the first two principal components from principal component analysis of cranial variables in Callitrichinae.

Fig. 3 Phylogenomic trees obtained through maximum likelihood and Bayesian inference of nuclear DNA (DDRadseq) from *Callibella*, *Mico*, *Callithrix* and *Cebuella* species. Each external branch represents an individual and the support probability value is given on each branch.

Table S1 Scores and contributions of each cranial variable in the first two principal components of a principal component analysis of Callitrichinae

Table S2 A comparison of mean measurements recorded for *Callibella humilis* and *Mico* sp. with values available for marmosets from previous studies.

Fig. S1 Anatomical comparison of the skull of *Callibella humilis* (right) and its sympatric Mico marcai (left) skull.

Fig. S2 Phylogenetic trees obtained through maximum likelihood and Bayesian inference from Cytochrome b sequences of *Callibella humilis*, *Mico* spp. and *Cebuella pygmaea*. Each terminal branch represents an individual and the support probability value is given on each branch.

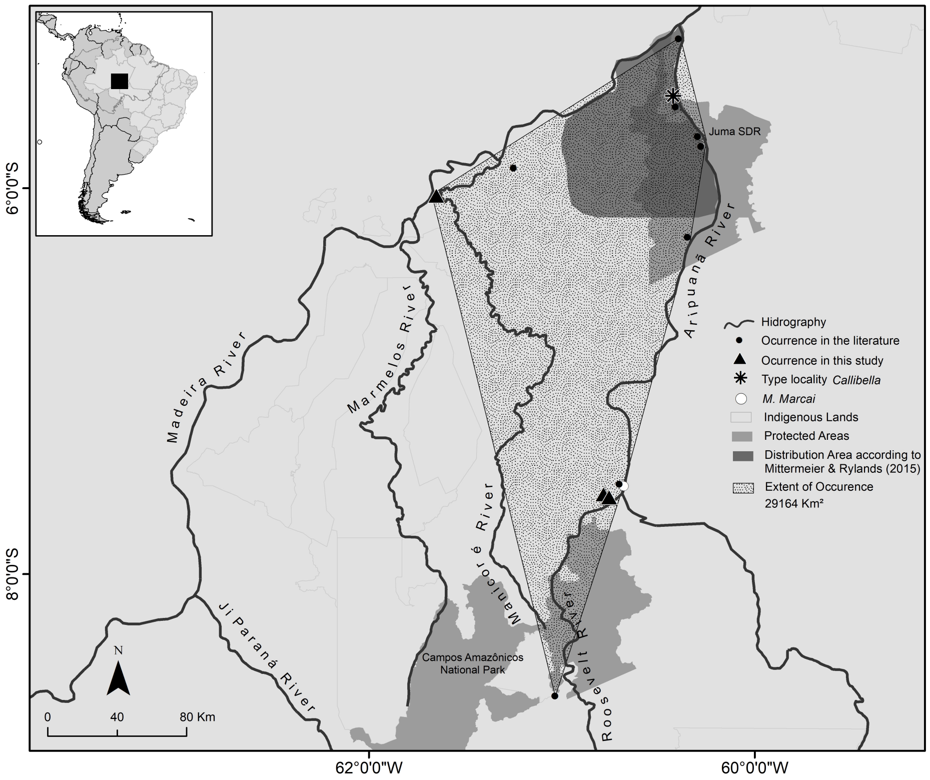
Juma SDR
Aripuanã River
Madeira River
Marmelos River
Manicoré River
Roosevelt River
Ji Paraná River
Campos Amazônicos National Park
Hidrography
Ocurrence in the literature
Ocurrence in this study
Type locality Callibella
M. Marcai
Indigenous Lands
Protected Areas
Distribution Area according to Mittermeier & Rylands (2015)
Extent of Occurence 29164 Km²
N
0
40
80 Km
6°0'0"S
8°0'0"S
62°0'0"W
60°0'0"W

Figure 1.

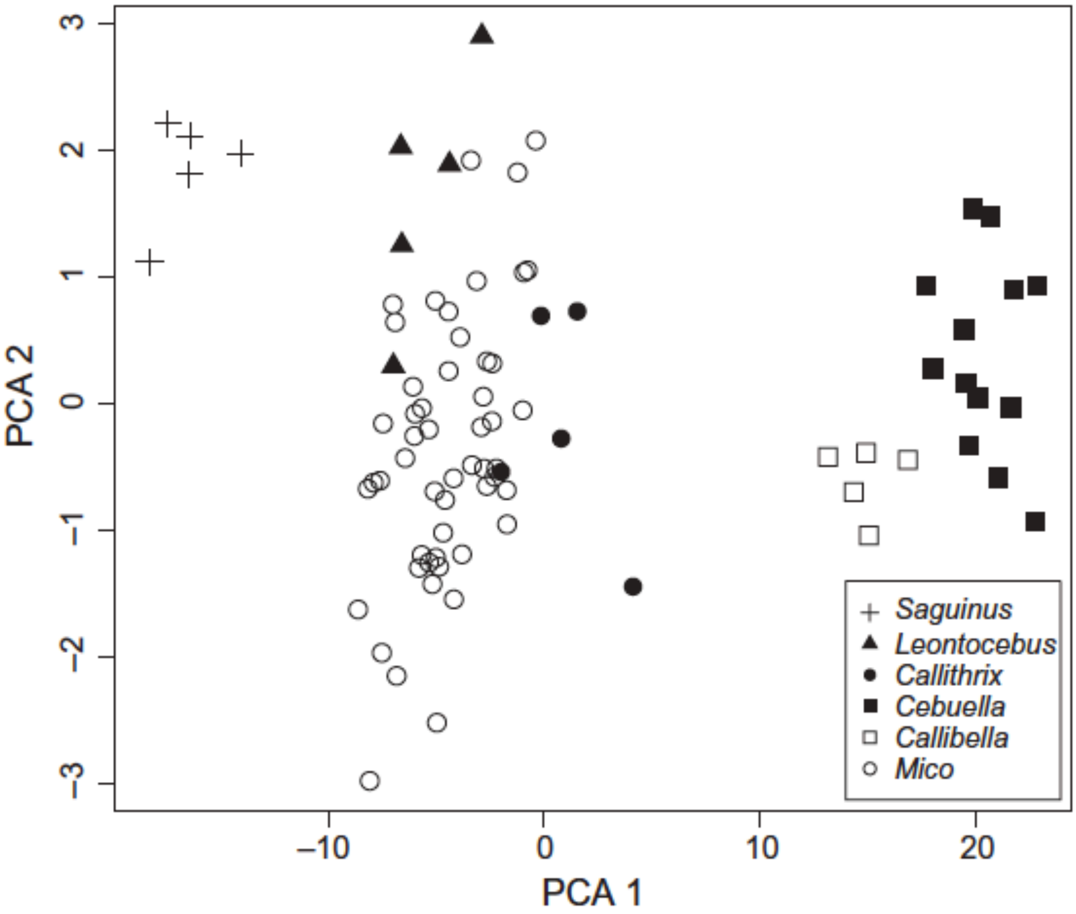
PCA 2
PCA 1
3
2
1
0
−1
−2
−3
−10
0
10
20
+ Saguinus
▲ Leontocebus
● Callithrix
■ Cebuella
□ Callibella
○ Mico

Figure 2

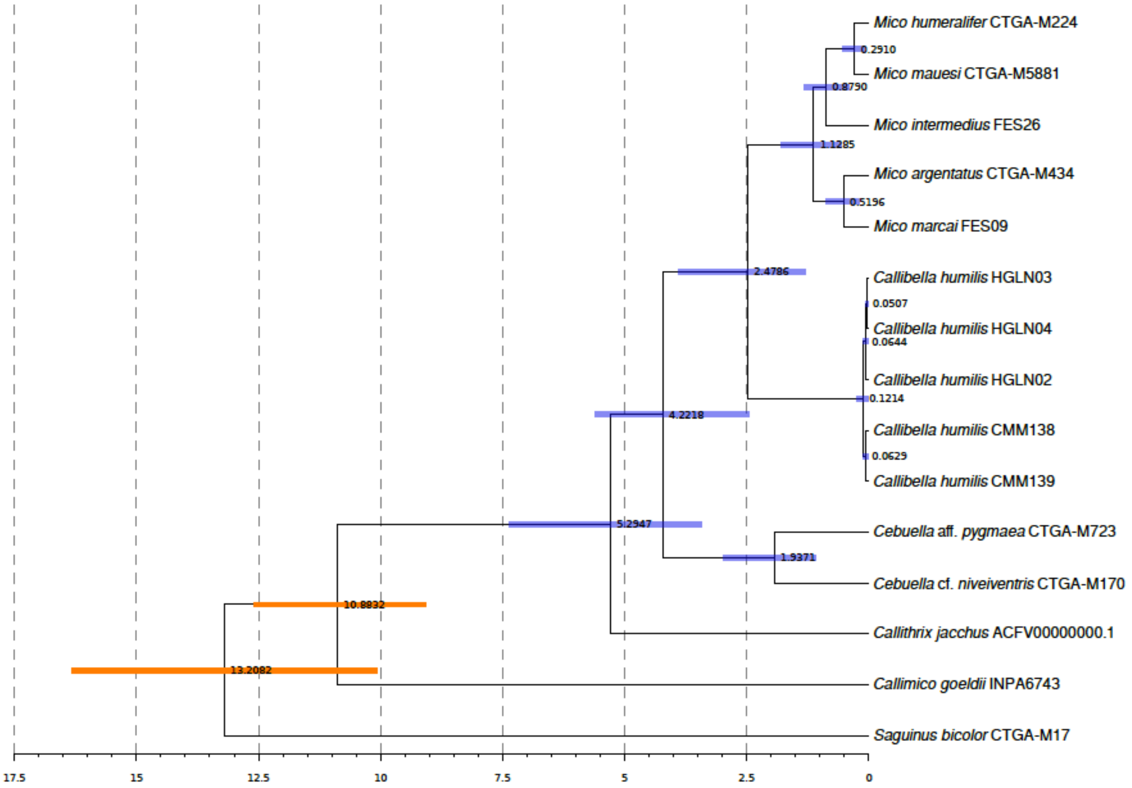
Mico humeralifer CTGA-M224
0.2910
Mico mauesi CTGA-M5881
0.8790
Mico intermedius FES26
1.1285
Mico argentatus CTGA-M434
0.5196
Mico marcai FES09
2.4786
Callibella humilis HGLN03
0.0507
Callibella humilis HGLN04
0.0644
Callibella humilis HGLN02
0.1214
4.2218
Callibella humilis CMM138
0.0629
Callibella humilis CMM139
5.2947
Cebuella aff. *pygmaea* CTGA-M723
1.9371
Cebuella cf. *niveiventris* CTGA-M170
10.8832
Callithrix jacchus ACFV00000000.1
13.2082
Callimico goeldii INPA6743
Saguinus bicolor CTGA-M17
17.5
15
12.5
10
7.5
5
2.5
0

Figure 3