



Taxonomic review of the New World tamarins (Primates: Callitrichidae)

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Twelve generic names have been ascribed to the New World tamarins but all are currently placed in just one: *Saguinus* Hoffmannsegg, 1807. Based on geographical distributions, morphology, and pelage patterns and coloration, they have been divided into six species groups: (1) *nigricollis*, (2) *mystax*, (3) *midas*, (4) *inustus*, (5) *bicolor* and (6) *oedipus*. Molecular phylogenetic studies have validated five of these groups; each are distinct clades. *Saguinus inustus* is embedded in the *mystax* group. Genetic studies show that tamarins are sister to all other callitrichids, diverging 15–13 Ma. The small-bodied *nigricollis* group diverged from the remaining, larger tamarins 11–8 Ma, and the *mystax* group diverged 7–6 Ma; these radiations are older than those of the marmosets (*Callithrix*, *Cebuella*, *Mico*), which began to diversify 6–5 Ma. The *oedipus* group diverged from the *midas* and *bicolor* groups 5–4 Ma. We review recent taxonomic changes and summarize the history of the generic names. Taking into account the Late Miocene divergence time (11–8 Ma) between the large- and small-bodied tamarin lineages, the small size of the *nigricollis* group species when compared with other tamarins, and the sympatry of the *nigricollis* group species with the larger *mystax* group species, we argue that the *nigricollis* group be recognized as a distinct genus: *Leontocebus* Wagner, 1839.

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ADDITIONAL KEYWORDS: *Leontocebus* – marmosets – phylogenetics – Platyrrhini – *Saguinus*.

INTRODUCTION

Tamarins, *Saguinus* Hoffmannsegg, 1807, are small (358–575 g; Smith & Jungers, 1997), diurnal, arboreal, frugivore-insectivores of the forests of South and Central America: in the Amazon basin, the

Guianas, northern Colombia and Panama. Herzhkovitz (1966b, 1977, 1979, 1982) recognized ten species and 33 subspecies, and since his synthesis the number of taxa has remained almost the same (Table 1). The few changes include: (1) the loss of *S. fuscicollis acrensis*, described by de Carvalho (1957a) as a subspecies of *Leontocebus melanoleucus* Miranda Ribeiro, 1912, but which was found to be a hybrid *S. f. fuscicollis* × *S. f. melanoleucus*

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Table 1. The taxonomy of the tamarins

Hershkovitz (1977, 1979, 1982)	Rylands & Mittermeier (2013)
White-mouthed or <i>nigricollis</i> group	White-mouthed or <i>nigricollis</i> group
<i>Saguinus fuscicollis fuscus</i> (Lesson, 1840)	<i>Saguinus fuscus</i>
<i>Saguinus nigricollis nigricollis</i> (Spix, 1823)	<i>Saguinus nigricollis nigricollis</i>
<i>Saguinus nigricollis graellsii</i> (Jiménez de la Espada, 1870)	<i>Saguinus nigricollis graellsii</i>
<i>Saguinus nigricollis hernandezii</i> Hershkovitz, 1982	<i>Saguinus nigricollis hernandezii</i>
<i>Saguinus fuscicollis leucogenys</i> (Gray, 1866)	<i>Saguinus leucogenys</i>
<i>Saguinus fuscicollis illigeri</i> (Pucheran, 1845)	<i>Saguinus illigeri</i>
<i>Saguinus fuscicollis lagonotus</i> (Jiménez de la Espada, 1870)	<i>Saguinus lagonotus</i>
<i>Saguinus fuscicollis tripartitus</i> (Milne-Edwards, 1878)	<i>Saguinus tripartitus</i>
<i>Saguinus fuscicollis fuscicollis</i> (Spix, 1823)	<i>Saguinus fuscicollis fuscicollis</i>
<i>Saguinus fuscicollis avilapiresei</i> Hershkovitz, 1966	<i>Saguinus fuscicollis avilapiresei</i>
<i>Saguinus fuscicollis primitivus</i> Hershkovitz, 1977	<i>Saguinus fuscicollis primitivus</i>
<i>Saguinus fuscicollis nigrifrons</i> (I. Geoffroy, 1850)	<i>Saguinus fuscicollis mura</i> Röhe <i>et al.</i> , 2009
<i>Saguinus fuscicollis cruzlimai</i> Hershkovitz, 1966	<i>Saguinus nigrifrons</i>
<i>Saguinus fuscicollis weddelli</i> (Deville, 1849)	<i>Saguinus cruzlimai</i> *
<i>Saguinus fuscicollis melanoleucus</i> (Miranda Ribeiro, 1912)	<i>Saguinus weddelli weddelli</i>
<i>Saguinus fuscicollis acrensis</i> (de Carvalho, 1957) [†]	<i>Saguinus weddelli melanoleucus</i>
<i>Saguinus fuscicollis crandalli</i> Hershkovitz, 1966	<i>Saguinus weddelli crandalli</i>
Moustached or <i>mystax</i> group	Moustached or <i>mystax</i> group
<i>Saguinus mystax mystax</i> (Spix, 1823)	<i>Saguinus mystax mystax</i>
<i>Saguinus mystax pileatus</i> (I. Geoffroy & Deville, 1848)	<i>Saguinus mystax pileatus</i>
<i>Saguinus mystax pluto</i> (Lönningberg, 1926)	<i>Saguinus mystax pluto</i>
<i>Saguinus labiatus labiatus</i> (É. Geoffroy, 1812)	<i>Saguinus labiatus labiatus</i>
<i>Saguinus labiatus thomasi</i> (Goeldi, 1907)	<i>Saguinus labiatus thomasi</i>
<i>Saguinus imperator imperator</i> (Goeldi, 1907)	<i>Saguinus labiatus rufiventer</i> (Gray, 1843) [‡]
<i>Saguinus imperator subgrisescens</i> (Lönningberg, 1940)	<i>Saguinus imperator imperator</i>
Mottled-face tamarin or <i>inustus</i> group	<i>Saguinus imperator subgrisescens</i>
<i>Saguinus inustus</i> (Schwarz, 1951)	<i>Saguinus inustus</i>
Midas tamarin or <i>midas</i> group	Midas tamarin or <i>midas</i> group
<i>Saguinus midas midas</i> (Linnaeus, 1758)	<i>Saguinus midas</i>
<i>Saguinus midas niger</i> (É. Geoffroy, 1803)	<i>Saguinus niger</i>
Brazilian bare-face tamarins or <i>bicolor</i> group	<i>Saguinus ursulus</i> Hoffmannsegg, 1807 [§]
<i>Saguinus bicolor bicolor</i> (Spix, 1823)	Brazilian bare-face tamarins or <i>bicolor</i> group
<i>Saguinus bicolor martinsi</i> (Thomas, 1912)	<i>Saguinus bicolor</i>
<i>Saguinus bicolor ochraceus</i> Hershkovitz, 1966	<i>Saguinus martinsi martinsi</i>
Colombian and Panamanian bare-face tamarins or <i>oedipus</i> group	<i>Saguinus martinsi ochraceus</i>
<i>Saguinus oedipus oedipus</i> (Linnaeus, 1758)	Colombian and Panamanian bare-face tamarins or <i>oedipus</i> group
<i>Saguinus oedipus geoffroyi</i> (Pucheran, 1845)	<i>Saguinus oedipus</i>
<i>Saguinus leucopus</i> (Günther, 1877)	<i>Saguinus geoffroyi</i>
	<i>Saguinus leucopus</i>

Arrangements proposed by Hershkovitz (1977, 1979, 1982) and Rylands & Mittermeier (2013), the latter with three modifications: (1) inclusion of *Saguinus inustus* in the moustached or *mystax* group as indicated by molecular data (Jacobs Cropp *et al.*, 1999; Boubli *et al.*, 2015; Buckner *et al.*, 2015); (2) the addition of *Saguinus ursulus* Hoffmannsegg, 1807, revalidated by Gregorin & de Vivo (2013); and (3) the elevation of *S. fuscicollis cruzlimai* to a species by Sampaio *et al.* (2015).

*Raised to species level by Sampaio *et al.* (2015).

[†]Found to be a hybrid *S. f. fuscicollis* × *S. f. melanoleucus* (Peres, 1993a; Peres *et al.*, 1996).

[‡]Revalidated by Groves (2001).

[§]Revalidated by Gregorin & de Vivo (2013).

(Peres, 1993a; Peres, Patton & da Silva, 1996); (2) the recognition of *S. labiatus rufiventer* (Gray, 1843) by Groves (2001, 2005); (3) the description of a new subspecies, *S. fuscicollis mura* Röhe *et al.*, 2009; and (4) the splitting of Hershkovitz's *S. midas niger* into *S. niger* (É. Geoffroy Saint-Hilaire, 1803) and *S. ursulus* Hoffmannsegg, 1807, by Gregorin & de Vivo (2013). The principal changes in the taxonomy of this genus have arisen from the trend to adopt the Phylogenetic Species Concept (Cracraft, 1983; Groves, 2001, 2004, 2012, 2014; Rylands & Mittermeier, 2014); a number of Hershkovitz's subspecies are now considered species, and the tally of tamarins currently stands at 22 species and 35 species and subspecies (Groves, 2001, 2005; Matauschek, Roos & Heymann, 2011; Rylands, Mittermeier & Silva-Júnior, 2012; Gregorin & de Vivo, 2013; Rylands & Mittermeier, 2008, 2013; Sampaio *et al.*, 2015).

Besides the tamarins, the Callitrichidae comprises the pygmy marmosets (*Cebuella*), the Amazonian marmosets (*Mico*), Goeldi's monkey (*Callimico*), the Atlantic forest marmosets (*Callithrix*) and the Atlantic forest lion tamarins (*Leontopithecus*) (Rylands *et al.*, 2012; Schneider *et al.*, 2012; Garbino, 2015; Schneider & Sampaio, 2015). The molecular genetic analysis of Perelman *et al.* (2011) indicated that the Callitrichidae diverged from the Aotidae (night monkeys) and Cebidae (squirrel monkeys and capuchin monkeys) about 20–19 million years ago (Ma) (see also Goodman *et al.*, 1998; Ray *et al.*, 2005; Schneider & Sampaio, 2015). The tamarins split early in the callitrichid radiation (Canavez *et al.*, 1999; see review by Osterholz, Walter & Roos, 2009), and are sister to all other extant callitrichids, with a Middle Miocene divergence estimated at 15–13 Ma (Matauschek *et al.*, 2011; Perelman *et al.*, 2011; Perez, Klaczo & dos Reis, 2012; Schneider *et al.*, 2012; Buckner *et al.*, 2015; Schneider & Sampaio, 2015).

Based on morphology, pelage and geographical distribution, Hershkovitz (1977: 604) separated his ten tamarin species into the following groups: (1) the white-mouthed tamarin or *nigricollis* group (*S. nigricollis* and *S. fuscicollis*); (2) the moustached tamarin or *mystax* group (*S. mystax*, *S. labiatus* and *S. imperator*); (3) the Midas tamarin group (*S. midas*); (4) the mottled-face tamarin group (*S. inustus*); (5) the Brazilian bare-face tamarin group (*S. bicolor*); and (6) the Colombian and Panamanian bare-face tamarin group (*S. leucopus* and *S. oedipus*) (Table 1, Figs 1–3). For shorthand, we refer to them as (1) the *nigricollis* group, (2) the *mystax* group, (3) the *midas* group, (4) the *inustus* group, (5) the *bicolor* group and (6) the *oedipus* group.

Molecular genetic studies have confirmed five of these six groups as distinct clades. The exception is

inustus, which occurs north of the Rio Solimões in Brazil and Colombia, and, having a bare-face, Hershkovitz (1977: 732) supposed that it came 'from the same stock that could have given rise to the *S. oedipus* group'. The results of the molecular genetic analyses of Jacobs Cropp, Larson & Cheverud (1999) and Boubli *et al.* (2015) who used mtDNA, Buckner *et al.* (2015) who used both mtDNA and nuclear sequences, and da Cunha *et al.* (2011) who analysed DNA sequences of five nuclear genes with *Alu* insertions, have indicated however, that it may be a sister to *S. mystax*, *S. labiatus* or *S. mystax* + *S. labiatus*, and as such is a well-embedded member of the *mystax* group.

In this article, we review changes to the taxonomy of the tamarins (species and subspecies) since Hershkovitz's synthesis (1977, 1979, 1982), and provide a summary of the history of the tamarin genus names. Taking into account new information from molecular phylogenetic studies concerning the ages of the tamarin clades – clades that are coincident with the species groups mentioned above – we suggest a taxonomy that recognizes two genera, not one. The argument for this separation, based on morphological, genetic, behavioural and ecological, and biogeographical evidence, follows the same reasoning as that for the split of the capuchin monkeys into two genera, *Cebus* Erxleben, 1777, and *Sapajus* Kerr, 1792, by Lynch Alfaro, Silva-Júnior & Rylands (2012).

OVERVIEW OF MOLECULAR PHYLOGENETIC EVIDENCE FOR TAMARIN RELATIONSHIPS

Since the Jacobs, Larson & Cheverud (1995) study of phylogenetic relationships in *Saguinus*, analyses of molecular, protein and cytogenetic data have consistently revealed a deep divergence between a small-bodied clade (the *nigricollis* group) and the remaining larger tamarins (Meireles *et al.*, 1997; Canavez *et al.*, 1999; Jacobs Cropp *et al.*, 1999; Tagliaro *et al.*, 2005; Araripe *et al.*, 2008; da Cunha *et al.*, 2011; Matauschek *et al.*, 2011; Perelman *et al.*, 2011; Springer *et al.*, 2012; Sampaio *et al.*, 2015) (Table 2, Fig. 4). Estimates of the divergence dates reported for this split range from 11 to 8 Ma, considerably older than the radiation of the marmosets that began to diversify about 6–5 Ma (Matauschek *et al.*, 2011; Perelman *et al.*, 2011; Schneider *et al.*, 2012; Buckner *et al.*, 2015). Studies have shown that genetic distances are generally greatest when members of the small-bodied group are compared with those of the large-bodied groups (Meireles *et al.*, 1997; Jacobs Cropp *et al.*, 1999; Canavez *et al.*, 1999; Araripe *et al.*, 2008; da Cunha *et al.*, 2011).

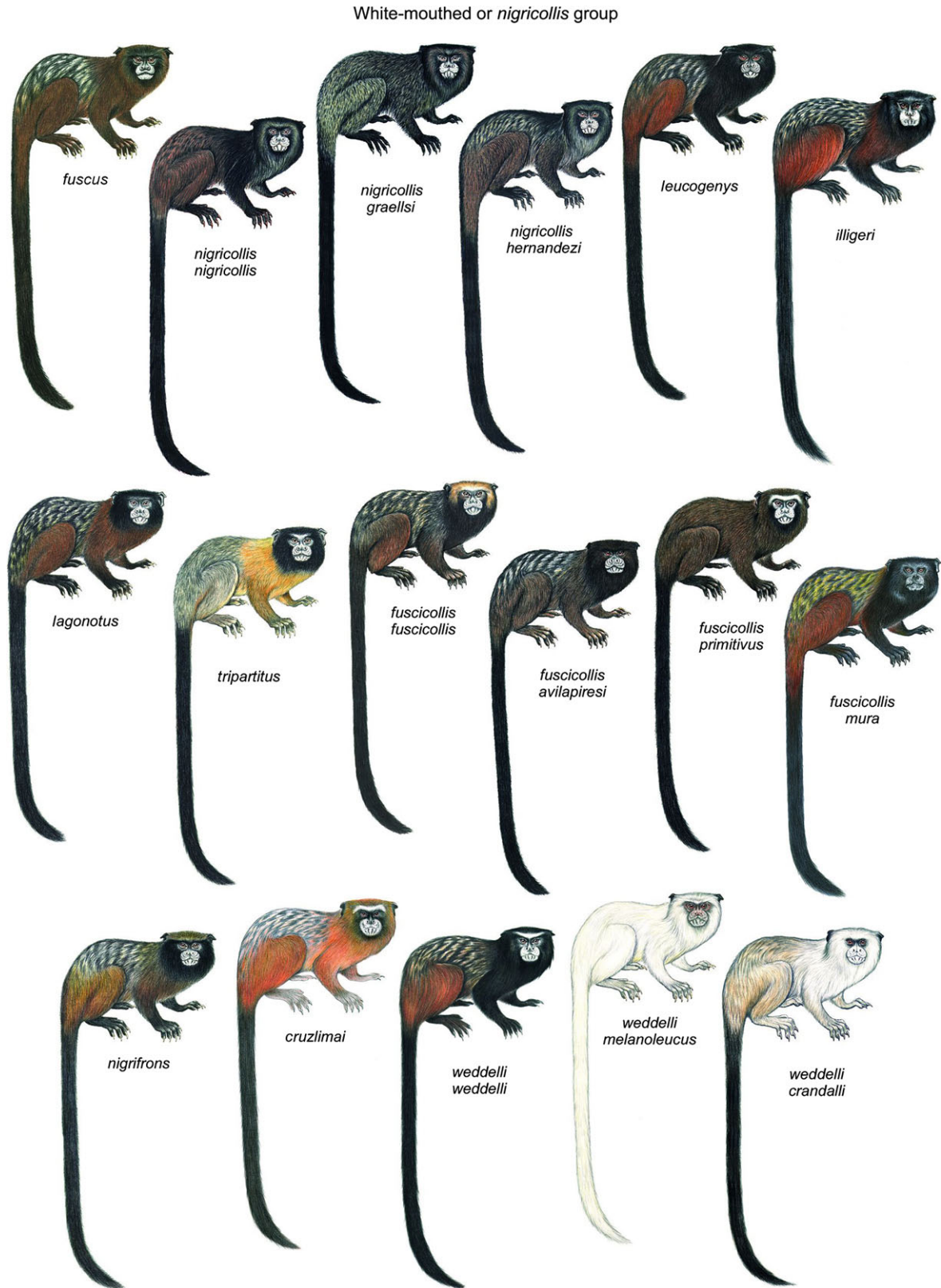


Figure 1. The white-mouthed tamarin or *nigricollis* group. Illustrations by Stephen D. Nash. © Conservation International.

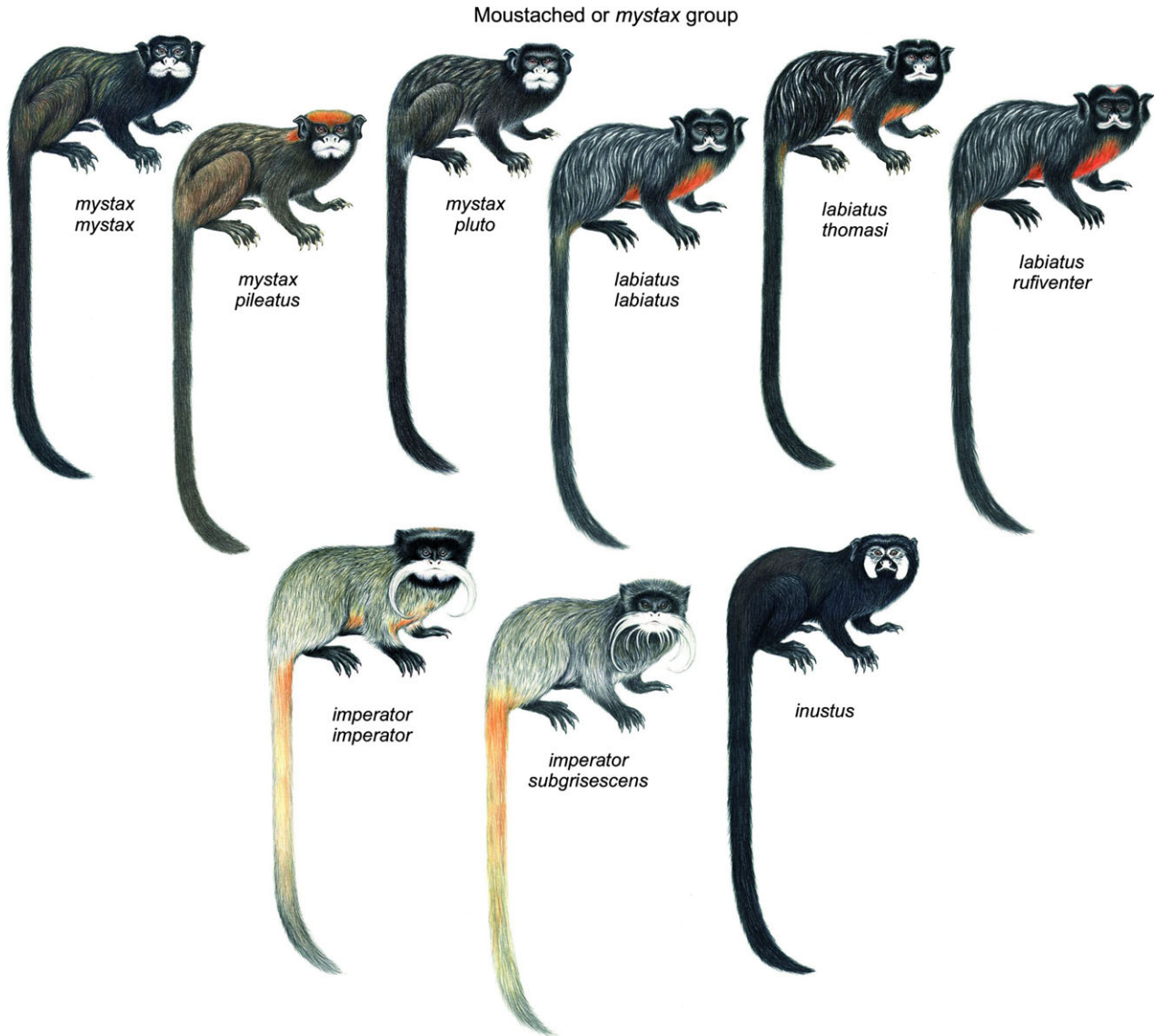


Figure 2. The moustached tamarin or *mystax* group. Illustrations by Stephen D. Nash. © Conservation International.

Genetic studies of the relationships within the *nigricollis* group have revealed *S. fuscicollis* to be a paraphyletic taxon (Jacobs Cropp *et al.*, 1999; Matauschek *et al.*, 2011). As a result, Matauschek *et al.* (2011) proposed a revision of the nomenclature that would involve either the reduction of all taxa to subspecies of *S. fuscicollis* or the raising of all taxa to full species. The latter is preferable if the current marmoset nomenclature is to be maintained (all as species), as well as to follow the current trend in Neotropical primate taxonomy that adopts the Phylogenetic Species Concept (PSC) (Groves, 2012). The PSC tends to increase the numbers of species often by raising taxa ranked as subspecies to species level.

In the most recent well-supported phylogenies, the *mystax* group, composed of (((*S. mystax*, *S. inustus*), *S. labiatus*), *S. imperator*), is recovered to have diverged from a common ancestor to the *oedipus*, *midas* and *bicolor* groups approximately 7–6 Ma (Perelman *et al.*, 2011; Springer *et al.*, 2012; Boubli *et al.*, 2015; Buckner *et al.*, 2015). Buckner *et al.* (2015) found that the *oedipus* group is composed of ((*S. oedipus*, *S. geoffroyi*), *S. leucopus*) and the *midas* and *bicolor* groups are composed of (*S. niger*, *S. midas*) and (*S. martinsi*, *S. bicolor*), respectively. The position of *S. leucopus* is still contentious as Springer *et al.* (2012) recovered it as the sister lineage to the *mystax* group, while Araripe *et al.* (2008) and Tagliaro *et al.* (2005), although analysing only single

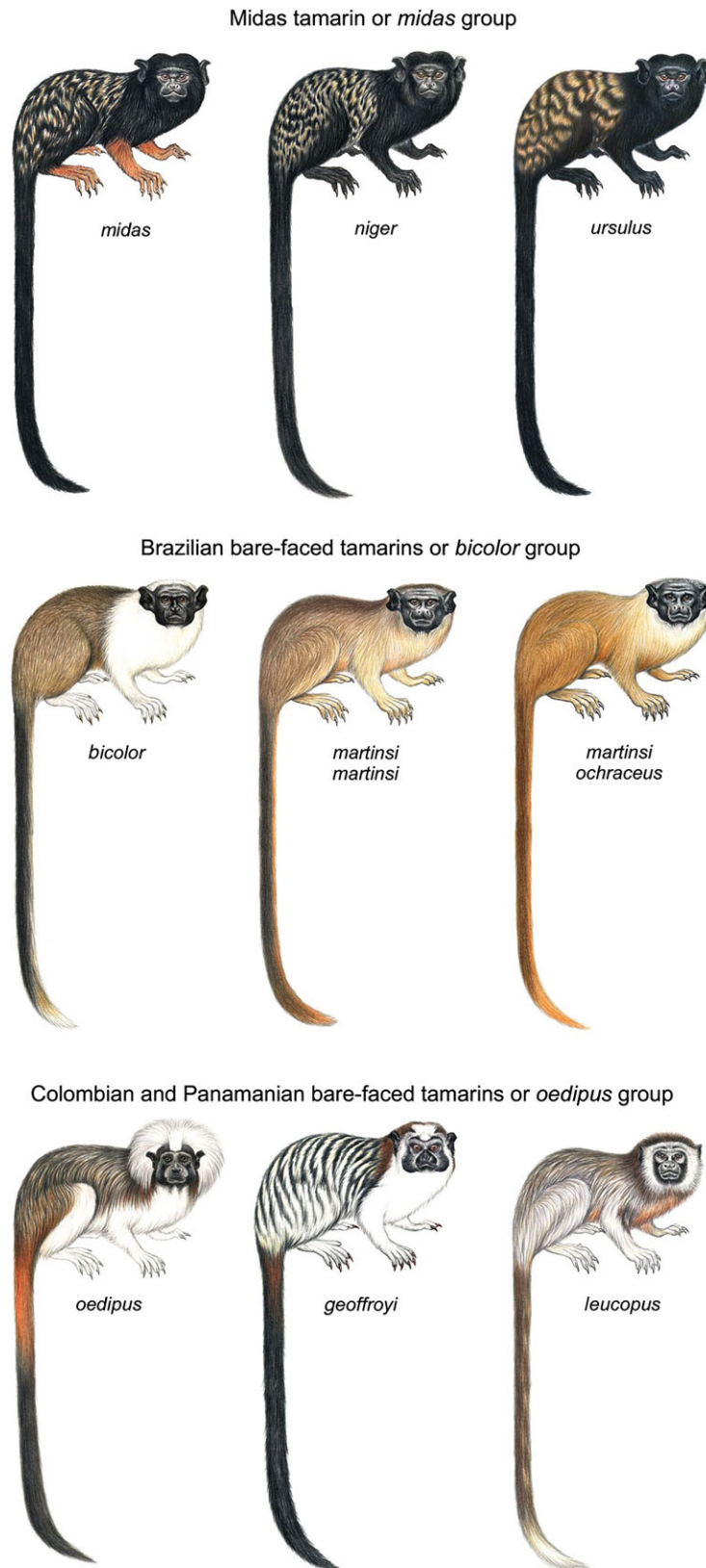


Figure 3. The Midas tamarin or *midas* group, the Brazilian bare-faced tamarin or *bicolor* group, and the Colombian and Panamanian bare-face tamarin or *oedipus* group. Illustrations by Stephen D. Nash. © Conservation International.

Table 2. Estimated divergence times of the *mystax*, *oedipus* and *midas/bicolor* groups, and species relationships for each of the large-bodied tamarin clades for studies including multiple genes

Study	Markers used	Inferred species relationships	Group node support	Age estimate (Ma)	Confidence interval (Ma)
<i>Mystax</i> group vs. <i>oedipus</i> + <i>midas/bicolor</i> groups					
Buckner <i>et al.</i> (2015)	16S rRNA, ABCA1, ADORA3, AFF2, VWF, COII, CytB, D-loop, DMRT1, FBN1	((<i>S. mystax</i> , <i>S. inustus</i>), <i>S. labiatus</i>), <i>S. imperator</i>)	0.99 (PP)	6.1	4.5–7.9
Springer <i>et al.</i> (2012)	76 genes*	(((<i>S. mystax</i> , <i>S. labiatus</i>), <i>S. leucopus</i>), <i>S. imperator</i>)	50–70 (ML)	5.7	4.1–7.4
Perelman <i>et al.</i> (2011)	54 genes (X-chromosome, Y-chromosome, autosome, intron, exon, and UTR segments)	((<i>S. mystax</i> , <i>S. labiatus</i>), <i>S. imperator</i>)	100/100/1.00 (ML/MP/PP)	7.0	4.7–9.4
da Cunha <i>et al.</i> (2011)	5 nuclear loci with <i>Alu</i> insertions	(((<i>S. labiatus</i> , <i>S. inustus</i>) <i>S. imperator</i>) <i>S. mystax</i>)	72/57/50/51 (ML/BI/NJ/MP for <i>S. labiatus</i> , <i>S. inustus</i> , <i>S. imperator</i> clade)	~12.5	n/a
<i>Oedipus</i> group vs. <i>midas/bicolor</i> groups					
da Cunha <i>et al.</i> (2011)	5 nuclear loci with <i>Alu</i> insertions	(<i>S. oedipus</i> , <i>S. leucopus</i>)	97/100/100/88 (ML/BI/NJ/MP)	~9.5	n/a
Buckner <i>et al.</i> (2015)	16S rRNA, ABCA1, ADORA3, AFF2, VWF, COII, CytB, D-loop, DMRT1, FBN1	((<i>S. oedipus</i> , <i>S. geoffroyi</i>), <i>S. leucopus</i>)	1.00 (PP)	4.9	3.6–6.6
Springer <i>et al.</i> (2012)	76 genes*	(<i>S. oedipus</i> , <i>S. geoffroyi</i>)	≥95 (ML)	4.7	3.1–6.5
Perelman <i>et al.</i> (2011)	54 genes (X-chromosome, Y-chromosome, autosome, intron, exon, and UTR segments)	(<i>S. oedipus</i> , <i>S. geoffroyi</i>)	100/100/1.00 (ML/MP/PP)	5.3	3.4–7.6
<i>Midas/bicolor</i> groups vs. <i>oedipus</i> group					
Buckner <i>et al.</i> (2015)	16S rRNA, ABCA1, ADORA3, AFF2, VWF, COII, CytB, D-loop, DMRT1, FBN1	((<i>S. martinsi</i> , <i>S. bicolor</i>), (<i>S. midas</i> , <i>S. niger</i>))	1.00 (PP)	4.9	3.6–6.6
Springer <i>et al.</i> (2012)	76 genes*	((<i>S. martinsi</i> , <i>S. bicolor</i>), (<i>S. midas</i> , <i>S. niger</i>))	70–<95 (ML)	4.7	3.1–6.5
Perelman <i>et al.</i> (2011)	54 genes (X-chromosome, Y-chromosome, autosome, intron, exon, and UTR segments)	((<i>S. martinsi</i> , <i>S. bicolor</i>), <i>S. midas</i>)	100/100/1.00 (ML/MP/PP)	5.3	3.4–7.6
da Cunha <i>et al.</i> (2011)	5 nuclear loci with <i>Alu</i> insertions	((<i>S. martinsi</i> , <i>S. bicolor</i>), (<i>S. midas</i> , <i>S. niger</i>))	97/100/94/97 (ML/BI/NJ/MP)	~9.5	n/a

MP, maximum parsimony; ML, maximum likelihood; NJ, neighbour joining; PP, posterior probability; BI, Bayesian Inference; Ma, million years ago; n/a, not available.

*Many species have only a small subset represented of the full set of genes included in the study.

genes, found this species to form the sister lineage to all other large-bodied tamarins, but with low support (50–70%). The 16S ribosomal RNA gene studied by

Araripe *et al.* (2008) is known to give inaccurate results when comparing species. The *oedipus* and *midas* and *bicolor* groups diverged from each other

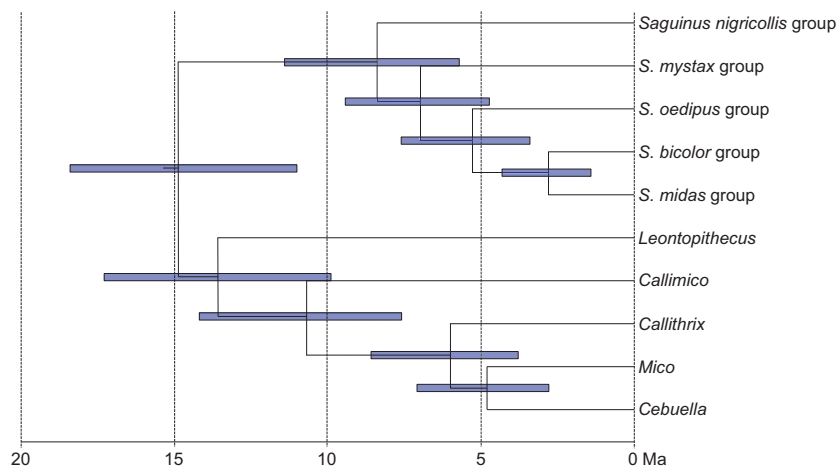


Figure 4. Ultrametric tree showing phylogenetic relationships and divergence ages among all callitrichid genera and tamarin species groups as reconstructed from nuclear sequence data (redrawn from Perelman *et al.*, 2011). All nodes are significantly supported by maximum-parsimony and maximum-likelihood bootstrap values of $\geq 98\%$, and Bayesian posterior probabilities of 1.0. Blue bars indicate 95% credibility intervals of divergence times and the time scale below shows million years before present.

Table 3. Divergence times for callitrichid lineages

Group or genus	Study	Age estimate (Ma)	Confidence interval (Ma)
<i>Nigricollis</i> group (<i>Leontocebus</i> vs. <i>Saguinus</i>)	Buckner <i>et al.</i> (2015)	9.1	7.1–11.6
	Perelman <i>et al.</i> (2011)	8.4	5.7–11.4
	Matauschek <i>et al.</i> (2011)	10.1	7.1–12.4
<i>Mystax</i> group vs. <i>midas</i> / <i>bicolor</i> + <i>oedipus</i> groups	Buckner <i>et al.</i> (2015)	6.1	4.5–7.9
	Boubli <i>et al.</i> (2015)	7.1	4.9–9.4
	Perelman <i>et al.</i> (2011)	7.0	4.7–9.4
<i>Oedipus</i> group vs. <i>midas</i> / <i>bicolor</i>	Buckner <i>et al.</i> (2015)	4.9	3.6–6.6
	Perelman <i>et al.</i> (2011)	5.3	3.4–7.6
<i>Callithrix</i> vs. <i>Cebuella</i> + <i>Mico</i>	Buckner <i>et al.</i> (2015)	5.4	4.3–6.7
	Schneider <i>et al.</i> (2012)	5.3	n/a
	Perelman <i>et al.</i> (2011)	6.0	2.9–7.2
	Buckner <i>et al.</i> (2015)	4.4	3.3–5.6
<i>Cebuella</i> vs. <i>Mico</i>	Schneider <i>et al.</i> (2012)	4.0	n/a
	Perelman <i>et al.</i> (2011)	4.8	2.9–7.2
	Buckner <i>et al.</i> (2015)	13.4	11.4–15.6
	Perelman <i>et al.</i> (2011)	13.6	9.9–17.3
<i>Leontopithecus</i> vs. <i>Callimico</i> + <i>Callithrix</i> + <i>Cebuella</i> + <i>Mico</i>	Opazo <i>et al.</i> (2006)	14.2	n/a
	Buckner <i>et al.</i> (2015)	11.2	9.2–13.3
	Schneider <i>et al.</i> (2012)	11.5	n/a
	Perelman <i>et al.</i> (2011)	10.7	7.6–14.2
<i>Callimico</i> vs. <i>Callithrix</i> + <i>Callithrix</i> + <i>Cebuella</i> + <i>Mico</i>	Opazo <i>et al.</i> (2006)*	12.1	n/a

Ma, millions of years ago; n/a, not available.

*Dates from Opazo *et al.* (2006) are from the ML/Bayesian tree.

about 5–4 Ma (Perelman *et al.*, 2011; Buckner *et al.*, 2015) (see Table 3, Fig. 4).

Marmosets, with 21 species and 22 subspecies, are less speciose than the tamarins. The

tamarins show divergence times between their lineages that are comparable to or older than those of the three currently recognized marmoset genera, *Callithrix*, *Mico*, and *Cebuella* (Perelman *et al.*,

2011; Buckner *et al.*, 2015) (see Fig. 4). Genetic distances among all the major clades of tamarins are also comparable to those between the genera of marmosets (Canavez *et al.*, 1999). All of the marmoset taxa except for the pygmy marmosets, *Cebuella*, are currently recognized as full species (Rylands, Coimbra-Filho & Mittermeier, 2009).

Molecular phylogenetic studies of the small-bodied tamarins (*nigricollis* group) and large-bodied tamarins (remaining groups) consistently recover four distinct clades, even though internal arrangements found within each of these groups have varied (Jacobs Cropp *et al.*, 1999; Tagliaro *et al.*, 2005; Ara-ripe *et al.*, 2008; Buckner *et al.*, 2015). They are (1) the *nigricollis* group, (2) the *mystax* + *inustus* group, (3) the *midas* and *bicolor* groups, and (4) the *oedipus* group. There is certainly agreement concerning the placement of the *mystax* group as sister to the *oedipus* and *midas/bicolor*, while the *nigricollis* group represents the first tamarin split (e.g. Perelman *et al.*, 2011).

As indicated by the varying results discussed, there are still doubts about some aspects of tamarin phylogenetics. There remain species that have little to no genetic information available and thus their relationship to other tamarins is unclear: for example, *S. nigricollis hernandezii*, *S. ursulus*, *S. mystax pluto* and *S. m. pileatus*. Additionally, most studies have used only one or a few markers to study the phylogenetics of this group, the shortcomings of which have been discussed extensively elsewhere (Maddison, 1997; see Table 2). Exceptions to this have been the efforts of Perelman *et al.* (2011), in which 54 genes were sequenced for all species in the study, and Springer *et al.* (2012), who used the Perelman *et al.* (2011) data set and, in addition, concatenated all available sequences for many other primate species. While Perelman *et al.* (2011) generated both nuclear and mitochondrial sequence data, Springer *et al.* (2012) harvested all their sequence data from GenBank. The Springer *et al.* (2012) study encompasses the largest number of primate taxa to date, but the number of genes available for each taxon varies considerably, and in some instances species are represented by as little as a single gene. Furthermore, the species identification of sequence data from GenBank is not always reliable.

TAXONOMY OF THE TAMARINS – CHANGES SINCE 1977

Hershkovitz's (1977) monograph on the taxonomy and biology of the Callitrichidae organized, clarified and rationalized a tortuous and complex taxonomic history for this family. He placed all of the tamarins in a single genus, *Saguinus* Hoffmannsegg, 1807.

His taxonomy has remained largely intact since then (Rylands *et al.*, 2012). Here we detail the few taxonomic changes since 1977.

As mentioned, in the *nigricollis* group one subspecies has been lost (*S. fuscicollis acrensis* found to be a hybrid) and one gained (*S. fuscicollis mura* described in 2009). Thorington (1988) believed that *S. fuscicollis tripartitus* was sympatric with *S. fuscicollis lagonotus* and raised the former to a full species. Further surveys and analysis showed that they are not in fact sympatric, but *tripartitus* continued to be considered a distinct species (Heymann, 2000a; Heymann, Encarnación-C & Canaquin-Y, 2002; Matauschek, 2010; Rylands *et al.*, 2011; Aquino *et al.*, 2014).

The distinctive white *S. f. melanoleucus* was first described as a full species (*Mico melanoleucus* Miranda Ribeiro, 1912), and was listed by Coimbra-Filho (1990) as such, with *acrensis* and *crandalli* as subspecies. As mentioned, *acrensis* is now believed to be a hybrid, and *crandalli*, known from a single specimen of unknown provenance (Hershkovitz, 1966b), may likewise be a hybrid. Coimbra-Filho's taxonomy in this case was taken up by Groves (2001, 2005) and Rylands & Mittermeier (2008). Tagliaro *et al.* (2005) used data on ND1 mitochondrial DNA from one specimen of *melanoleucus* and six specimens of *S. fuscicollis weddelli* to test this hypothesis. Differences between *melanoleucus* and *weddelli* were no larger than among the *weddelli* specimens, thus failing to support Coimbra-Filho's (1990) separation. Matauschek *et al.* (2011) also found that the forms *weddelli* and *melanoleucus* were genetically very closely related. They recommended, however, that, due to its distinctive pelage colour (white), *melanoleucus* should continue to be considered a valid taxon, but as a subspecies of *Saguinus weddelli* until further genetic analyses are carried out.

The northernmost of Hershkovitz's (1977) saddle-back tamarins, *Saguinus fuscicollis fuscus*, occurring north of the Río Putumayo-Içá in Colombia and Brazil, is evidently geographically isolated from other saddle-back tamarins (*S. n. nigricollis* occurs along the right bank of the Putumayo-Içá) (see Rylands *et al.*, 2011). The geographical proximity of *S. f. fuscus* and *S. nigricollis* is concordant with the phylogenetic affinity of the two found by Jacobs Cropp *et al.* (1999), who suggested that *fuscus* should be considered a separate species as a result; a suggestion supported by Cheverud & Moore (1990) who studied facial morphology.

Matauschek *et al.* (2011) carried out a molecular genetic analysis of the Peruvian saddle-back tamarins and black-mantle tamarins. They identified four clades and recommended that *tripartitus*, *lagonotus*, *leucogenys*, *illigeri*, *nigrifrons* and *weddelli*, all

placed as subspecies of *S. fuscicollis* by Hershkovitz (1977), be considered species. Rylands & Mittermeier's (2013) taxonomy of the saddle-back tamarins (Table 1), influenced particularly by Matauschek *et al.* (2011), included eight species and 14 taxa (species and subspecies). Sampaio *et al.* (2015) subsequently reported on the provenance of *S. f. cruzlimai*, unknown to Hershkovitz (1966b, 1977), and argued that it too should be classified as a species. The Brazilian saddle-back tamarins *avilapirensi*, *primitivus* and *mura* remain as subspecies of *S. fuscicollis* pending equivalent molecular phylogenetic analyses.

The study of Matauschek *et al.* (2011) revealed intergradation between *Saguinus fuscicollis illigeri* and *S. f. leucogenys*, especially in San Martín, Moyobamba, Peru, and further north in the Río Mayo valley. There, phenotypes were more similar to *S. f. illigeri*, otherwise known along the ríos Ucayali, Tapiche and Pacaya. Hershkovitz (1977) also noted that Moyobamba specimens were similar to *S. f. illigeri*, but assigned them to *S. f. leucogenys*. This finding of similarity was reflected in the genetic data. North of the Río Pachitea in the northern part of the range, *S. f. leucogenys* (*sensu* Hershkovitz, 1977) formed a clade with *S. f. illigeri*. Samples of *S. f. leucogenys* south of the Río Pachitea formed part of the clade with other eastern/south-eastern taxa (*S. w. weddelli*, *S. f. fuscicollis*, *S. f. nigrifrons* and *S. f. melanoleucus*). Matauschek *et al.* (2011: 571) wrote that 'morphological and mitochondrial evidence suggested a range limit for *S. f. leucogenys* far more southwards than described by Hershkovitz (1977) and an inclusion of the northern populations of *S. f. leucogenys* into *S. f. illigeri*'.

In Hershkovitz's (1977, 1982) taxonomy there is just one species of black-mantle tamarin, *Saguinus nigricollis*, with three subspecies: *nigricollis*, *graellsi* and *hernandezii*. Hernández-Camacho & Cooper (1976) and Defler (1994) suggested that *graellsi* was a full species on the basis of supposed sympatry with a population of *S. n. nigricollis* in the region of Puerto Leguizamo in southern Colombia. Groves (2001, 2005) maintained *graellsi* as a full species based on Hernández-Camacho & Cooper's (1976) supposition of its sympatry with *nigricollis*. Defler (2004) and Hershkovitz (pers. comm. to Defler, 2004), concluded, however, that the specimens considered to be *S. n. nigricollis* were in fact just dull-coloured *S. fuscicollis fuscus*, and Hernández-Camacho & Defler (1989) and Defler (2004) listed *graellsi* as a subspecies of *S. nigricollis*. Molecular genetic data have indicated that *graellsi* and *nigricollis* are inseparable (Matauschek *et al.*, 2011), and there seems to be no identifiable geographical or ecological barrier separating their ranges between the

ríos Putumayo and Napo (Matauschek *et al.*, 2011; Rylands *et al.*, 2011). Furthermore, *S. nigricollis* is more closely related to some taxa previously considered as subspecies of *S. fuscicollis* than these are amongst each other (Matauschek *et al.*, 2011). This renders *S. fuscicollis* a polyphyletic taxon and provides additional arguments for giving species rank to its subspecies.

Currently, the *nigricollis* group is considered to comprise ten species and 17 species and subspecies. Molecular phylogenetic analyses have yet to be carried out on the forms *S. nigricollis hernandezii*, *S. fuscicollis avilapirensi*, *S. f. mura*, *S. f. primitivus* and *S. weddelli crandalli*.

In the *mystax* group, Hershkovitz (1977, 1979) listed *Jacchus rufiventer* Gray, 1843, as a synonym of *S. l. labiatus*. He recognized that red-bellied tamarins in the north of their range were distinct but argued that it was probably a clinal variation. Groves (2001, 2005) revalidated *rufiventer* with a provisional distribution (indicated by Hershkovitz) that extends south from the Rio Solimões between the rios Madeira and Purus to the Rio Ipixuna, an east bank tributary of the Rio Purus. Groves (2001) also argued that, while *S. m. mystax* and *S. m. pluto* are quite similar to each other, the red-capped *pileatus* is distinct, and he listed it as a separate species, *S. pileatus*. Current evidence indicates that the ranges of *S. m. mystax* and *S. m. pluto* are separated by *pileatus* (Rylands, Coimbra-Filho & Mittermeier, 1993; Rylands & Mittermeier, 2008), indicating that *pluto* would then need to be considered a distinct species as well. The affinities of the little known *S. inustus*, forming a monotypic mottled-face tamarin group, were a mystery for Hershkovitz and for all. The surprising (but geographically reasonable) finding that *inustus* is genetically aligned with the *mystax* group means we have provisionally placed it with the mustached tamarins, although more research is needed. Hershkovitz (1979) reviewed the taxonomy and distributions of *S. imperator*, resurrecting *imperator subgriseus*, earlier (1977) considered a synonym.

Vallinoto *et al.* (2006) found that *S. midas* from the Rio Uatumã separated out from the populations from the Rio Trombetas to the east, about 200 km, indicating a possibility that red-handed (western) and yellow-handed (eastern and northern) forms of *S. midas* may be geographical races or distinct species. Hershkovitz (1977) listed the black-handed tamarin, (*niger*) as a subspecies of *S. midas*. It is now considered a full species, and Tagliaro *et al.* (2005) and Vallinoto *et al.* (2006) indicated that the Rio Tocantins is a barrier to gene flow, and that *S. niger* on either side of the river may be distinct taxa. Gregorin & de Vivo (2013) subsequently revalidated *Saguinus ursulus* Hoffmannsegg as the form

east of the Rio Tocantins, with *S. niger* restricted to the west of the river.

Herskovitz (1977) placed the forms *ochraceus* Herskovitz, 1966, and *martinsi* Thomas, 1912, as subspecies of *S. bicolor*. Groves (2001, 2005) listed them as subspecies of *martinsi*. Coimbra-Filho, Pissinatti & Rylands (1997) indicated the possibility that *ochraceus* may have arisen as a natural hybrid, intermediate between *bicolor* to its west and *martinsi* to the east.

For the *oedipus* group, Herskovitz (1977) considered the Panamanian *geoffroyi* to be a subspecies of *S. oedipus*. Thorington (1976), Hanihara & Natori (1987), Kanazawa & Rosenberger (1988) and Skinner (1991) argued that it should be considered a distinct species (see Rylands *et al.*, 2006).

TAMARINS: DISTRIBUTIONS, ECOLOGY, BEHAVIOUR AND SYMPATRY

The tamarins are very largely Amazonian, extending outside of the basin only into the Guianas (*midas* group) and northern Colombia and Panama (*oedipus* group) (see Figs 5, 6).

Nigricollis group – south of the ríos Caquetá, Caguán and Orteguzza, south through Ecuador and Peru, east of the Andes, to about 16°S in Bolivia, and east to the Rio Ji-Paraná in the state of Rondônia, Brazil.

Mystax/inustus group – south of the Rio Solimões-Amazonas, east of the Río Ucayali, extending east to

the Rio Madeira, east and south to the ríos Uribamba and Inuya in Peru, and as far as the southern bank of the Río Muyumanu in Bolivia, with *inustus* between the Rio Negro and the Rio Solimões, extending west into Colombia.

Midas/bicolor groups – Guiana Shield, east of the ríos Negro and Branco and the Essequibo River in Guyana, north of the Rio Amazonas, and east of the Rio Xingu, south of the Rio Amazonas.

Oedipus group – northern Colombia, basins of the ríos Cauca and Magdalena, and Panama.

The *mystax* group tamarins are broadly sympatric with the *nigricollis* group south of the Rio Solimões-Amazonas and west of the Rio Madeira, and they commonly form mixed-species groups (Heymann, 1997; Bicca-Marques, 1999; Buchanan-Smith, 1999; Heymann & Buchanan-Smith, 2000). The *nigricollis* group tamarins are smaller than those of the *mystax* group. Garber (1992: 470) indicates a body mass of 310–410 g for *S. fuscicollis*, 475–525 g for *S. labiatus* and 525–650 g for *S. mystax*. The *midas/bicolor* and *oedipus* groups are entirely allopatric.

White-mouthed tamarins (the *nigricollis* group) have been the subject of several ecological and behavioural studies, although most have focused on only two taxa, *S. nigrifrons* and *S. w. weddelli* (Table S1). Despite this bias, existing studies suggest that white-mouthed tamarins are ecologically and behaviourally relatively uniform. A striking feature of their ecology, notable even during short observations, is the prevailing use of lower forest strata and the



Figure 5. The geographical distribution of the *nigricollis* group tamarins. Map by Stephen D. Nash. © Conservation International.

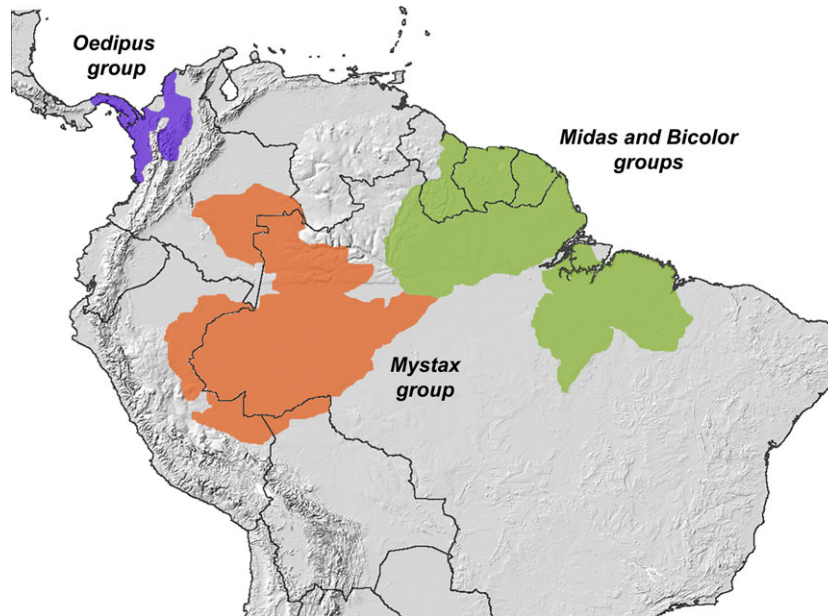


Figure 6. The geographical distributions of the tamarins of the *mystax* group (orange), the *oedipus* group (purple), and the *midas* and *bicolor* groups (green). Map by Stephen D. Nash. © Conservation International.

higher proportion of leaping between vertical trunks in their locomotor repertoire (Yoneda, 1981, 1984; Garber, 1991, 1992; Nyakatura & Heymann, 2010). This is even more noticeable in areas of sympatry with species of the *mystax* group that occupy higher strata than white-mouthed tamarins and more often employ movements along horizontal branches and leaping from canopy to canopy (Garber, 1991; Buchanan-Smith, 1999; Heymann & Buchanan-Smith, 2000; Heymann, 2001; Nyakatura & Heymann, 2010). Comparison of different taxa of white-mouthed tamarins reveals that the prevailing use of lower forest strata is independent of sympatry or allopatry with other tamarin taxa (Yoneda, 1981, 1984; Soini, 1987; Buchanan-Smith, 1999; Heymann, 1997). It is thus not the consequence of vertical displacement by the larger taxa of the *mystax* group but rather represents a uniform trait of white-mouthed tamarins (Buchanan-Smith, 1999).

White-mouthed tamarins are also highly distinct from other tamarin taxa in their prey foraging behaviour. They search for prey concealed in knotholes, crevices, bromeliad tanks and leaf litter, amongst other substrates (Terborgh, 1983; Yoneda, 1984; Peres, 1993b; Smith, 2000; Nadjafzadeh & Heymann, 2008). This is in contrast to the foraging behaviour of larger tamarins, which focus on exposed prey on the surface of leaves, branches and trunks (Terborgh, 1983; Yoneda, 1984; Peres, 1993b; Smith, 2000; Nadjafzadeh & Heymann, 2008). Notably, the hands of white-mouthed tamarins are relatively

longer and narrower than those of other tamarin taxa (Bicca-Marques, 1999), probably as an adaptation to this extractive foraging behaviour.

Interspecific differences in prey foraging behaviour led Garber (1993) to identify three patterns in *Saguinus*. These patterns correspond to the Panamanian tamarin (*S. geoffroyi*; Pattern 1), the *mystax* group and perhaps *S. midas* (Pattern 2), and the white-mouthed tamarins (Pattern 3). While Patterns 2 and 3 are confirmed by several independent studies on different taxa and populations (see above), the validity of Pattern 1 and whether it extends to the sister species of *S. geoffroyi* – *S. oedipus* and *S. leucopus* – remains to be determined. In any case, the ecological distinctiveness of the white-mouthed tamarins provides additional arguments for their taxonomic separation.

While their prey foraging behaviour is distinct, there seem to be few differences between white-mouthed and other tamarins with regard to social organization and group size. In all tamarins, groups contain between two and 11 individuals (reviewed by Digby, Ferrari & Saltzman, 2011). Breeding is generally restricted to a single female, although both successful and unsuccessful breeding by multiple females have been observed (Calegari-Marques, Bicca-Marques & de Azevedo, 1995; Goldizen *et al.*, 1996; Tirado Herrera, Knogge & Heymann, 2000). The prevailing social mating system (*sensu* Kappeler & van Schaik, 2002) is polyandry, but monogamy, polygyny and polygynandry also occur (Terborgh &

Goldizen, 1985; Goldizen, 1988; Heymann, 2000b; Garber *et al.*, 2016).

In contrast to the lack of obvious differences in social organization and mating system, clear differences seem to exist with regard to olfactory communication. While all tamarins studied so far employ anogenital, suprapubic and sternal scent marking (Epple *et al.*, 1993), suprapubic marking seems to be much more frequent in white-mouthed than in other tamarins (Heymann, 2001). Furthermore, scent marking is more complex, i.e. involves the combination of more single acts and more different types of scent marking, in white-mouthed tamarins (Heymann, 2001). Such differences may relate to subtle and, to date, unrecognized differences in social organization, social structure and mating system (*sensu* Kappeler & van Schaik, 2002). However, the scarcity of data on scent marking behaviour in tamarins except for *S. nigrifrons* and *S. mystax* makes this interpretation tentative.

In sum, white-mouthed tamarins differ from other tamarins primarily with regard to forest strata use, locomotion and prey foraging. These differences are substantial and support a generic separation of the white-mouthed from other tamarins.

Except for the recognition of a separate foraging type (Pattern 1) for *S. geoffroyi* by Garber (1993), behavioural or ecological differences between the different species groups of the larger tamarins are less obvious or currently unknown. However, as with the *nigricollis* group, intensive and long-term studies are restricted to a few species, namely from the *mystax* group, currently restricting detailed comparisons (Table S2). The recognition by Ackermann & Cheverud (2002) of a distinct cranio-facial morphology in the *oedipus* group (see also below) suggests that concomitant behavioural or ecological differences may exist, at least between it and the other groups.

TAXONOMIC HISTORY OF GENUS NAMES FOR THE TAMARINS

The generic classification of the tamarins has a complex and confused history. Groves (2001) listed 11 genus names attributed specifically to tamarins, the long-tusked callitrichids, a number of which included the lion tamarins. Here we note some pertinent aspects of callitrichid nomenclature and the genus names attributed to the tamarins, particularly the use of the name *Leontocebus* Wagner, and how, despite its meaning lion monkey, came to be attached to the tamarins, and the *nigricollis* group tamarins in particular.

The first valid name attributed specifically to the tamarins was *Saguinus* Hoffmannsegg, 1807, but this was not recognized for most of the history of

their taxonomic classification – Hershkovitz in 1958 was the first to pull it out of obscurity. In 1812, Étienne Geoffroy Saint-Hilaire created the name *Midas*, with Hoffmannsegg's *Saguinus ursula* as the type, but *Midas* had already been taken for a genus of Diptera.

The name *Leontocebus* was created by Wagner (1839) as a subgenus that included, implicitly, the following species: *Hapale chrysomelas*, *H. chrysopyga*, *H. leonina*, *H. rosalia*, *H. bicolor* and *H. oedipus*. Except for *leonina*, these species' names are in use today. *Simia leonina* was named by von Humboldt (1805) and means lion monkey, *leonina* alluding to the long hair on the neck and mantle giving the appearance of a mane (Palmer, 1904). The description was based on two tamarins that Humboldt saw in captivity in Popayán, Colombia, which were said to have been brought from Mocoa (a river and town at the head of the Río Caquetá) and the Río Putumayo, at the eastern base of the Andean Cordillera Oriental (Hershkovitz, 1949, 1957, 1977; Cabrera, 1956). Wagner (1839) did not designate a type species for *Leontocebus*. Miller (1912) was the first to do so, selecting *Midas leoninus* É. Geoffroy Saint-Hilaire (a synonym of *Simia leonina* von Humboldt, 1805).

Lesson (1840) ordered the subfamily Hapalinae in two genera: (1) the marmosets *Hapale* Illiger, with two subgenera *Hapale* (ear tufts and ringed tail) (= *Callithrix* Erxleben, 1777) and *Mico* (no ear tufts and no rings on the tail) (the latter in use today for the Amazonian marmosets); and (2) the tamarins *Midas* É. Geoffroy Saint-Hilaire, with three subgenera: *Midas*, *Oedipus* Lesson and *Leontopithecus* Lesson. *Oedipus* as a genus name was preoccupied by *Oedipus* Tschudi, 1838, for a group of New World salamanders. *Leontopithecus* comprised three species: *Leontopithecus marikina* (from Rio de Janeiro and Cabo Frio = golden lion tamarin *Leontopithecus rosalia* [Linnaeus, 1766]) (p. 200), *Leontopithecus fuscus* (from Mocoa, Colombia = *Simia leonina* Humboldt) (p. 202) and *Leontopithecus ater* (from São Paulo = black lion tamarin *Leontopithecus chrysopygus* [Mikan 1820]), with a *variété* from the forests between São Pedro d'Alcantara and the Sertão d'Ilhéos and the rios Belmonte (= Jequitinhonha) and Pardo = golden-headed lion tamarin *Leontopithecus chrysomelas* (Kühl, 1820) (p. 204). Lesson was familiar with the name *chrysopygus*, and the reason for his use of *ater* is unknown. Lesson (1840) did not name a type species for this subgenus. Although not stating specifically that it was a subgenus, Lesson (1840: 199) also listed *Marikina* for the pied tamarin, *bicolor* Spix, 1823, which Hershkovitz (1949: 411) used as the genus name for all the tamarins.

So why did Lesson (1840) change the name of *Simia leonina*? Cabrera (1956) noted that *Simia leonina* Humboldt, 1805, was a homonym of *Simia leonina* Shaw, 1800; which he said was the Wanderer or Malabar monkey, which are common names of the lion-tailed macaque, *Macaca silenus*. There is an illustration of the lion-tailed macaque *Macaca silenus* (Linnaeus, 1758) with the caption *Simia silenus* L. (Plate XI) in Wagner (1839) and, following it (Plate XIB), one by a different artist, evidently also of a lion-tailed macaque, that is captioned '*Simia leonina*'. Fooden (1975: 75) noted that '[*Simia*] *leonina*: G. Cuvier, 1817, p.108, (not Shaw, 1800)' was a synonym of *Macaca silenus*.

Reichenbach (1862) was the first to use Lesson's (1840) *Leontopithecus*, and included only *leonina*. Gray (1870) used the name *Leontopithecus* Lesson for the lion tamarins (*rosalia* and *chrysomelas*; no mention of *Leontocebus*), *Oedipus* Lesson for the cotton-top tamarin and Geoffroy's tamarin in northern Colombia and Panama (the latter in a subgenus *Hapanella* Gray), and *Seniocebus* Gray for the pied tamarin, *bicolor* Spix. The remaining tamarins he placed in the genus *Midas* Geoffroy with three subgenera: *Mystax* Gray (*mystax* group), *Midas* (*nigricollis* group) and *Tamarin* Gray (*midas* group). As mentioned, *Oedipus* was preoccupied by a salamander genus, but *Mystax* too was preoccupied by a genus of caddis fly, Trichoptera, *Mystax* Stephens, 1829. *Tamarin*, with the type species *Midas ursulus* Geoffroy, was antedated by *Saguinus* Hoffmannsegg.

The *Catalogus Mammalium* of Trouessart (1904) placed the tamarins in the genus *Midas* É. Geoffroy Saint-Hilaire with the following subgenera: *Leontopithecus* Lesson (including '?*leoninus*?'), *Oedipomidas* Reichenbach, *Tamarinus* nom. nov. (*nigricollis* and *mystax* groups + *chrysopygus*) and *Midas* (*midas* and *bicolor* groups). *Midas mystax* Spix was designated the type species of *Tamarinus* by Pocock (1917).

Elliot (1913) applied the name *Leontocebus* for all the lion tamarins and the moustached and *nigricollis* group tamarins. Evidently ignorant of Miller's (1912) designation of *Midas leoninus* he named *Hapale chrysomelas* Wied (the golden-headed lion tamarin) as the type species of the genus. He divided *Leontocebus* into two subgenera: *Tamarinus* (moustached and *nigricollis* group tamarins, and *L. chrysopygus*) and *Marikina* Reichenbach (lion tamarins *Leontocebus leoninus*, *L. rosalia* and *L. chrysomelas*, but not *L. chrysopygus*). The Colombian and Panamanian bare-face tamarins (*oedipus* and *geoffroyi*) he placed in the genus *Oedipomidas* Reichenbach. The Brazilian bare-face tamarins (*bicolor* and *martinsi*) were placed in the genus *Seniocebus* Gray, and the *midas* group was placed in the genus *Cercopithecus* Gronov.

Elliot (1913) placed *Leontopithecus* Lesson as a junior synonym of *Leontocebus*, because the publication date of Wagner's *Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber*, following Palmer (1904), was given as 1839. In a footnote (p. 225), however, Pocock (1917) cast doubts on the date: 'Elliot, following Palmer gives 1839 as the date of this name, presumably on Sherborn's authority (P.Z.S. 1891, p.587); but although the part of Wagner's edition of Schreber dealing with the monkeys was published, according to Sherborn, in 1839, it is not obvious that the "Übersicht" [overview] and preface were published till 1840. The name may be given the benefit of the doubt, thus carrying priority over *Leontopithecus*.' Pocock cites Sherborn (1891), but in the subsequent work of the same author (Sherborn, 1922–1932) the name *Leontocebus* is clearly stated as being dated from 1839. This is a moot point, however, because Miller (1912) had already designated *Simia leonina* as the type species for *Leontocebus*, and Cabrera (1956) showed that Humboldt's *Simia leonina* was in fact a saddle-back tamarin (see below). Pocock (1917) designated Lesson's *Leontopithecus marikina* [= *L. rosalia*] as the type species for *Leontopithecus* (see Kleiman, 1981), while following Elliot (1913) in placing *Leontopithecus* as a synonym of *Leontocebus*.

In his mordant review of the genera of Hapalidae, then the family name for the marmosets and tamarins, Pocock (1917) restricted the name *Leontocebus* (synonyms: *Leontopithecus* Lesson and *Marikina* Reichenbach) to the lion tamarins based on their long-palmed, syndactylous hands. He included *chrysomelas* and *rosalia*, and wrote (p. 255) that 'this genus probably contains *L. leonina*, Humb., a species about which practically nothing is known apart from the colour.' The black lion tamarin was evidently very little known as well, and Pocock made no comment on Elliot's placement of *Leontocebus chrysopygus* (Wagner) in the subgenus *Tamarinus*. Referring particularly to the morphology of the ear (pinna) he separated the Colombian bare-face tamarins (*oedipus* and *geoffroyi*) in the genus *Oedipomidas* Reichenbach, and placed all the remaining tamarins in the genus *Mystax* Gray. He discounted as such Elliot's use of the names *Seniocebus* (*bicolor* and *martinsi*) and *Cercopithecus* (the *midas* group). Thomas (1922) agreed with Pocock's (1917) revision, but re-introduced *Seniocebus* Gray for *leucopus*, *bicolor* and *martinsi*.

da Cruz Lima (1945), dealing only with the tamarins of Amazonia, adopted a taxonomy with just two genera: *Marikina* Lesson (*bicolor*, *martinsi*) and *Tamarin* Gray (*mystax* group, *nigricollis* group and *midas* group). Simpson (1945) listed *Leontocebus* Wagner as the generic name for all the tamarins and lion tamarins.

Herskovitz (1949) placed the tamarins and lion tamarins in two genera, as follows: *Marikina* Lesson, with three subgenera *Marikina* (*bicolor* group and *leucopus*), *Tamarin* Gray (*nigricollis* group, *midas* group, *mystax* group) and *Oedipomidas* Reichenbach (*oedipus* group, but not *leucopus*); and *Leontocebus* Wagner (lion tamarins, *rosalia*, *chrysomelas* and *chrysopygus*). Herskovitz (1949: 424) concluded that the original description and coloured plate of *Simia leonina* Humboldt indicated ‘a marmoset whose identifiable characters correspond to those of *Leontocebus rosalia*’, and that ‘it is fitting to dispose of *leonina* in the synonymy of *rosalia*’.

Hill (1957) divided the tamarins into four genera as follows: *Tamarin* Link (*midas* group + *inustus*), *Marikina* Lesson (*bicolor* and *martinsi*), *Oedipomidas* Reichenbach (*oedipus* and *geoffroyi*) and *Tamarinus* Trouessart (the entire *nigricollis* group along with the moustached tamarins and *leucopus*). He placed the three lion tamarins (*rosalia*, *chrysomelas* and *chrysopygus*) in the genus *Leontocebus*, with *Leontopithecus* Lesson, 1840 a junior synonym. He did not refer to a type species and did not make reference to Miller (1912). Hill (1957: 262) explained that *Leontocebus leoninus* (Humboldt) was based on two specimens seen living in captivity at Popayán, Colombia ‘at the opposite end of the New World tropics from the natural habitat of the other maned tamarins’ and, with the lack of information (no other evidence of a hapalid occurring in Colombia), and based on the fact that the ‘original description and plate recall *rosalia*’, considered it a synonym.

It was Cabrera (1956) who clarified that Humboldt’s *Simia leonina* was not a lion tamarin, but a member of the white-mouthed tamarin or *nigricollis* group. Herskovitz (1957) reported on his examination of 16 specimens of hairy-faced tamarins that he collected between the ríos Caquetá and Putumayo – the type region of *Simia leonina* – in 1952. Herskovitz (1957: 17) confirmed that ‘except for the very different pygmy marmoset, *Cebuella pygmaea*, no other member of the family *Callitrichidae* [sic] occurs in the area [and that] Discounting vagaries of the original description of *Simia leonina* and liberties taken by the artist in depicting an animal he never saw, the [...] series exhibits all positive diagnostic characters of Humboldt’s monkey.’ With *Simia leonina* being a tamarin and the type species for *Leontocebus* Wagner, Cabrera (1957) placed all the tamarins in the genus *Leontocebus* with three subgenera: *Leontocebus* (*nigricollis* group, *mystax* group, *midas* group), *Oedipomidas* Reichenbach (type *Simia oedipus* Linnaeus: *oedipus* group, but not *leucopus*) and *Marikina* Lesson (type *Midas bicolor* Spix: *bicolor* group and *leucopus*).

In a preface of nomenclatural emendations, Hill (1960: xxi–xxii), having read Cabrera (1956) and Herskovitz (1957), acknowledged that *Leontocebus* pertained to a ‘white-faced’ tamarin, and affirmed that *Leontideus* Cabrera, 1956, was the correct name for the lion tamarins. He informed that the genus names *Tamarin* and *Tamarinus* used in his 1957 volume should, as a result, be considered junior synonyms of *Leontocebus*.

Herskovitz (1958: 53) established *Saguinus* Hoffmannsegg as the ‘first valid generic name for the group of marmosets characterized by normal lower canines’. He cited as synonyms the following: *Leontocebus* Wagner, *Leontopithecus* Lesson, *Tamarin* Gray, *Cercopithecus* Gronov (rejected), *Midas* Humboldt (pre-occupied), *Mystax* Gray (pre-occupied) and *Tamarinus* Trouessart. His 1958 arrangement took into account Hill (1957) and included three subgenera: *Saguinus*, *Oedipomidas* Reichenbach (synonyms *Oedipus* Lesson [pre-occupied] and *Hapanella* Gray) and *Marikina* Lesson (synonym *Seniocebus* Gray). The lion tamarins he placed in the genus *Leontideus* Cabrera (synonyms *Marikina* Reichenbach, and *Leontocebus* of authors not Wagner, 1839). Napier & Napier (1967: 376) followed Herskovitz’s (1958) arrangement. In his *magnum opus* of 1977, Herskovitz avoided the use of subgenera, and instead classified the diversity of the tamarins, all in the genus *Saguinus*, in the six species’ groups discussed at the beginning of this article (see Table 1).

SPECIES GROUPS AND A PROPOSAL FOR THE USE OF THE GENUS NAME *LEONTOCEBUS* FOR THE *NIGRICOLLIS* GROUP

Since 2005, molecular genetic studies have been shedding light on the phylogeny of the callitrichids. They have clearly confirmed the taxonomic arrangement of the tamarin species’ groups proposed by Herskovitz (1977). All but the little known mottled-face tamarin group, *S. inustus*, fall into distinct clades that conform to his groups. *Saguinus inustus*, first described as *Leontocebus midas inustus*, was thought to be a hybrid of *midas* × *nigricollis* by Hill (1957), who put it in the genus *Tamarin* (as *Tamarin inustus*) with the *midas* group (but could not accommodate it in the taxonomic key). Napier & Napier (1967) placed it in the subgenus *Marikina* with the *bicolor* group and *S. leucopus*. Herskovitz (1977) placed it in its own group. A molecular genetic reanalysis by Buckner *et al.* (2015), using a D-Loop sequence for this species from Jacobs Cropp *et al.* (1999), placed *inustus* in the *mystax* group, as did Boubli *et al.* (2015), using cytochrome *b* sequences

from three *S. inustus* individuals wild-caught from known provenance.

The place of *Saguinus leucopus* was for many years in doubt. Elliot (1913) made no reference to it. Thomas (1922) placed it in the genus *Seniocebus* Gray, along with *bicolor* and *martinsi*. Hershkovitz (1949), Cabrera (1957) and Napier & Napier (1967), likewise, aligned it with *bicolor* and *martinsi*, but in the subgenus *Marikina* Lesson. Hill (1957) considered it to be anomalous and placed it in *Tamarinus* Trouessart, but, as with *inustus*, was unable to accommodate it in his taxonomic key. Hershkovitz (1977) placed it as a member of the *oedipus* group, an arrangement borne out in subsequent morphological (Hanihara & Natori, 1987; Natori, 1988; Moore & Cheverud, 1992; Natori & Hanihara, 1992) and molecular genetic analyses (Tagliaro *et al.*, 2005; Buckner *et al.*, 2015).

The estimated ages of the lineages are shown in Tables 2 and 3 and indicate the phylogeny summarized in Fig. 4. The earliest lineage leading to a crown group of tamarins was the *nigricollis* group (the small-bodied tamarins) that appeared in the early Late Miocene, around 9 Ma, the second to appear was the *mystax* group in the middle Late Miocene, around 7 Ma, and the third was the *oedipus* group, right at the end of the Miocene, entering the Pliocene, around 5 Ma. The lineages of the *bicolor* and *midas* groups appeared around 2.5 Ma, during the Pliocene–Pleistocene transition. In comparison, the diversification of the marmosets began much later, with the lineage of the Atlantic forest marmosets, *Callithrix*, appearing about 5.4 Ma (end of the Miocene) and the Amazonian marmoset split of *Cebuella* and *Mico* occurring about 4.4 Ma, in the Early Pliocene.

Our proposal here is that the Late Miocene divergence (11–8 Ma) between small- and large-bodied tamarin lineages be reflected in tamarin taxonomy by raising the *nigricollis* group to the generic level. This is in accordance with the recommendations of Goodman *et al.* (1998); (see also Groves, 2001: 17–20) regarding an age-related taxonomic classification of the primate clades. As stated by Groves (2001: 18), one of the authors of the proposed classification of Goodman *et al.* (1998), a proviso is that any alterations must be made in line with the ‘principle of least violence’, meaning that it is important to preserve the ranks with the content with which they are widely recognized. Goodman *et al.* (1998) proposed 11–7 Ma (Late Miocene) as the appropriate age of the last common ancestor of different crown groups that should be considered distinct genera.

In addition to the evidence for at least 8 Myr of evolutionary isolation of the *nigricollis* group, as has already been discussed, the morphology (smaller size) and ecological differences that permit sympatry

and mixed-species groups with the *mystax* group tamarins also support a distinction at the generic level. The *oedipus* group (Panama and northern Colombia) and the *midas/bicolor* groups (Guiana Shield) are entirely allopatric.

The assessment of the interspecific affinities in the tamarins has been based on pelage, size, appearance and geographical distribution (sympatry and proximity), but morphological studies in recent times have focused on the cranio-facial and dental morphology. Hanihara & Natori (1987) made dental measurements and, applying a numerical taxonomy, found that the *nigricollis* group (*S. nigricollis* and *S. fuscicollis*) was distinct from the *mystax* group (*S. labiatus* and *S. mystax*), and that the *oedipus* group (*S. oedipus*, *S. geoffroyi* and *S. leucopus*) was clearly separated from both. A cladistic analysis of dental and cranial morphology by Natori (1988) had the *oedipus* group again separate, and the *nigricollis* group, with *inustus*, separate from the *mystax* group and the *bicolor/midas* groups. Although the cladogram conformed to the species groups, it contained a trichotomy and a pentachotomy, and Natori (1988) indicated that more characters need to be included to obtain a clearer phylogenetic pattern. A study of tooth shape by Natori & Hanihara (1992) again separated out *S. oedipus* and *S. geoffroyi*, the *midas* group and the *nigricollis* group. *Saguinus leucopus* and *S. imperator* formed a separate pair in the dendrogram, *S. inustus* grouped with *S. mystax* and *S. labiatus*, and *S. bicolor* aligned with the *midas* group. A combined dental and cranial morphometric analysis of the hairy-faced tamarins by Hanihara & Natori (1989) clearly separated the *nigricollis* group (*S. nigricollis* and *S. fuscicollis*) from the *mystax* group (*S. imperator*, *S. labiatus* and *S. mystax*), and both were distinct from the *midas* group (*S. midas* and *S. niger*).

Ackermann & Cheverud (2002), also studying cranio-facial variation in the tamarins, concluded that there was divergent size selection responsible for the morphological diversification of the two major clades – the large-bodied tamarins and the small-bodied *nigricollis* group – but that diversification was not due to convergent size selection alone, occurring also for non-allometric aspects of the cranial shape. Their results were consistent with Garber’s (1992) proposal that selection was occurring for specialization in the use of vertical postures to forage for animal prey on large vertical supports (tree trunks). While the patterns of interspecific cranio-facial variation did not match DNA-based phylogenetic relationships, their results did largely agree with the species groups, the exceptions being that although *Saguinus geoffroyi* and *S. oedipus* came out as extreme outliers, *S. leucopus* was more similar to the other *Saguinus*, and

the *bicolor* group was more similar to the *nigricollis* group than the *midas* group (Ackermann & Cheverud, 2000).

A distinctive feature of the *oedipus* group, which impressed Pocock (1917), is their small square ears, and through all the confused taxonomic history of the tamarins described above, the *oedipus* group has consistently been singled out, either as a subgenus (Lesson, 1840; Gray, 1870; Trouessart, 1904; Hershkovitz, 1949, 1958; Napier & Napier, 1967) or as a genus (Reichenbach, 1862; Elliot, 1913; Pocock, 1917; Thomas, 1922; Cabrera, 1957; Hill, 1957). In conclusion, the patterns in dental and cranial morphology agree with the species groups of *nigricollis*, *mystax*, *oedipus*, *midas* and *bicolor*.

GENUS *LEONTOCEBUS* WAGNER

Wagner, J. A. 1839. *Schreber's Säug.* Suppl. 1. 1839: 9th page [marked v, the 3rd page of the *Übersicht*]. Type species designated by Miller (1912: 380) *Midas leoninus* É. Geoffroy Saint-Hilaire, 1812 (= *Simia leonina* Humboldt, 1805; = *Leontopithecus fuscus* Lesson, 1840). Type species designated by Elliot (1913: 194) *Hapale chrysomelas* Wied, 1820 (a lion tamarin). Pocock (1917: 255) followed Elliot (1913) in listing *chrysomelas* as the type species.

Synonyms

Saguinus Hoffmannsegg, G. von. 1807. *Mag. Gesellsch. Naturforsch. Freunde, Berlin* 1: 102. Type species *Saguinus ursula* Hoffmannsegg, 1807. In part. For the *nigricollis* group as applied by Napier and Napier (1967), Napier (1976), Hershkovitz (1977, 1982), Rylands *et al.* (1993, 2000, 2012), Groves (2001, 2005), and Rylands & Mittermeier (2013).

Marikina Lesson, R.-P. 1840. *Spec. Mamm. Bim. Quadrum.* p. 199. Type species *Marikina bicolor* [= *Midas bicolor* Spix, 1823]. In part. Vieira (1955) and Hershkovitz (1949) applied this genus name to all tamarins.

Tamarin Gray, J. E. 1870. *Cat. Monkeys, Lemurs, Fruit-eating Bats. Brit. Mus.*, p. 68. Subgenus of *Midas*. Type species *Midas ursulus* É. Geoffroy Saint-Hilaire (= *Saguinus ursula* Hoffmannsegg, 1807). In part. For the *nigricollis* group as applied by da Cruz Lima (1945).

Tamarinus Trouessart, E.-L. 1904. *Cat. Mamm., Suppl.*, p. 29. Type species designated by Pocock, 1917, *Ann. Mag. Nat. Hist.*, ser. 8, 20: 256 *Midas mystax* Spix, 1823. In part. Hill (1957) applied this genus name to the *mystax* and *nigricollis* groups, and *Saguinus leucopus*.

White-mouthed tamarins, *nigricollis* species group

Facial skin, rhinarium, ears, and external genitalia, blackish; cheeks, temple, forehead, and crown densely covered with long hairs; broad circumbuccal band thickly haired white and not encircling muzzle; long and conspicuous moustache absent in adults; ears thinly haired and mostly or entirely exposed, not concealed by mane or preauricular tufts; colour of middle or lower back more or less well defined from shoulders; terminal half or more of tail uniformly coloured, not banded, barred, or with nearly entire dorsal surface sharply defined from ventral (Hershkovitz, 1977: 621–622). Restricted to the Amazon forests, east of the Andes, east to the rios Madeira and Ji-Paraná and Mamoré-Guaporé. Smaller than other tamarins of the genus *Saguinus*. Mean body weights of free-ranging *nigricollis* group tamarins provided by Smith and Jungers (1997) are as follows: *L. nigricollis* males 468 g ($N = 8$) and females 484 g ($N = 6$); *L. fuscicollis* males 343 g ($N = 69$) and females 358 g ($N = 55$). Soini (1983, 1990) recorded the mean adult body mass of three species: *L. illigeri* males 292 g ($N = 9$) and females 296 g ($N = 4$); *L. fuscicollis* males 328 g ($N = 9$) and females 338 g ($N = 10$); and *L. nigrifrons* males 354 g ($N = 51$) and females 369 g ($N = 41$). By comparison, mean body weights of free-ranging *S. mystax mystax* provided by Soini and Soini (1990) are as follows: males 501 g ($N = 161$) and females 530 g ($N = 104$). *Saguinus l. labiatus* males average 477 g ($N = 34$) and females 515 g ($N = 18$) (F. Encarnación in Snowdon & Soini, 1988). *Saguinus imperator* males average 474 g ($N = 4$) and a female weighed 475 g ($N = 1$). Mean body weight of *S. midas* males was 533 g ($N = 3$) and a female weighed 450 g ($N = 1$) (Fleagle & Mittermeier, 1980). Mean body weight of *S. oedipus* males was 418 g ($N = 37$) and females 404 g ($N = 29$) (Smith & Jungers, 1997).

White-mouthed tamarins differ from other tamarins regarding strata use, locomotion, and foraging. A number are sympatric with moustached tamarins, forming mixed-species groups. They travel and forage in the lower strata, below the moustached tamarins, and, associated with this, use a higher proportion of leaping between vertical supports in their locomotory repertoire, compared with the moustached tamarins that use more quadrupedal walking and running and leaping on horizontal branches. The white-mouthed tamarins' use of the lower forest strata is independent of sympatry or allopatry with other tamarin taxa.

The *nigricollis* group tamarins forage more for concealed animal prey in specific sites (e.g. knotholes, crevices, bromeliad tanks) than the moustached tamarins, which forage more by foliage gleaning and looking along branches for exposed, camouflaged prey. Associated with their manipulative foraging, white-mouthed tamarins have hands that are longer

and narrower than those of other tamarins (Bicca-Marques, 1999).

The lineage that led to the *nigricollis* species group diverged from other tamarins 11–8 Ma. The *nigricollis* species group is sister to all other tamarins.

Leontocebus fuscus (Lesson, 1840). Lesson's saddle-back tamarin

Leontopithecus fuscus Lesson, R.-P. 1840. *Spec. Mamm. Bim. Quadrup.*, p. 202.

Type locality. Colombia: Plaines de Mocoa, Putumayo, between the ríos Putumayo and Caquetá.

Leontocebus nigricollis nigricollis (Spix, 1823). Spix's black-mantle tamarin

Midas nigricollis Spix, J. B. von. 1823. *Sim. Vespert. Brasil.*, p. 28.

Type locality. Brazil: near São Paulo de Olivença, north bank of the Rio Solimões, Amazonas (Hershkovitz, 1977: 632).

Leontocebus nigricollis graellsii (Jiménez de la Espada, 1870), Graells' black-mantle tamarin

Midas graellsii Jimenez de la Espada, M. 1870. *Bol. Rev. Univers. Madrid*, p.19.

Type locality. Peru: restricted by Hershkovitz (1977: 629) to right bank Río Napo, opposite Tarapoto and above the mouth of the Río Curaray.

Leontocebus nigricollis hernandezi (Hershkovitz, 1982). Hernández-Camacho's black-mantle tamarin
Saguinus nigricollis hernandezi Hershkovitz, P. 1982. *Proc. Biol. Soc. Wash.* 95(4): 649.

Type locality. Colombia: Río Peneya, a small tributary of the Río Caquetá, entering from left (north) about 15 km above mouth of the Río Caguán, and about 50 km in a straight line below village of La Tagua, Intendencia de Caquetá, approximately 150 m above sea level.

Leontocebus leucogenys (Gray, 1866). Andean saddle-back tamarin

Midas leucogenys Gray, J. E. 1866. *Proc. Zool. Soc. Lond.* 1865: 735.

Type locality. Brazil. The type (British Museum) is a juvenile of unknown origin. Restricted by Hershkovitz (1966a) to the Department of Huánaco, Peru. Fixed by Napier (1976) as Peru, Sarayacu.

Leontocebus illigeri (Pucheran, 1845). Illiger's saddle-back tamarin

Hapale illigeri Pucheran, J. 1845. *Rev. Mag. Zool., Paris* 8: 336.

Type locality. Colombia: restricted to the Colombian bank of the Rio Solimões by Hershkovitz (1949),

but altered to the left bank of the lower Río Ucayali near its mouth in Loreto, Peru, by Hershkovitz (1966a: 328).

Leontocebus lagonotus (Jiménez de la Espada, 1870). Red-mantle saddle-back tamarin

Midas lagonotus Jimenez de la Espada, 1870. *Bol. Rev. Univers. Madrid*, p. 11.

Type locality. Peru: Destacamento (=Francisco de Orellana), confluence of the ríos Napo and Amazonas. Forests on the right bank of the Río Napo (Hershkovitz, 1977: 655).

Leontocebus tripartitus (Milne-Edwards, 1878). Golden-mantle saddle-back tamarin

Midas tripartitus Milne-Edwards, A. 1878. *Bull. Nouv. Arch. Mus. Hist. Nat. Paris*, sér. 2, 1: 161.

Type locality. Ecuador: Rio Napo, Oriente.

Leontocebus fuscicollis fuscicollis (Spix, 1823). Spix's saddle-back tamarin

Midas fuscicollis Spix, J. B. von. 1823. *Sim. et Vespert. Brasil.*, p. 27, fig. 20.

Type locality. Brazil. 'It occurs near the district of São Paulo de Olivença in the forests between the Solimões and Içá'. Restricted by Hershkovitz (1977: 645) to the vicinity of São Paulo de Olivença on the south bank of the Rio Solimões.

Leontocebus fuscicollis avilapiresi (Hershkovitz, 1966). Ávila Pires' saddle-back tamarin

Saguinus fuscicollis avilapiresi Hershkovitz, P. 1966. *Folia Primatol.* 4: 386.

Type locality. Brazil: mouth of the Lago de Tefé, Rio Solimões, Amazonas.

Leontocebus fuscicollis primitivus (Hershkovitz, 1977). Hershkovitz's saddle-back tamarin

Saguinus fuscicollis primitivus Hershkovitz, P. 1977. *Living New World Monkeys (Platyrrhini) With an Introduction to Primates*, 1: 1022.

Type locality. Brazil: Rio Juruá, Amazonas.

Leontocebus fuscicollis mura (Röhe, Silva-Júnior, Sampaio & Rylands, 2009). Gray-fronted saddle-back tamarin

Saguinus fuscicollis mura Röhe, F., Silva-Júnior, J. de S., Sampaio, R. & Rylands, A. B. 2009. *Int. J. Primatol.* 30: 536.

Type locality. Brazil: Campina Tupana, near the Rio Tupana, interfluvium of the lowest (northernmost) reaches of the rios Madeira and Purus, north (left bank) of the Rio Tupana, tributary of the Rio Madeira; 04°09'26.5"S; 60°07'56.0"W.

Leontocebus nigrifrons (I. Geoffroy Saint-Hilaire, 1850). Geoffroy's saddle-back tamarin
Hapale nigrifrons Geoffroy Saint-Hilaire, I. 1850. *C. R. Acad. Sci. Paris*, 31: 875.

Type locality. Unknown. Restricted by Hershkovitz (1977: 646) to lower Río Yavari, Loreto, Peru.

Leontocebus cruzlimai (Hershkovitz, 1966). Cruz Lima's saddle-back tamarin
Saguinus fuscicollis cruzlimai Hershkovitz, P. 1966. *Folia Primatol.* 4: 388.

Type locality. Brazil: said to be from upper Rio Purus region, Amazonas. The description by Hershkovitz (1966b) was based on a painting by Eládio da Cruz Lima published in his book *Mammals of Amazônia. Volume 1. General Introduction and Primates* (1945). The painting was of a specimen in the Museu Paraense Emílio Goeldi, Belém. The specimen was lost and never seen by Hershkovitz (1966b). Sampaio *et al.* (2015) designated a neotype from the 'Vicinity of the Cujuri community (about six families) in the Purus National Forest, left bank of the Rio Inauini (left bank affluent of the middle Rio Purus), municipality of Pauini, Amazonas, Brazil (8°11'12.3" S; 67°11'12.3"W)'.
Leontocebus weddelli weddelli (Deville, 1849). Weddell's saddle-back tamarin
Midas weddelli Deville, É. 1849. *Rev. Mag. Zool.*, 2^e série, 1, 1849: 55.

Type locality. Bolivia, Apolobamba (=Caupolicán) Province, La Paz (Hershkovitz, 1977: 661).

Leontocebus weddelli melanoleucus (Miranda Ribeiro, 1912). White saddle-back tamarin, White mantled tamarin
Mico melanoleucus Miranda Ribeiro, A. de. 1912. *Brasil. Rundsch.* 2(1): 22.

Type locality. Brazil: Pará. Restricted to Santo Antônio, Rio Eirú, Amazonas, by de Carvalho (1957b: 222).

Leontocebus weddelli crandalli (Hershkovitz, 1966). Crandall's saddle-back tamarin
Saguinus fuscicollis crandalli Hershkovitz, P. 1966. *Folia Primatol.* 4: 389.

Type locality. Unknown provenance.

GENUS SAGUINUS HOFFMANNSEGG

Hoffmannsegg, G. von. 1807. *Mag. Gesellsch. Naturforsch. Freunde, Berlin* 1: 102. Type species, by monotypy, *Saguinus ursula* Hoffmannsegg, 1807.

Synonyms

Cercopithecus Gronovius, L. T. 1763. *Zoophylacium Gronovianus*, fasc. 1, p. 5. Included *Simia midas* Linnaeus, 1758, designated by Elliot (1911) as the type species. Name unavailable: Opinion 89, ICZN 1925.

Midas Geoffroy-Saint-Hilaire, É. 1812. *Rec. Obs. Zool. Anat. Comp.* p.361. Type species *Midas ursulus* É. Geoffroy Saint-Hilaire (= *Saguinus ursula* Hoffmannsegg, 1807). Preoccupied by *Midas* Latreille, 1796, a genus of Diptera.

Leontocebus Wagner, J. A. 1839. *Schreber's Säug. Suppl.* 1. 1839: xi [marked v]. Type species designated by Miller (1912; 380) *Midas leoninus* É. Geoffroy Saint-Hilaire, 1812 [= *Simia leonina* Humboldt, 1805; = *Leontopithecus fuscus* Lesson, 1840]. Type species designated by Elliot (1913; 194) *Hapale chrysomelas* Wied, 1820. Pocock (1917; 255) followed Elliot (1913) in listing *chrysomelas* as the type species. In part. Elliot (1912) and Cabrera (1957) applied this genus name to all of the tamarins.

Marikina Lesson, R.-P. 1840. *Spec. Mamm. Bim. Quadrum.* p. 199. Type species *Marikina bicolor* [= *Midas bicolor* Spix, 1823].

Oedipus Lesson, R.-P. 1840. *Spec. Mamm. Bim. Quadrum.* 184, 197–200, 1840. Subgenus of *Midas*. Type species *Oedipus titi* (= *Simia oedipus* Linnaeus), from Pará, Brazil. Name preoccupied by *Oedipus* Tschudi, 1838; a genus of Amphibia.

Oedipomidas Reichenbach, H. G. L. 1862. *Vollständ. Naturgesch. Affen.* 5, pl. 11, figs 18–20, 1862. New name for *Oedipus* Lesson, 1840. Type species designated by Elliot (1913: 213): *Simia oedipus* Linnaeus.

Hapanella Gray, J. E. 1870. *Cat. Monkeys, Lemurs and Fruit-eating Bats, Brit. Mus.*, 65, 1870. Subgenus of *Oedipus* Lesson. Type *Hapale geoffroyi* Pucheran, 1845 [= *Saguinus geoffroyi*].

Mystax Gray, J. E. 1870. *Cat. Monkeys, Lemurs and Fruit-eating Bats, Brit. Mus.*, 66, 1870. (subgenus of *Midas*). Type species *Midas mystax* Spix, and included *M. labiatus* É. Geoffroy Saint-Hilaire and *M. Rufiventer* Gray. Preoccupied by *Mystax* Stephens, 1829; a genus of Trichoptera.

Tamarin Gray, J. E. 1870. *Cat. Monkeys, Lemurs, Fruit-eating Bats. Brit. Mus.*, p. 68. Subgenus of *Midas*. Type species *Midas ursulus* É. Geoffroy Saint-Hilaire (= *Saguinus ursula* Hoffmannsegg, 1807).

Seniocebus Gray, J. E. 1870. *Cat. Monkeys, Lemurs, Fruit-eating Bats. Brit. Mus.*, p. 68. Type species *Seniocebus bicolor* (= *Midas bicolor* Spix, 1823).

Tamarinus Trouessart, E.-L. 1904. *Cat. Mamm., Suppl.*, p.29. Type species designated by Pocock,

1917, *Ann. Mag. Nat. Hist.* ser. 8, 20: 256, *Midas mystax* Spix, 1823.

Moustached tamarins and the mottled-face tamarin, *mystax* species group

Saguinus mystax mystax (Spix, 1823). Spix's moustached tamarin

Midas mystax Spix, J. B. von. 1823. *Sim. Vespert. Brasil.*, p. 29, pl. 22.

Type locality. Brazil: near São Paulo de Olivença, south bank of Rio Solimões, Amazonas.

Saguinus mystax pileatus (I. Geoffroy Saint-Hilaire & Deville, 1848). Red-cap moustached tamarin

Midas pileatus Geoffroy Saint-Hilaire, I & Deville, E. 1848. *Comptes Rendus Acad. Sci., Paris* 27: 499.

Type locality. Brazil: Rio Javari. Near Pebas, Peru. Hershkovitz (1977) informed that it occurs in neither location and restricted it to Lago de Tefé (Ega), near its mouth at the Rio Solimões, Brazil, where collections were made by the Castelnau Expedition.

Saguinus mystax pluto (Lönnerberg, 1926). White-rump moustached tamarin

Mystax pluto Lönnerberg, E. 1926. *Ark. Zool., Stockholm* 18B(9): 1.

Type locality. Brazil: Ayapuá [Lago], Rio Purus, Amazonas. Lago Ayapuá is west of the Rio Purus. Hershkovitz (1977) believed that the type locality would in fact have been opposite the Lago Ayapuá, on the right bank of the Rio Purus, due to his conviction that its range was between the rios Purus and Madeira, and as such in sympatry with the red-bellied tamarin (*labiatus*). Based on the three available specimen localities used by Hershkovitz (1977) to delimit the distribution of this subspecies, Rylands *et al.* (1993) argued that in fact the more likely range for this very little known tamarin would lie between the rios Purus and Coari, west of the Purus. *Tamarinus mystax pileatus* occurs west of the Rio Coari to the Rio Tefé.

Saguinus labiatus labiatus (É. Geoffroy Saint-Hilaire, 1812). Geoffroy's red-bellied tamarin

Simia labiata Geoffroy-Saint-Hilaire, É. 1812. *Rec. Observ. Zool. Anat. Comp.* 1: 361.

Type locality: 'Probablement le Brésil'; restricted by Cabrera (1957) to Lago Joanacan [=Lago Janauacá], Amazonas, Brazil; type locality of *Midas erythrogaster* Reichenbach, 1862. Lago Janauacá is in the supposed range of *rufiventer* Gray, considered a synonym by Cabrera (1957). The type locality suggested by Hershkovitz (1977: 692) is 'somewhere between the rios Purus and Madeira, south of the

Rio Ipixuna, in the region of *griseovortex* Goeldi, 1907'. The type of *Midas griseovortex* was collected during Goeldi Museum expeditions (1903–1904) in the Purus and Acre regions (Goeldi, 1907). de Carvalho (1959: 460) restricted it to upper Rio Purus, Bom Lugar, Amazonas.

Saguinus labiatus thomasi (Goeldi, 1907). Thomas's red-bellied tamarin

Midas thomasi Goeldi, E. A. 1907. *Proc. Zool. Soc. Lond.* (1907): 89.

Type locality. Brazil: Tonantins, Rio Tonantins, north bank of the Rio Amazonas [=Solimões], below mouth of Rio Içá, Amazonas, Brazil (Hershkovitz, 1977).

Saguinus labiatus rufiventer (Gray, 1843). Gray's red-bellied tamarin

Jacchus rufiventer Gray, J. E. 1843. *Ann. Mag. Nat. Hist.* 1st series, 12: 398.

Type locality. Unknown. Gray (1843) informed that it came from Mexico. Oldfield Thomas told Goeldi (1907) that the specimen had been obtained from a dealer. Recognized as valid by Groves (2001), who indicated that it occurred south of the Rio Solimões between the rios Purus and Madeira, below the Rio Ipixuna, based on Hershkovitz's (1977) description of geographical variation in *S. labiatus labiatus*. According to Cabrera (1957), the type locality of *Midas erythrogaster* Reichenbach, 1862, is Lago Janauacá, south of the Rio Solimões, Amazonas, Brazil, and this would be appropriate for this subspecies, presuming that *erythrogaster* is a synonym. Reichenbach (1862: 14) stated that his *Midas erythrogaster* is very similar to *M. rufiventer*.

Saguinus imperator imperator (Goeldi, 1907). Black-chinned emperor tamarin

Midas imperator Goeldi, E. A. 1907. *Proc. Zool. Soc. Lond.* (1907): 93.

Type locality. Brazil: Upper Rio Purus. Two [cotypes] from the Rio Acre and three from the upper Rio Purus. de Carvalho (1959: 460) designated a lectotype from 'upper Rio Purus, state of Amazonas, in Bom Lugar (or perhaps Monte Verde)'. From a map published by Sneath (1909), a member of the expedition that resulted in the collection of the types of this species, Hershkovitz (1979) placed Monte Verde on the right bank of the Rio Purus, just above the mouth of the Rio Acre, and Bom Lugar on the right bank the Rio Purus just below the mouth of the Acre, a little north of what is today the town of Boca do Acre. From our understanding of the distributions of *S. labiatus labiatus* and *S. i. imperator* today, it is

evident that Monte Verde, not Bom Lugar, should be the type locality for the black-chinned emperor tamarin. Goeldi's (1907) *Midas griseovertex*, a junior synonym of *S. l. labiatus*, was collected in Bom Lugar (de Carvalho, 1959). As such, Monte Verde should be considered the type locality, and not Bom Lugar.

Saguinus imperator subgrisescens (Lönningberg, 1940). Bearded emperor tamarin

Mystax imperator subgrisescens Lönningberg, E. 1940. *Ark. Zool., Stockholm* 32A(10): 9.

Type locality. Brazil: Santo Antônio, western bank of the Rio Eiru, near its confluence with the upper Rio Juruá, Amazonas.

Saguinus inustus (Schwarz, 1951). Mottled-face tamarin

Leontocebus midas inustus Schwarz, E. 1951. *Am. Mus. Novit.* (1508): 1.

Type locality. Brazil: Tabocal, between Rio Japurá and Rio Negro, state of Amazonas.

Midas tamarins, *midas* species group

Saguinus midas (Linnaeus, 1758). Midas tamarin, golden-handed tamarin

[*Simia*] *midas* Linnaeus, C. 1758. *Syst. Nat.* 10th ed., p. 28.

Type locality. 'America' as given by Linnaeus. Restricted by Schreber (1775, *Säugetiere* 1: 132) to Suriname (Hershkovitz, 1977).

Saguinus niger (É. Geoffroy Saint-Hilaire, 1803). Western black-handed tamarin

Sagouin niger Geoffroy Saint-Hilaire, É. 1803. *Cat. Mamm. Mus. Hist. Nat., Paris*, p. 13.

Type locality. Said to be from Cayenne, but restricted by Hershkovitz (1977) to Belém do Pará, Pará, the type locality of *ursula* Hoffmannsegg. Hershkovitz considered *ursula* to be a junior synonym. Voss, Lunde, and Simmons (2001) designated a neotype of *niger* from Cametá, western bank of the Rio Tocantins, Pará, Brazil. Gregorin and de Vivo (2013) re-validated *ursulus*.

Saguinus ursulus Hoffmannsegg, 1807. Eastern black-handed tamarin

Saguinus ursula Hoffmannsegg, G. von. 1807. *Mag. Gesell. Naturf. Fr., Berlin* 1: 102.

Type locality. Brazil: Vicinity of Pará (=Belém do Pará), Pará.

Brazilian bare-face tamarins, *Saguinus bicolor* species group

Saguinus bicolor (Spix, 1823). Pied tamarin, pied bare-face tamarin

Midas bicolor Spix, J. B. von. 1823. *Sim. Vespert. Brasil.*, p. 30, pl. 24.

Type locality. Brazil: near the village of Rio Negro (=Manaus), Barra do Rio Negro, Amazonas.

Saguinus martinsi martinsi (Thomas, 1912). Martins' bare-face tamarin

Leontocebus martinsi Thomas, O. 1912. *Ann. Mag. Nat. Hist.* 8th ser., 9: 85.

Type locality. Brazil, Faro, north side of the Rio Amazonas, near mouth of Rio Nhamundá, Pará.

Saguinus martinsi ochraceus Hershkovitz, 1966. Ochraceous bare-face tamarin

Saguinus bicolor ochraceus Hershkovitz, P. 1966. *Folia Primatol.* 4: 391.

Type locality. Brazil: mouth of Rio Paratucú, a right bank tributary of the Nhamundá, Amazonas.

Colombian and Panamanian bare-face tamarins, *oedipus* species group

Saguinus oedipus (Linnaeus, 1758). Cotton-top tamarin

[*Simia*] *oedipus* Linnaeus, C. 1758. *Syst. Nat.* 10th ed., p. 28.

Type locality. 'America' as given by Linnaeus. Determined as western Colombia by Humboldt (1812, *Rec. Obs. Zool. Anat. Comp.* p. 337), and restricted to the lower Río Sinú, Córdoba, Colombia, by Hershkovitz (1949: 415).

Saguinus geoffroyi (Pucheran, 1845). Geoffroy's tamarin

Hapale geoffroyi Pucheran, J. 1845. *Rev. Mag. Zool. Paris*, 8: 336.

Type locality. 'Panamá'. Restricted to the Canal Zone by Hershkovitz (1949: 417).

Saguinus leucopus (Günther, 1877). Silvery-brown bare-face tamarin, white-footed tamarin

Hapale leucopus Günther, A. 1877. *Proc. Zool. Soc. Lond.* (1876): 743.

Type locality. Colombia: near Medellín, Antioquia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Ecological and behavioural field studies of white-mouthed tamarins.

Table S2. Ecological and behavioural field studies of large-bodied tamarins.