
















Molecular systematics of tamarins with emphasis on genus *Tamarinus* (Primates, Callitrichidae)

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Abstract

The genus *Saguinus* comprises three principal clades that diverged in the Middle to Late Miocene. Their taxa are ecologically differentiated and allopatrically distributed. These clades were recently recognized as different genera, *Saguinus*, *Tamarinus* and *Oedipomidas*. In *Tamarinus*, the phylogenetic relationships among

Gerson Paulino Lopes and Fábio Rohe first two authors should be regarded as joint first authors.

We dedicate this paper to Professor Marcelo Menin, our friend who passed away in January 2021. He was a valued mentor, colleague, and a friend to many of the authors of this paper, all of whom were privileged for having been part of the enormous legacy that Prof. Menin leaves behind and will always remember him as a world class scientist, and a passionate admirer and lover of amphibians.

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species/subspecies are poorly understood. Thus, in this study we present a comprehensive dated genomic phylogeny based on double digest restriction associated DNA for all known species and subspecies of *Tamarinus*. We also tested whether that *Tamarinus imperator* and *Tamarinus subgriseus* are different species, as morphology-based taxonomy, phenotypical divergences and mitochondrial genes recognized them as two different species. Additionally, we reconstructed time-calibrated phylogenetics tree hypotheses of all extant species and subspecies of the genera *Saguinus*, *Tamarinus* and *Oedipomidas*. Our analysis robustly supported the phylogenetic hypothesis of all species/subspecies of the genus *Tamarinus*; strongly supported a divergence between the three clades, *Saguinus*, *Oedipomidas* and *Tamarinus*; and provided support for *T. imperator* and *T. subgriseus* as distinct species. Therefore, we reiterate and ratify the division of *Saguinus* into three genera, supporting the taxonomic proposal for these genera.

KEYWORDS

Divergence times, Genera, Neotropical Primates, Phylogeny

1 | INTRODUCTION

The Neotropical family of primates Callitrichidae includes marmosets, callimicos, lion tamarins and tamarins, the smallest and morphologically most distinct Neotropical primates (Hershkovitz, 1977; Rylands & Mittermeier, 2013; Rylands et al., 2000). The callitrichids range from Panama to southern Brazil (Hershkovitz, 1977), and currently are classified in 10 genera: the marmosets: *Callithrix* Erxleben, 1777, *Mico* Lesson, 1840, *Cebuella* Gray, 1866, and *Callibella* van Roosmalen & van Roosmalen, 2003; callimicos: *Callimico* Miranda-Ribeiro, 1911; the lion tamarins: *Leontopithecus* Lesson, 1840; and the tamarins: *Saguinus* Hoffmannsegg, 1807, *Leontocebus* Wagner, 1839, (Buckner et al., 2015; Rylands et al., 2000, 2016; van Roosmalen & van Roosmalen, 2003). In mid-2022 Brcko et al. (2022) proposed *Tamarinus* Trouessart, 1904 and *Oedipomidas* Reichenbach, 1862 as genera for the western Amazonian and trans-Andean *Saguinus* species, respectively.

Historically, the taxonomy of Callitrichidae was addressed in Hershkovitz's (1977) extensive monography. For tamarins of the genus *Saguinus*, Hershkovitz (1977) proposed an intra-generic classification based on morphology, coat colour and geographic distribution, and divided *Saguinus* into three sections and six species groups:

Section: Hairy-faced tamarins:

The White-mouthed tamarins or *Saguinus nigricollis* group – *Saguinus nigricollis* and *Saguinus fuscicollis* species and subspecies.

The Moustached tamarins or *Saguinus mystax* group – *Saguinus mystax mystax* (Spix, 1823), *Saguinus mystax pileatus* (I. Geoffroy Saint-Hilaire & Deville, 1848), *Saguinus mystax pluto* (Lönnerberg, 1926), *Saguinus labiatus labiatus* (É. Geoffroy Saint-Hilaire, 1812), *Saguinus labiatus thomasi* (Goeldi, 1907), *Saguinus imperator imperator* (Goeldi, 1907).

The Midas tamarins or *Saguinus midas* group – *Saguinus midas midas* (Linnaeus, 1758), *Saguinus midas niger* (É. Geoffroy Saint-Hilaire, 1803).

Section: Mottle-faced section:

The *Saguinus inustus* group – *Saguinus inustus* (Schwarz, 1951).

Section: Bare-faced tamarins:

The Brazilian bare-face tamarins or *Saguinus bicolor* group – *Saguinus bicolor bicolor* (Spix, 1823), *Saguinus bicolor martinsi* (Thomas, 1912), *Saguinus bicolor ochraceus* Hershkovitz, 1966.

The Colombian and Panamanian bare-face tamarins or *Saguinus oedipus* group – *Saguinus oedipus oedipus* (Linnaeus, 1758), *Saguinus oedipus geoffroyi* (Pucheran, 1845), *Saguinus leucopus* (Gunther, 1877).

The molecular phylogenetic studies using mitochondrial sequences: (Cyt-b and D-Loop) (Cropp et al., 1999; Jacobs et al., 1995), ND1 (Tagliaro et al., 2005), 16S (Araripe et al., 2008), Cyt-b and HVI (Matauschek et al., 2011); nuclear sequences: β -2-microglobulin (Canavez et al., 1999), ALU insertions (da Cunha et al., 2011); proteins (Meireles et al., 1997); and combined nuclear and mitochondrial DNA (Buckner et al., 2015; Perelman et al., 2011) has recovered two major clades, which corresponding to the *Saguinus nigricollis* group (small-bodied tamarins), and all other *Saguinus* groups (large-bodied tamarins).

The phylogenetic analyses and divergence time at 9.1 ma (95% HDP 7.1–11.6 ma), allied to the differences in morphology, behaviour, ecology and biogeography, suggested the division of the genus *Saguinus* in two, with the name *Leontocebus* Wagner, 1839 for *Saguinus nigricollis* group (Buckner et al., 2015). Subsequently, Rylands et al. (2016), in their taxonomic review of tamarins, reinforced the differences between small-bodied tamarins and large-bodied tamarins, and supported the division into two genera, *Leontocebus* and *Saguinus*.

For genus *Saguinus* sensu Buckner et al. (2015), some studies also consistently recovered the *Saguinus bicolor* + *S. midas*, *Saguinus mystax* + *S. inustus* and *Saguinus oedipus* groups (Athaydes et al., 2021; Brcko et al., 2022; Buckner et al., 2015). However, only Brcko et al. (2022) proposed to classify the *Saguinus bicolor* + *midas*, *Saguinus mystax* + *inustus* and *Saguinus oedipus* groups as the genera *Saguinus* Hoffmannsegg, 1807, *Tamarinus* Trouessart, 1904 and *Oedipomidas* Reichenbach, 1862, respectively. Brcko et al. (2022) based their proposal on the robustly supported phylogeny, divergence time, and the morphological and ecological divergence and geographic distribution of these groups (Figure 1).

Within the genera *Saguinus* and *Oedipomidas*, there were taxonomic revisions for some species. *Saguinus midas niger* (É. Geoffroy Saint-Hilaire, 1803) was elevated to full species, *S. niger* (É. Geoffroy Saint-Hilaire, 1803), based on analyses of morphological and molecular data (Natori & Hanihara, 1992; Rylands & Mittermeier, 2009; Vallinoto et al., 2006). Molecular phylogenies also indicated that the *S. niger* population on the right bank of the Tocantins River was a distinct taxon (Tagliaro et al., 2005; Vallinoto et al., 2006). Thus, based on these studies and on craniometric and phenetic data, this population was revalidated as a full species, *Saguinus ursulus* Hoffmannsegg, 1807, previously considered a synonym of *S. niger* by Hershkovitz (1977) (Gregorin & Vivo, 2013). Unlike Hershkovitz (1977), Groves (2001) considered *S. bicolor* (Spix, 1823) a full species and reclassified *S. bicolor ochraceus* and *S. bicolor martinsi* as *S. martinsi* (Thomas, 1912), with two subspecies, *S. m. martinsi* (Thomas, 1912) and *S. m. ochraceus* Hershkovitz, 1966.

Comparative morphological studies also resulted in the recognition of *O. oedipus* (Linnaeus, 1758) and *O. geoffroyi* (Pucheran, 1845) as a separate species (Hanihara & Natori, 1987; Kanazawa & Rosenberger, 1988; Moore & Cheverud, 1992; Rylands, 1993; Skinner, 1991). These findings were confirmed by subsequent molecular phylogenies (Araripe et al., 2008; Brcko et al., 2022; Buckner et al., 2015; Perelman et al., 2011; Ruiz-García et al., 2014).

For genus *Tamarinus*, Lopes et al. (2023) recently published a taxonomic revision of the *Tamarinus mystax*, the authors described a new species from the Juruá-Tefé interfluvia, while Hrbek et al. (T. Hrbek, G. P. Lopes, F. Bertuol, F. Rohe, F. E. Silva, R. Gregorin, I. P. Farias, L. Portela, unpublished data) revised the taxonomy of the *Tamarinus labiatus* species, finding support for *Tamarinus thomasi* (Goeldi, 1907), but no support for a species-level divergence of *T. labiatus labiatus* and *T. labiatus rufiventer*. This supports the taxonomy of Hershkovitz (1977) who recognized only *Tamarinus labiatus* albeit showing clinal phenotypic variation across a north–south gradient, while Groves (2001) revalidated the subspecies *T. labiatus rufiventer* (Gray, 1843) for individuals in the northern portion of the distribution of *Tamarinus labiatus*. Recently, the taxonomic status of *Tamarinus imperator* (Goeldi, 1907) was evaluated (Gregorin et al., 2023). This species has two subspecies, *Tamarinus imperator imperator* (Goeldi, 1907), and *Tamarinus imperator subgriseus* (Lönnerberg, 1940). This evaluation was based on phenotypical divergences, craniometric data and mitochondrial DNA, leading to rise of the two subspecies to species level. Although a substantial number of samples were used for phenotypical divergences and craniometric data, only three specimens were used for genetic analysis, using a uniparental molecular marker only. Thus, the use of double digestion restriction associated DNA (ddRAD) data to conduct coalescent-based tests of taxonomic hypotheses for these species can be prolific (Fujita et al., 2012), as it is an adaptable inexpensive technique which do not require a reference genome. Currently seven species of the genus *Tamarinus* are recognized. *Tamarinus thomasi* and *T. inustus* occur west of the Negro and north of the Solimões/Amazonas rivers, while the remaining species occur west of the Madeira and south of the Solimões/Amazonas rivers (Figure 2). Therefore, rivers delimit the ranges of all taxa.

Despite all phylogenetic and taxonomic information presented above, the phylogenetic relationships of species of genus *Tamarinus* are poorly known due to a lack of samples, since no study has complete taxonomic sampling of all recognized species and subspecies. In this study, we conducted a time-calibrated species tree test of all extant species and subspecies of the genera *Saguinus*, *Tamarinus* and *Oedipomidas* using the ddRAD sequence data. We also

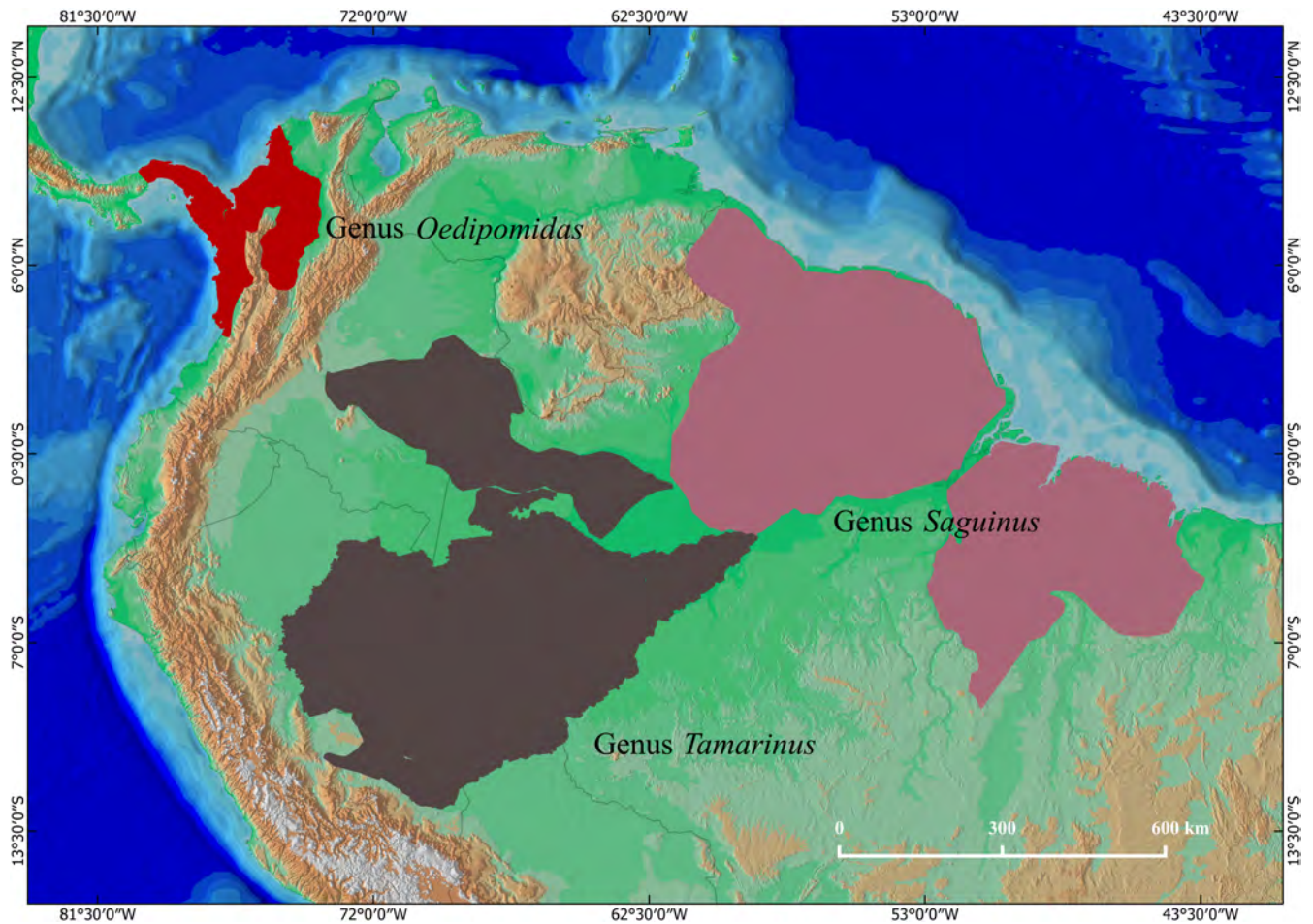


FIGURE 1 The geographical distributions of tamarins of genus *Tamarinus* (brown), *Oedipomidas* (red), and *Saguinus* (wine).

discussed the recent proposal of Brcko et al. (2022) to classify the *Saguinus bicolor*+*midas*, *Saguinus mystax*+*inus-tus* and *Saguinus oedipus* groups as the genera *Saguinus* Hoffmannsegg, 1807, *Tamarinus* Trouessart, 1904 and *Oedipomidas* Reichenbach, 1862, respectively.

2 | MATERIALS AND METHODS

2.1 | Collection of ddRAD data

We extracted DNA from tissues deposited at Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil, Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Tefé, Brazil, Universidade Federal do Amazonas (UFAM), Manaus, Brazil, Instituto de Pesquisas Científicas e Tecnológicas do Estado de Amapá (IEPA), Macapá, Brazil, Association KWATA, Cayenne, French Guiana, The Field Museum of Natural History (FMNH), Chicado, United States of America, and Pontificia Universidad Javeriana, Bogotá, Colombia. We obtained tissue samples from 46 specimens of the genus *Tamarinus*, 26 specimens of genus *Saguinus*, six

specimens of genus *Oedipomidas*, and 10 specimens of *Leontocebus* (outgroup) (Table S1).

We performed a partial representational genome sequencing using the SdaI and Csp6I restriction enzymes (ThermoFisher), through the double-digest RAD sequencing protocol (ddRAD) (Peterson et al., 2012), modified and optimized for the IonTorrent PGM (Boubli et al., 2018; see: <https://github.com/legalLab/protocols-scripts>), and selected fragments in the range of 320–400 bp using PippinPrep (Sage Science) Samples were sequenced on the IonTorrent PGM using the manufacturer's recommended protocol. We generated data for the 88 specimens of tamarins (Table S1). These specimens represented all known species and subspecies of the ingroup. These specimens were also sampled across the known geographic distribution of the taxa.

Sequencing reads were processed using the pyRAD pipeline (Eaton, 2014), as follows: During the de novo assembly, we used a minimum coverage of 6× per locus, assembling all fragments in the 300–400 bp range. Nucleotides with PHRED scores <30 were excluded, and loci with more than six low-quality nucleotides were excluded. Following demultiplexing and extraction of loci

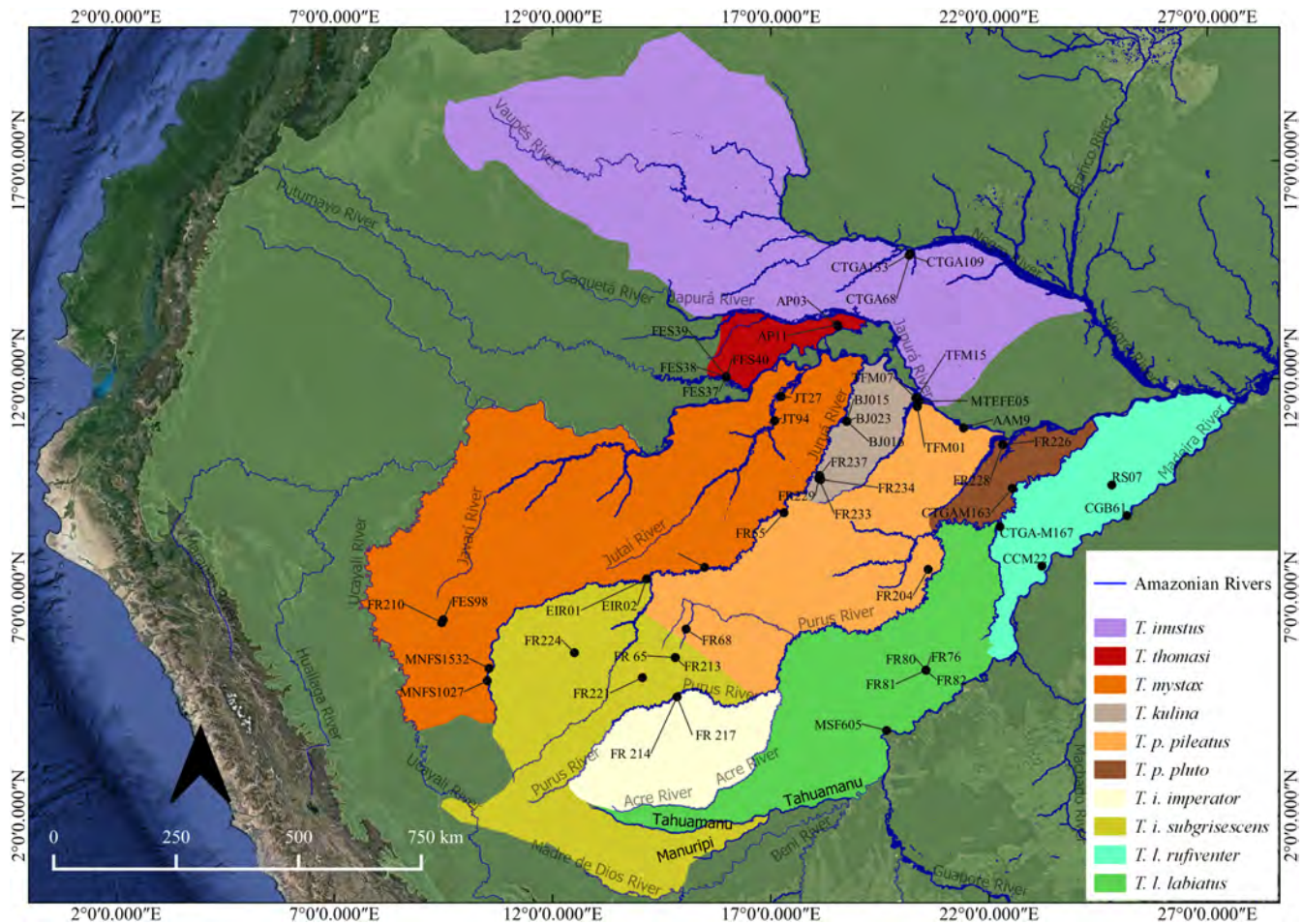


FIGURE 2 Distribution of species/subspecies of the genus *Tamarinus*. Black circles represent localities of the genetic samples. Polygons modified from IUCN and Sampaio et al. (2018).

using the above criteria, we proceeded with the clustering of alleles within loci, and of loci across individuals, and the generation of the dataset for analyses. The minimum similarity to allow the union of reads in the same cluster was 88%, and the minimum individual coverage for a cluster to be accepted as valid was 26 reads. We subsequently filtered the clusters, excluding all loci with more than 50% heterozygotes – likely paralogues. The resulting dataset contained 512 loci and 180,043 nucleotides.

We also processed our raw reads using DiscoSnpRAD (Gauthier et al., 2020), which uses De Bruijn graphs to circumvent the need for clustering of reads, reducing data loss due to low coverage within individuals. We extracted single nucleotide polymorphisms (SNPs) from our reads using a minimum read depth of 5. Furthermore, we filtered these loci on rank (Gauthier et al., 2020), retaining those SNPs with rank >0.9 —a statistic incorporating the discriminant power as function of read coverage of each SNP—and those that were present in at least 90% of the samples, that is, no more than nine individuals had missing data at any particular SNP

locus. The resulting variant call file (VCF) was filtered to retain one SNP per RAD locus resulting in a 95.87% complete matrix comprising 13,242 loci. Using the same filtering procedure, we also generated a VCF file containing individuals of *Tamarinus imperator*, *Tamarinus subgriseus* and *Tamarinus inustus*, which resulted in 6522 loci and 100% complete.

2.2 | Species hypotheses tests

2.2.1 | Tests of taxonomic hypotheses for *Tamarinus imperator*

We carried out a path sampling analysis in BEAST2 (Bouckaert et al., 2014) testing competing taxonomic hypotheses derived from current taxonomy. The potential taxa whose taxonomic status was tested were *Tamarinus imperator imperator* and *Tamarinus imperator subgriseus*. The taxonomic hypotheses were: (1) one species – (*T. imperator*); (2) two species – (*T. imperator* and *T. subgriseus*). Marginal probabilities of the competing

taxonomic hypotheses were then compared by Bayes factors (Kass & Raftery, 1995).

2.3 | Phylogenetic analyses

We estimated a species tree phylogeny using SVDquartets (Chifman & Kubatko, 2014) implemented in PAUP (Swofford, 2002) and the STARBEAST2 package of BEAST v2.6 (Ogilvie et al., 2017). We opted to use both methods because they are fully coalescent methods for species tree phylogenetic reconstruction, and they have slightly different premises and use data in a different form (SNPs vs. sequences). For both analyses, we inferred phylogenetic relationships of all valid species and subspecies.

The SVDquartets method infers quartets based on summaries of SNPs in a concatenated sequence matrix using a full coalescent model (Chifman & Kubatko, 2014). We assessed the robustness of the species tree topology using 1000 bootstrap replicates. For species tree analyses in STARBEAST2, we first ran PartitionFinder2 (Lanfear et al., 2017) on our genomic alignment to select an optimal number of partitions and their respective models of molecular evolution, grouping the 512 ddRAD loci into 140 partitions. We analysed these data in BEAST v2.6 (Bouckaert et al., 2014), implementing the Yule tree prior, generating 10^8 topologies, sampling every 10^4 th topology and discarding the first 15% topologies as burn-in after verifying stationarity in Tracer v1.7 (Rambaut et al., 2018). Topologies were visualized in DensiTree (Bouckaert et al., 2014), and a final maximum clade credibility tree was generated using TreeAnnotator v1.6.2 (Rambaut & Drummond, 2015) after discarding 15% burn-in. The maximum clade credibility tree and divergence times were calibrated using the age of the root of the phylogeny at 8.42 (5.72–11.31), from soft calibration prior derived from Perelman et al. (2011). Divergence times tree was visualized and edited in FigTree v1.3 (Rambaut, 2010).

3 | RESULTS

3.1 | Test of phylogenetic hypotheses for *Tamarinus imperator*

The marginal likelihood of the one-species hypothesis was -82298.756 while the two-species hypothesis was -81374.587 , resulting in a Bayes Factor of 1848.338. Bayes Factors >10 are considered decisive (Kass & Raftery, 1995), and therefore there is decisive support for the existence of two species: *Tamarinus imperator* and *Tamarinus subgriseus*. This inference is supported by diagnostic phenotypic differences between the two species

(Gregorin et al., 2023; Figures S1 and S2) and disjunct distribution (Figure 2). Synonyms, diagnostic characters, type locality, and geographic distribution for two species are in Appendix S1.

3.2 | Phylogenetics inferences

Our phylogenetic reconstructions were robustly supported. The topologies of the SVDQ and STARBEAST2 species tree analyses are identical except for the phylogenetic position of *Tamarinus thomasi* (Figures 3–5). In the SVDQ phylogeny *Tamarinus thomasi* is sister to *Tamarinus labiatus* (Figure 3), while in the STARBEAST2 phylogeny it is sister to *Tamarinus inustus* (Figures 4 and 5). In both analyses we recovered strong support for the monophyly of the genera *Leontocebus*, *Oedipomidas*, *Saguinus* and *Tamarinus*. Using the 8.42 ma (HPD = 5.72–11.38 ma) divergence of *Leontocebus* and all other tamarins reported in Perelman et al. (2011), we estimated the divergence of *Tamarinus* and *Oedipomidas/Saguinus* at 7.21 ma (HPD = 4.88–9.85 ma; Figure 5), and of *Oedipomidas* and *Saguinus* at 5.35 ma (HPD = 2.99–7.41 ma; Figure 5).

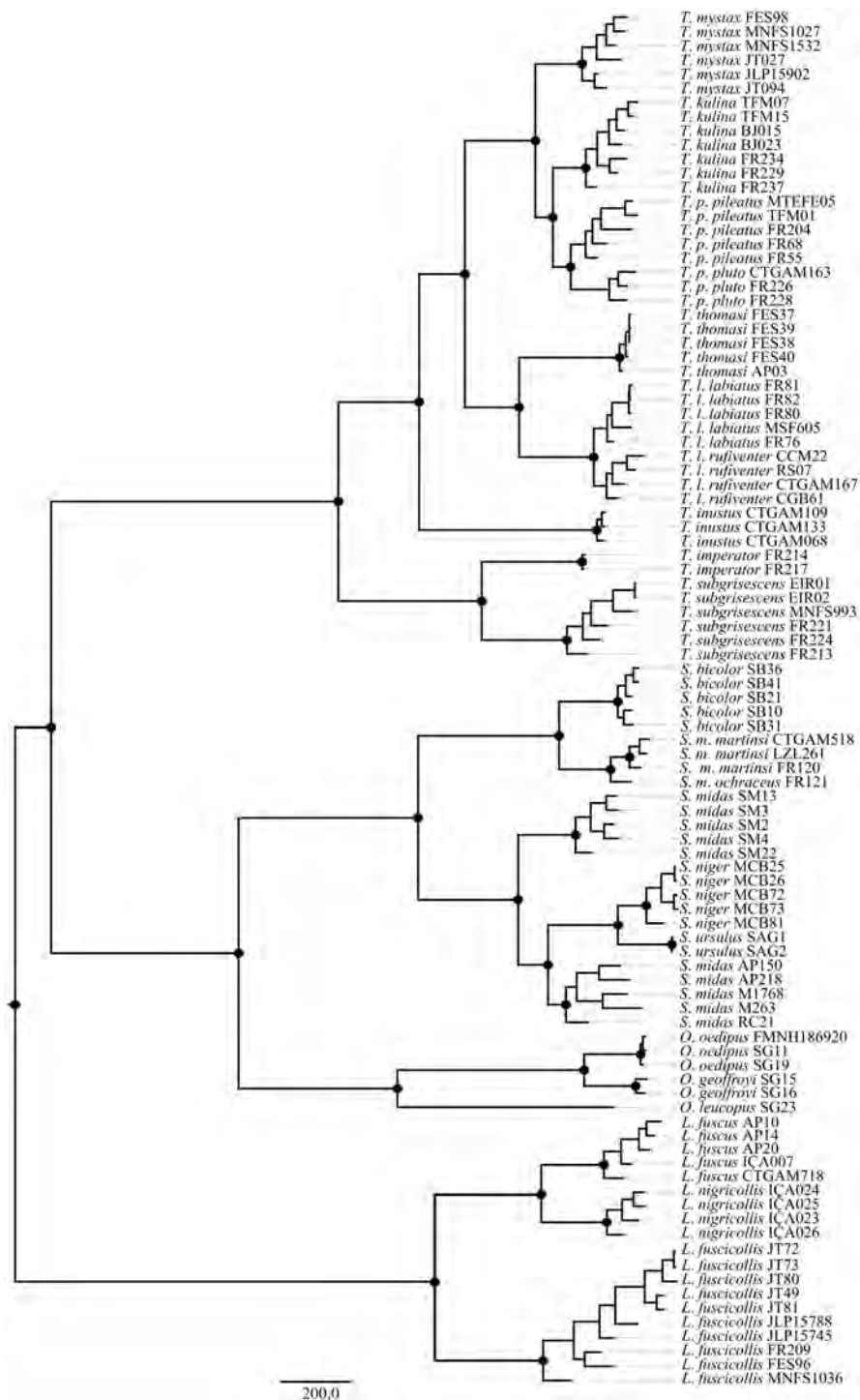
4 | DISCUSSION

Here, we use the ddRAD data set to generate the most complete phylogeny of the genus *Tamarinus*, including all subspecies and, a recently described species. Likely it is also the first study to assess the evolutionary history of the *Tamarinus*. Furthermore, this is the first study to include all species of the genera *Oedipomidas* and *Saguinus*. Although the taxonomy and systematics of the genera *Tamarinus*, *Oedipomidas* and *Saguinus* have been the subject of discussion since Hershkovitz's (1977) seminal study, the taxonomy of *Tamarinus* remained virtually unchanged, thus, we provide the first comprehensive phylogeny for genus *Tamarinus* throughout an extensive molecular analysis.

4.1 | *Tamarinus imperator* and *Tamarinus subgriseus*

Our analyses confirm the existence of two species of *Tamarinus* previously subsumed under the specific epithet of *Tamarinus imperator*, as did Gregorin et al. (2023). Not only is there decisive support for the two species *T. imperator* and *T. subgriseus*, but these species are also estimated to have diverged 1.64 ma. The time of this divergence is greater than all other sister species divergences observed in the genera

FIGURE 3 SVDQuartet phylogeny of genus *Oedipomidas*, *Saguinus* and *Tamarinus*. Black dots on major clades indicate supported clades by a 100% bootstrap value, sensu Hillis & Bull (1993).



Tamarinus, *Saguinus* and *Oedipomidas*. *Tamarinus imperator* and *T. subgriseus* also exhibit markedly different phenotypes and have non-overlapping geographic distributions. Despite the distinct phenotypes of the two species, *T. imperator* was considered a single species with great individual and ontogenetic variation (Hershkovitz, 1977). Hershkovitz (1977) based his taxonomy mostly on specimens of *T. subgriseus*. Thus, after analysing other specimens of *T. imperator*, Hershkovitz (1979) realized that the phenotypes were

different and that they were two subspecies. Recent phylogenetics studies could not clarify the taxonomy of these species as only *T. subgriseus* were analysed (Athaydes et al., 2021; Brcko et al., 2022). Only Araripe et al. (2008) enclosed both species in their study, and two significant lineages were found, suggesting the existence of two species. Furthermore, the most recent phylogenetics studies could not clarify the taxonomy of these species (Athaydes et al., 2021; Brcko et al., 2022).

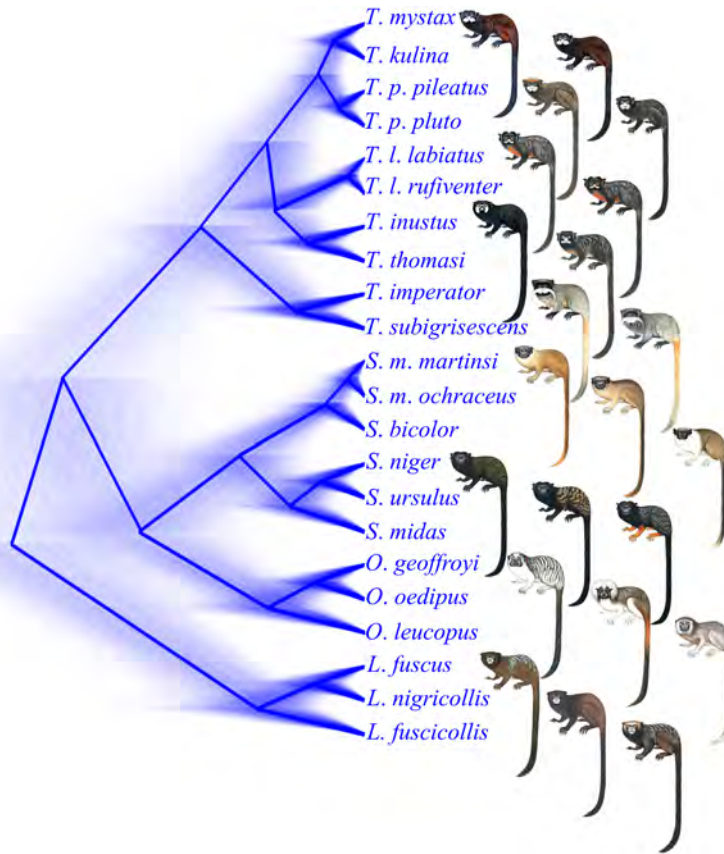


FIGURE 4 DensiTree and coat colour of three species of genus *Leontocebus* (outgroup), and all species/subspecies of genera *Oedipomidas*, *Saguinus* and *Tamarinus*.

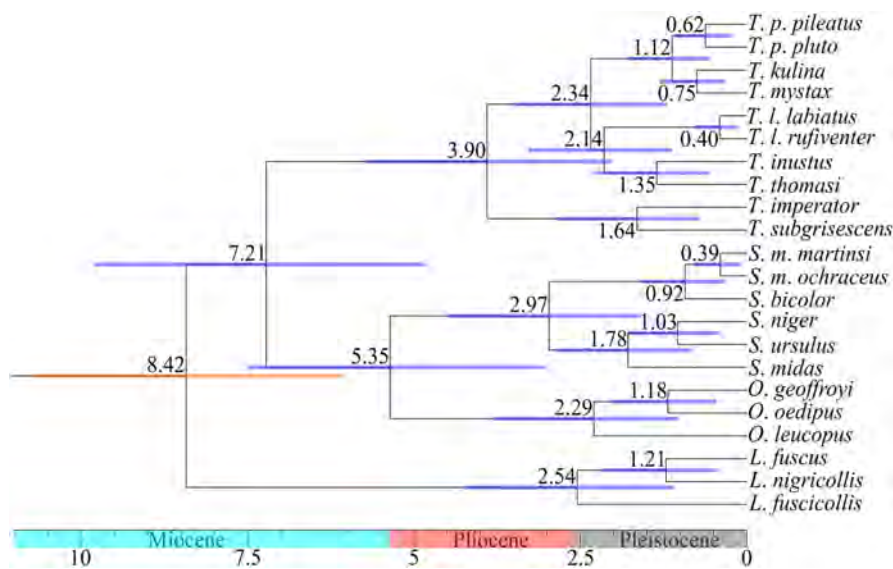


FIGURE 5 Bayesian phylogenetic time species tree of tamarins of the genera *Leontocebus* (outgroup) *Tamarinus*, *Oedipomidas* and *Saguinus*. Numbers in nodes correspond to time in millions of years and error bars represent 95% HPD intervals. Divergences represented by orange error bars were used as calibration points. Bayesian posterior probabilities are all equal to 1. See Table S1 for all specimens used in this phylogenetic analysis.

4.2 | *Tamarinus inustus*

We confirmed that *T. inustus* is a member of the genus *Tamarinus*. While Hershkovitz (1977) considered *T. inustus* an enigma due to its unclear relationship to other tamarins and proposed a separate species group to accommodate it, molecular and morphological phylogenies as well as dental morphology have supported its close, although often unresolved phylogenetic relationship

to another member of the genus *Tamarinus* (Athaydes et al., 2021; Boubli et al., 2015; Brcko et al., 2022; Buckner et al., 2015; Cropp et al., 1999; Natori & Hanihara, 1992). In our analyses we find two alternates, albeit strongly supported phylogenetic relationships. In the STARBEAST2 analysis, *T. inustus* is sister to *T. thomasi* (Figures 4 and 5). In the SVDquartets analysis, *T. inustus* is sister to the clade formed by *T. thomasi* and *T. labiatus* (Figure 3).

Both phylogenetic relationships are plausible, and potentially reflect a complex history of divergence of *T. thomasi*. Since *T. thomasi* is phenetically similar to *T. labiatus*, the sister taxon relationship of *T. inustus* and *T. thomasi*+*T. labiatus* as inferred in SVDquartets would appear non-controversial. *Tamarinus thomasi* is, however, separated by over 300 km and the Amazon River from *T. labiatus*, but its distribution is parapatric to that of *T. inustus*. This parapatry might have permitted hybridization between *T. thomasi* and *T. inustus* indicated at sister taxon relationship recovered in the STARBEAST2 analysis. While the raw genomic data for both analyses is identical, extraction of SNPs in DiscoSnp-RAD (Gauthier et al., 2020) and sequences in pyRAD (Eaton, 2014) results in slightly different final datasets. Similarly, while both SVDquartets and STARBEAST2 analyses are both fully coalescent analyses, they may recover alternate evolutionary histories (Collins & Hrbek, 2018).

4.3 | Phylogeny of tamarins

Our phylogenetic analyses recover high clade support for all species, and for relationships between species. The divergence of *Tamarinus*, *Oedipomidas*, *Saguinus*, and *Leontocebus* occurred in the Middle to Late Miocene. The timing of this diversification coincides with the diversification of other primate groups such as *Sapajus*, *Cebus*, *Cheracebus* and *Plecturocebus* (Byrne et al., 2016; Lima et al., 2018; Lynch Alfaro et al., 2012a; Ruiz-García et al., 2016, 2018), which may indicate geological or climatic events that may have similarly affected different groups.

4.4 | One genus or three? Assessing whether large-bodied tamarins should be divided into three genera

Although there are taxonomic proposals for defining supraspecific categories (Avisé & Johns, 1999; Dubois, 1988a, 1988b; Schaefer, 1976), genera generally represent a consensual classification among taxonomists, as the use of these categories is relevant not only because it reflects phylogenetic relationships (de Queiroz, 1988; Dubois, 1988a, 1988b), but are also relevant in communicating, estimating, evaluating, investigating patterns and processes, and retrieving information on biodiversity (Barraclough, 2010; Clayton, 1972; Dubois, 1988b; Nee et al., 1994; Simpson, 1961). Within a zoological concept, a genus would be a well-defined and well-supported monophyletic group of closely related species that share several characters, with morphological,

behavioural, and ecological diagnoses (Dubois, 1988a, 1988b; Dubois & Raffaëlli, 2009).

Some authors have even discussed what a genus means and have proposed some criteria to recognize and delimit genera (Allmon, 1992; Cain, 1956, 1958; Dubois, 1982, 1988a, 1988b; Garbino, 2015, 2015b; Garbino et al., 2019; Goodman et al., 1998; Groves, 2001, 2004; Hennig, 1966; Inger, 1958; Isler et al., 2013; Mayr, 1943, 1950, 1969; Michener, 1957; Simpson, 1945, 1961; Vences et al., 2013). One of the few widely accepted criteria for delimiting a genus is that the genus in question be monophyletic (Dubois, 1982; Garbino, 2015; Groves, 2001, 2004; Hennig, 1966; Isler et al., 2013; Mayr, 1969; Vences et al., 2013), the other criteria would be divergence time, phylogenetic gaps, and adaptive zone (Avisé & Johns, 1999; de Queiroz, 1994; Groves, 2001, 2004; Groves & Grubb, 2011; Hennig, 1966; Mayr, 1950, 1969; Simpson, 1944, 1953; Vences et al., 2013; Wood & Collard, 1999). The adoption of these criteria was to make the delimitation of genera objective (Groves, 2001, 2004; Groves & Grubb, 2011). However, there are several criticisms of applying these criteria in isolation, as some of them are not comparable across animal genera (Avisé & Mitchell, 2007; Garbino, 2015; Talavera et al., 2013; van Valen, 1973). Thus, using multiple lines of evidence makes genus delimitation more robust (Garbino, 2015; Lynch Alfaro et al., 2012b).

There are several arguments against changes in the number of Neotropical primates genera (Garbino, 2015; Rosenberger, 2012, 2020; Ruiz-García et al., 2012, 2016), and to the callitrichids species in particular (Garbino, 2015b; Garbino et al., 2019; Garbino & Martins-Junior, 2018). The arguments are largely based on the convenience of taxonomic stability (Garbino & Martins-Junior, 2018). Garbino (2015) and Garbino and Martins-Junior (2018) proposed the use of subgenera to avoid change and maximize taxonomic stability. However, stable classifications are not the goal of phylogenetic systematics (Baird et al., 2022; Dominguez & Wheeler, 1997; Gaffney, 1979; Grant & Kluge, 2005; Isler et al., 2013; Kluge, 1989; Padiá & De la Riva, 2006) and taxonomy must be constantly updated in the face of new data (Baird et al., 2022; Baker et al., 2021; Dominguez & Wheeler, 1997; Isler et al., 2013; Padiá & De la Riva, 2006; Tello et al., 2014).

Although the divergence times in primates have been used as a criterion for determining divisions into separate genera (Goodman et al., 1998; Groves, 2001), divergence time alone is insufficient and a phylogenetic approach, and must be associated with morphological, behavioural and ecological characteristics for the reclassification of any group (Byrne et al., 2016; Dubois, 1982; Garbino, 2015; Isler et al., 2013; Lynch Alfaro, Silva-Júnior, & Rylands, 2012; Matauschek, 2010; Rylands et al., 2016). In this sense, we

support the division of the genus *Saguinus* into three genera as proposed by Brcko et al. (2022). In addition to the divergence found here in relation to the genera *Saguinus* and *Oedipomidas*, the genus *Tamarinus* is also differentiated by phenotypic distinctiveness, morphology, and behavioural characters (Brcko et al., 2022; Garbino & Martins-Junior, 2018; Hershkovitz, 1977; Natori, 1988). The phylogenetic relationships found here for *Tamarinus*, *Oedipomidas* and *Saguinus* are also supported by phylogenetic signal based on morphology and behavioural characters (Garbino & Martins-Junior, 2018; Snowdon, 1993; Wittiger, 2002). This shows the consistency of these data in reflecting the molecular phylogeny of the three genera and reinforces the synapomorphies of each of these genera. Furthermore, the patterns found in cranial and dental morphology suggest a reorganization during the diversification of three genera (Ackermann & Cheverud, 2000, 2002). These genera are also geographically disjoint, which reinforces their distinct radiations and ecological differences (Dubois, 1982, 1988a, 1988b; Garber, 1993; Lemen & Freeman, 1984; Simpson, 1944, 1953; Wood & Collard, 1999). Contents, diagnostic characters, and geographic distribution of these genera are in Appendix S1.

The taxonomic proposal of three genera reflects the relatively old divergence comparable to the divergence of other genera of Neotropical primates, and the phenotypic, morphological, and behavioural discontinuities among the species of the different genera. This taxonomic proposal clearly conveys this information. Other taxonomic scenarios such as species groups are informal and non-standard classification schemes, while subgenera are even more polemic and arbitrary taxonomic categories, and do not appear in the species name (Dubois, 1988a, 1988b; Garbino, 2015b; Garbino & Martins-Junior, 2018). Finally, the current taxonomic proposal requires no nomenclatural novelty, since the genus names *Tamarinus* and *Oedipomidas* are available, were used on previous occasions and are non-controversial with respect to species membership (Cabrera, 1957; Elliot, 1913; Garbino & Martins-Junior, 2018; Hershkovitz, 1949; Hill, 1957; Pocock, 1917; Reichenbach, 1862; Rylands et al., 2016; Thomas, 1922; Trouessart, 1904).

5 | CONCLUSION

The taxonomy of the *Tamarinus* has remained practically the same since the seminal review of Hershkovitz (1977, 1979). Here, we provide the first complete phylogeny for the genus *Tamarinus*, with clarification of the phylogenetic relationships of all species in this genus. In addition, we also support the species-level division between *Tamarinus imperator* and *Tamarinus subgriseus* based on robust

genomic evidence. Here, we use all species and subspecies of the genera *Saguinus*, *Oedipomidas* and *Tamarinus* to generate the first complete phylogeny using ddRAD for these three callitrichid genera, assessing the phylogenetic relationships of all species and subspecies in these genera. Therefore, we reiterate and ratify the division of *Saguinus* into three genera, which supports the taxonomic proposal for these three genera.

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