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Taxonomy and systematics of the Neotropical primates: a review and update

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The database of the IUCN SSC Primate Specialist Group currently (December 2023) registers 218 species and subspecies of Neotropical primates in 24 genera and five families. In the early 1960s, the diversity of Neotropical primates was estimated to be around 200 species and subspecies. From then, through the 1970s to the mid-1990s, however, the perception of the region's primate diversity dropped, and reached an all-time low at 83 species and subspecies in 1980 (*A World List of Mammalian Species*, G. B. Corbet and J. E. Hill, British Museum (Natural History), Comstock Publishing, Cornell University Press, London and Ithaca). Interest in taxonomy and primate field research in the Neotropics was subdued up to the late 1970s. Change was sparked by the burgeoning capture of primates for biomedical research in the 1950s and 1960s, and the increasing destruction of the Amazon rainforests from the late 1970s. The numbers increased, at first slowly, but then, in 1995, they leapt back to the 200s in anticipation of a book by C. P. Groves (2001, *Primate Taxonomy*, Smithsonian Institution Press, Washington, DC). The species' counts (not including subspecies) rose due to the adoption of the Phylogenetic Species Concept over the Biological Species Concept, the former favoring the category of species over subspecies. In this article, we discuss the changes in species and subspecies numbers in the classification of the Neotropical primates, and report on the taxonomic changes resulting from taxonomic research ongoing since 2012. We emphasize the importance of taxonomic research for an understanding of the diversity of primates, and for conservation planning, not least in identifying the populations that are threatened.

KEYWORDS

Platyrrhini, systematics, Phylogenetic Species Concept, Biological Species Concept, taxonomic inflation, new species

Introduction

The fundamental importance of a solid understanding of the diversity of life, pursued through the scientific disciplines of systematics and taxonomy, is well emphasized, reviewed, and discussed by [Mayr and Ashlock \(1991\)](#). They cited [Elton \(1947\)](#), who explained that without it “the ecologist is helpless” (p.116). Systematics and taxonomy (the

naming of species) (see Simpson, 1961) are the bedrock of both theoretical and applied biology, and Mayr and Ashlock included as examples of the latter medicine, public health, agriculture, the management of natural resources, and conservation.

Here we report on some aspects of the progress and current status of the taxonomy and systematics of the Neotropical primates, emphasizing particularly the preeminent need to identify how many species and subspecies there are and where they occur as the baseline for their conservation. Phylogenetic and phylogenomic analyses are not only an extraordinarily helpful means by which we can distinguish species, but named, they can be identified in evolutionary lineages, providing for conservation strategies based on what have been termed Evolutionarily Significant Units (ESU), prioritizing all taxonomic levels, to subspecies and populations (Ryder, 1986; Avise, 1989; Mello et al., 2018), and allowing for adaptive evolutionary conservation (Fraser and Bernatchez, 2001).

In the case of the Neotropics, concern for primate conservation arose in the 1970s, when Amazonia became a target for development and the exploitation of its natural resources (Goodland and Irwin, 1975). One of those coveted natural resources concerned the use of Neotropical primates for biomedical research (PAHO, 1976; Mittermeier et al., 1993; Rylands and Anzenberger, 2012; Rylands and Mittermeier, 2022). In an address to the Pan American Health Organization (PAHO), Thorington (1976) provided a summary of the incipience and disarray, and, frankly, disregard in the classification of the New World monkeys at that time. Thorington explained that zoological classifications could serve different utilitarian purposes. He suggested that one based on morphology could well serve dental research, while another on serum proteins could “provide better hypotheses for hematological research.” (p.9). The classification of primates in the Neotropics, till then a largely academic pursuit, had found a purpose in biomedicine. In a letter to *Science*, Hershkovitz (1965) ridiculed the lack of attention given to the taxonomy of the Neotropical primates being, as it is, a fundamental aspect of their use and for the study of primates. In 1976, Colombia, Peru and Brazil banned or restricted primate exports, and PAHO, in desperation, promoted the establishment of in-country primate breeding centers, accompanied by an ambitious program of field surveys to establish ‘stocks’ and evaluate the methods and effects of trapping (cf. Arámbulo III et al., 1993; Rylands and Mittermeier, 2022). These surveys marked the beginning of Neotropical primatology, the focus of which, with the burgeoning exploitation and destruction of the forests of the Amazon basin, quickly changed to the need to document and protect the immense and complex diversity of primates that has been uncovered over the last 50 years. The classification of the Neotropical primates underpins all efforts for their conservation.

William C. Osman Hill, in his three treatises *Primates: Comparative Anatomy and Taxonomy* of the Platyrrhini in 1957, 1960 and 1962, listed 207 species and subspecies. In 1967, however, John and Prudence Napier published the influential *A Handbook of Living Primates* (Academic Press, London), which listed 159 species and subspecies. Estimates of the diversity of the Neotropical primates continued to decline from 1970 to 1990. In 1995, however, Rylands et al. published a list more redolent of Hill

(1957, 1960, 1962), at least in numbers if not in content. Following the 1970–1990 doldrums, the increase in numbers was quite severely contested, being seen as unnecessarily disruptive to conservation planning, notably the prioritization provided by the Red List of Threatened Species and legislation (Isaac et al., 2004; Mace, 2004). Here, we compare the lists provided by Cabrera (1957) through to Groves (2001) to Rowe and Myers (2016) and that maintained by the IUCN SCC Primate Specialist Group (Rylands and Mittermeier, 2024), among others, to indicate the trends in the overall numbers of the Neotropical primates over the last 110 years and stress the importance of a solid, researched taxonomy, based on morphology, phylogenetics and a consistent, scientific proposition for the delimitation of species. Nicely put by Gutiérrez and Helgen (2013) in a letter to *Nature* “Mammalogy is beleaguered by a dogmatic regard for mid-twentieth-century propositions, which were seldom based on critical study and lacked phylogenetic information. Species were lumped together and incorporated into influential classification checklists to simplify regional faunas and make them more manageable for non-taxonomists. Modern integrative approaches have shown that this tactic has hidden an incommensurable number of distinctive species from conservation efforts (Morrison et al., 2009), thereby increasing the risk of extinctions.” An example of this is provided by Oates and Ting (2015), who indicated that the demise of Miss Waldron’s Red Colobus, *Piliocolobus waldroni*, may well have resulted from lack of consideration of its plight due to its classification as a subspecies.

In 2012, Rylands et al. provided a summary update on the, then prevailing, taxonomy and systematics of the platyrrhines, counting 204 species and subspecies in 20 genera. Following on from Rylands et al. (2012), we provide a summary update regarding newly described species, and the changes in the taxonomy and systematics of the Neotropical primates as they stand in our current list of 2024. There have been revisions of the taxonomy of the, now, 24 genera, and 15 new species have been described (Table 1). In March 2024, the database of the IUCN SSC Primate Specialist Group registered 218 species and subspecies of primates for the Neotropical region – 29 of them subspecies (Rylands and Mittermeier, 2024).

Number of species and subspecies

The numbers of species and subspecies recognized as comprising the Platyrrhini, the Neotropical primates, has varied considerably since the early 20th century – 110 years from 1913 to 2024. It has ranged from 149 (Elliot, 1913) to a nadir of 59 (Corbet and Hill, 1980) to the current appraisal in 2024 that has 218 (Rylands and Mittermeier, 2024). This indecision as to the identity and diversity of primates on the American continent has multiple causes and is also, of course, serious in the sense of being highly consequential, not just in terms of setting up an accurate catalogue, but regarding efforts to conserve their (the primates’) contribution to biodiversity – their genes, the species and their forests.

The reasons for this variation in numbers can be found in the history of taxonomy and systematics, for long a concern principally

TABLE 1 Neotropical primate species described from 2012 to 2023.

Munduruku Marmoset	<i>Mico munduruku</i>	Costa-Araújo et al., 2019	Brazil
Schneider's Marmoset	<i>Mico schneideri</i>	Costa-Araújo et al., 2021	Brazil
Kulina's Mustached Tamarin	<i>Tamarinus kulina</i>	(Lopes et al., 2023)	Brazil
Vieira's Titi	<i>Plecturocebus vieirai</i>	(Gualda-Barros et al., 2012)	Brazil
Milton's Titi	<i>Plecturocebus miltoni</i>	(Dalponte et al., 2014)	Brazil
Urubamba Brown Titi	<i>Plecturocebus urubambensis</i>	(Vermeer and Tello-Alvarado, 2015)	Peru
Groves' titi	<i>Plecturocebus grovesi</i>	Boubli et al., 2018	Brazil
Parecis Titi	<i>Plecturocebus parecis</i>	Gusmão et al., 2019	Brazil
Aquino's Collared Titi	<i>Cheracebus aquinoi</i>	Rengifo et al., 2023	Peru
Cazuza's Saki	<i>Pithecia cazuzai</i>	Marsh, 2014	Brazil
Isabel's Saki	<i>Pithecia isabela</i>	Marsh, 2014	Peru
Mittermeier's Tapajós Saki	<i>Pithecia mittermeieri</i>	Marsh, 2014	Brazil
Rylands' Bald-faced Saki	<i>Pithecia rylandsi</i>	Marsh, 2014	Bolivia, Brazil, Peru
Pissinatti's Bald-faced Saki	<i>Pithecia pissinattii</i>	Marsh, 2014	Brazil
Kanamari Bald Uakari	<i>Cacajao amuna</i>	F.E. Silva et al., 2022	Brazil

of museum collections. As mentioned above, field primatology in the Neotropics was incipient in the mid- to late 1960s and 1970s and began in earnest only towards the end of that decade, inspired as it was by the burgeoning destruction of the Amazon rain forests and the massive trade in South America's primates for biomedical research (Rylands and Anzenberger, 2012; Rylands and Mittermeier, 2022). Field research clearly revealed the need to better understand their occurrence and distributions for species-based conservation programs (Ennos et al., 2005), not least in the discovery of unknown species and subspecies. Figure 1 shows the numbers of Neotropical primate species and subspecies listed in 14 publications. Elliot's 1913 monograph *A Review of Primates* counted 142 species and seven subspecies, an increase from Forbes (1896), who listed 88 species. Groves (2001) clarified, however, that Elliot's review was immensely useful but that "one does not want to take any notice of the taxonomy" (p.43) – Elliot paid little attention to individual or age variation, and there is no indication that he listed anything but the type specimens. Subsequent lists, starting with Cabrera (1957), included numerous subspecies, surpassing even the number of species. Osman Hill in the three volumes dedicated to the platyrrhines (1957, 1960, and 1962) of his encyclopedic series *Primates. Comparative Anatomy*

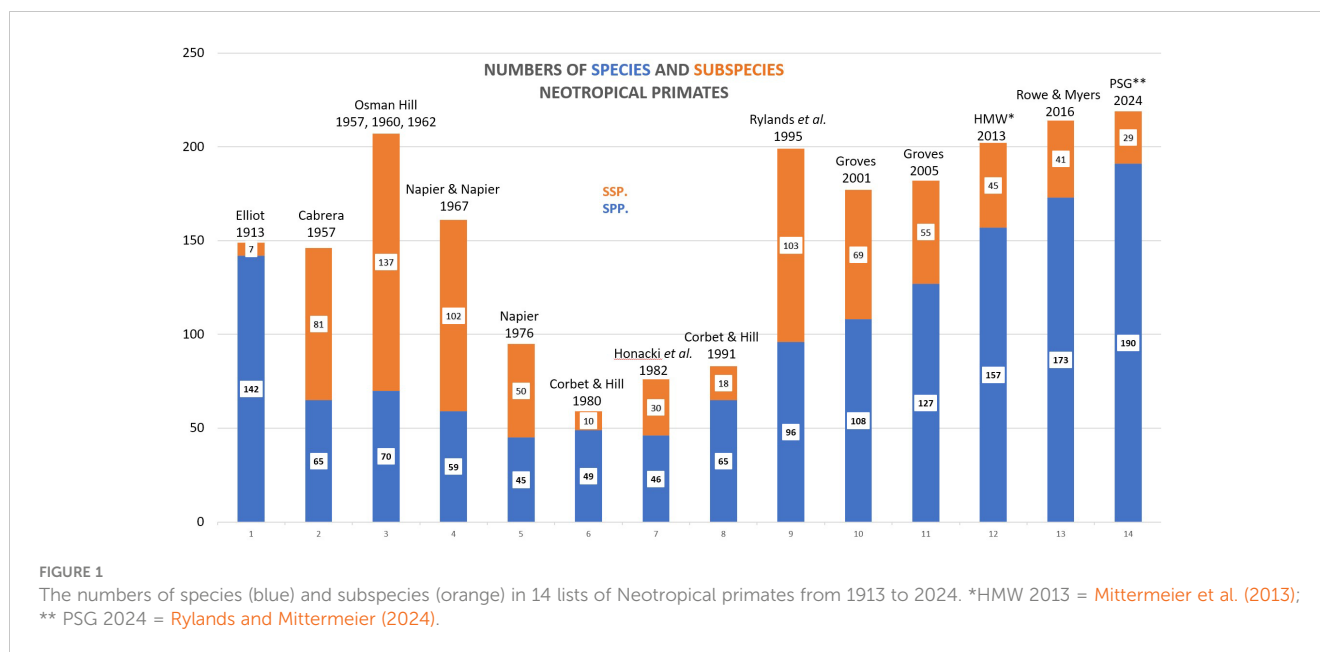
and *Taxonomy* listed 70 species and 137 subspecies. Napier and Napier (1967) recognized fewer species (57) and subspecies (102). From there, Corbet and Hill in 1980 recognized just 49 species and 10 subspecies. In 1995, Rylands et al. published a list that, while not increasing the numbers of species to any great extent – 96 compared to 84 listed by Groves (1983) in the second edition of *Mammal Species of the World*¹ – recognized 103 subspecies. Rylands et al. (1995), informed by Osman Hill's volumes and especially by the taxonomic and systematic revisions of Philip Hershkovitz, were aware of the overriding need to emphasize the full gamut of Neotropical primate diversity for its conservation. Four years earlier, Corbet and Hill (1991) had provided a list of a mere 83 species and subspecies.

Ignoring Elliot's (1913) compilation, the numbers of platyrrhine species were relatively constant for more than 35 years, ranging from a high of 70 (Hill, 1957, 1960, 1962) to a low of 46 (Honacki et al., 1982) but recovering to 65 in 1991 (Corbet and Hill, 1991). The increase in numbers from the 1995 (Rylands et al.) assessment, and those of Groves (2001, 2005) reaching 127 – almost a 50% increase – resulted in accusations of bias and "taxonomic inflation" (Isaac et al., 2004). Isaac et al. (2004) conflated the increase in the number of taxa (from newly discovered species and taxonomic revisions) with the increase in number of species by the elevation of subspecies to species. The outcry arose not just because of the increase in the numbers of platyrrhines but of all the primates. Napier and Napier (1967), the established taxonomy for too many years, counted 180 species worldwide. Groves (2005) listed 376, and today we count 539 (Rylands and Mittermeier, 2024).

The increase in numbers – the inflation – was largely attributed to Groves' and others' adoption of the Phylogenetic Species Concept (PSC) over the prevailing Biological Species Concept (BSC), associated with the subjective use of the polytypic principal that assigns look-alikes to subspecies, even those that are allopatric with no intermediates. The main concern of Isaac et al. (2004; see also Mace, 2004) was the importance of lists, such as those of national and international legislation and for conservation initiatives and programs, that need to be stable in length and content but are vulnerable to the chaos of changing taxonomies because of changes in the rules of delimiting species. Mace (2004) advocated for the continued use of the BSC and an independence from the vagaries of taxonomic lists and, most pertinently, their unwanted "inflation."

Groves' (2001, 2004, 2012, 2014) cogently defended his use of the PSC, defined by Cracraft (1983) as "an irreducible cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." It is essentially an evolutionary notion of the species as was argued by Simpson (1951). De Queiroz (1998, 2005) proposed a general lineage concept of species that reconciled many of the numerous species concepts (see Mallet, 2001) as just being different methods to delimit species. De Queiroz (2007) emphasized that "One of the

1 The 2nd (1983) edition of *Mammal Species of the World*, D. E. Wilson and D. M. Reeder (eds.), Smithsonian Institution Press, Washington, DC, listed subspecies as synonyms.



most important consequences of a unified species concept is that it clarifies the issue of species delimitation by clearly separating the conceptual problem of defining the species category (species conceptualization) from the methodological problem of inferring the boundaries and numbers of species (species delimitation)” (p.883). Numerous species concepts are not, in fact, concepts, they are merely methods to delimit species. Groves (2014) subsequently outlined his “diagnosability criterion for species delimitation” based on the PSC, in which each species is a testable hypothesis – a species is a population (or aggregation of populations) and differences between species are heritable and fixed (100% of individuals). It being consistently testable distinguishes it from the BSC. The BSC is testable for sexually reproducing organisms when they are sympatric, taking into account that any hybrids produced between them do not have exactly the same reproductive or fitness characteristics as the parental species (Zachos, 2016). It should also be said that the PSC has the practical limitation that, often in order to define the exact lines of descent, it is essential to carry out in-depth genetic analyses on all similar populations. Furthermore, applying this concept of species, very often all of the subspecies of a particular species automatically become distinct species with a consequent notable proliferation in their number (cf. Zachos, 2016).

However, the taxonomic changes and the increase in the numbers of platyrrhine taxa (as opposed to just species) was not entirely due to Groves’ adoption of the PSC and his use of the diagnosability criterion for species delimitation. Hershkovitz’s taxonomic revisions considerably increased the number of taxa without citing any particular species concept. He looked at their morphology, distinguishing characters and their distributions. The renewed interest in taxonomy was stimulated especially by the studies of Hershkovitz, providing, as it did, the wherewithal, the foundation for finding new species, for systematic revisions of species groups and genera, and subsequently for the phylogenetic studies that allowed for extraordinary revelations of their

relationships and lineages. Besides this, traditional knowledge of local populations and other indirect testimonies have often contributed to alerting specialists to distinct forms that can then be formally described – from 1980 to 2018, 31 new platyrrhine species were discovered in this way (Rossi et al., 2018).

Eighty-three species and subspecies of Neotropical primates considered valid today have been described since 1913, 34 of them since 1990. An indication of the influence of new species on the authors’ lists since that of Elliot (1913) is given in Table 2. Eliminating the taxa in each list that are today not considered valid and then adding the new species give a hypothetical approximation of the numbers each author might have listed today. For example, Hill (1957, 1960, 1962) listed 207 species and subspecies, 137 of which were subspecies. Fifty-eight of the primates he listed are no longer considered valid (synonyms). Fifty-one taxa that are currently considered valid, were described subsequently. If he were to accept all the newly discovered primates and the synonymy of the 58 no longer recognized, his taxonomic list would today have 200 Neotropical primate species and subspecies – seven less than his total in 1962. This is only hypothetical, of course. It does not include those taxa which Hill, for example, considered to be synonyms that have subsequently been considered valid. It does indicate, however, that the number of Neotropical primate taxa has not changed that much. The concern of Mace (2004) was the elevation of subspecies to species, evident in Figure 1, that would overwhelm the IUCN Red List of Threatened Species. It has not, however. All subspecies are now assessed in the Red List, and taxonomic changes are accounted for. Mace (2004) even suggested a separate, stable conservation-management taxonomy, independent of the changing taxonomic lists from 1995 – perhaps harking back to Napier and Napier (1967) and Thorington’s (1976) suggestions of a menu of classifications to serve different purposes. Gippoliti and Amori (2007) and Gippoliti et al. (2017) argued cogently the importance of robust and unbiased taxonomies and expounded the dangers of conservation management ill-informed by poor taxonomy.

TABLE 2 A comparison of seven taxonomic lists of Neotropical primates.

	Species	# ssp.	Taxa	Genera	Taxa not recognized today	Spp. & ssp. described since publication	Estimated # taxa today ³
Elliot (1913)	142	7	149	14	53	83	179
Cabrera (1957) ¹	65	81	146	16	24	51	185 ¹
Hill (1957, 1960, 1962)	70	137	207	17	58	51	200
Napier & Napier (1967)	59	102	161	16	24	51	188
Rylands et al. (1995)	96	103	199	15	10	28	217
Groves (2001)	108	69	177	18	7	27	197
Groves (2005)	127	55	182	20	13	18	187
Mittermeier et al. (2013) ²	157	45	202	19	6	15	211
Rylands and Mittermeier (2024)	190	29	218	24	–	–	219

¹Cabrera's 1957 monograph was limited to the South American primates. The estimated number of taxa today includes 12 currently accepted primates of Mexico and Central America not listed by Cabrera (1957).

²Mittermeier et al. (2013) encompasses: Fernandez-Duque et al. (2013) – Aotidae; Ferrari et al. (2013) – Pitheciidae; Rylands and Mittermeier (2013) – Callitrichidae; Rylands et al. (2013a) – Cebidae; and Rylands et al. (2013b) – Atelidae.

³To estimate the number of taxa which might be indicated for each list today (column 8), the taxa not recognized today (column 6) are subtracted from the taxa listed (column 4), and the number of taxa listed which have been described since the publication (column 7) are added.

Taxonomic changes since 2012

In 2012, Rylands et al. estimated 152 species and 204 species and subspecies (taxa) of Neotropical primates. Today we list 218 taxa (Rylands and Mittermeier, 2024) and here we briefly summarize the taxonomic and systematic changes, including 15 species described for the first time since Rylands et al. (2012).

Genera

A number of studies on the phylogenetic affinity of the pygmy marmoset, *Cebuella pygmaea*, to the Amazonian marmosets (formerly *Callithrix*, now *Mico*) indicated that it should be considered congeneric (e.g., Rosenberger, 1981; Barroso et al., 1997; Tagliaro et al., 1997). Schneider and Sampaio (2015) concluded, however, that *Cebuella* is a valid genus, separate from the Amazonian marmosets (see also Buckner et al., 2015). Garbino (2015) and Garbino and Martins Junior (2018) carried out a comparative study based on genetics, osteology, pelage and vocalizations and also concluded that it should be classified in a genus distinct from *Mico*.

The white-mouthed tamarin group of Hershkovitz (1977) currently comprises 16 black-mantled and saddle-back tamarins. The phylogenetic studies of Mataushek (2010; Mataushek et al., 2011) and Buckner et al. (2015) showed that they diverged from the tamarin lineage between 9 and 11 million years ago. Mataushek (2010) suggested that this would qualify for a distinct genus. Rylands et al. (2016) placed them in the genus *Leontocebus* Wagner, 1840. *Leontocebus* is the earliest name available with a type species that is a member of the *nigricollis* group—*Simia leonina* Humboldt, 1805. Humboldt's "lion marmoset" was re-named by

Lesson (1840, p.202) as *Leontocebus fuscus*. The name *Leontocebus* derives from the fact that *Simia leonina* was thought to be a lion marmoset (see Hershkovitz, 1949). In fact, it was a white-mouthed tamarin (see Hershkovitz, 1957). This use of *Leontocebus* was not a novelty. Cabrera (1957) placed all the tamarins in the genus *Leontocebus*, with three subgenera: *Leontocebus*, *Oedipomidas* (*geoffroyi* and *oedipus*) and *Marikina* (*leucopus*, *bicolor*, and *martinsi*). Garbino and Martins Junior (2018) preferred a subgeneric classification of *Saguinus* in three tamarin groups: *Saguinus* (*Saguinus*); *Saguinus* (*Leontocebus*); and *Saguinus* (*Tamarinus*). Brcko et al. (2022) followed Garbino and Martins Junior's (2018) arrangement but placed the groups as genera, not subgenera and added a fourth genus *Oedipomidas*: *Saguinus* Hoffmannsegg, 1807 (*S. midas*, *S. niger*, *S. ursulus*, *S. bicolor* and *S. martinsi*); *Leontocebus* Wagner, 1840 (white-mouthed tamarins); *Tamarinus* Trouessart, 1904 (moustached tamarins, *T. mystax*, *T. kulina*, *T. labiatus*, *T. imperator*, and *T. inustus*); and *Oedipomidas* Reichenbach, 1862 (the northern Colombian and Panamanian tamarins, *O. oedipus*, *O. geoffroyi*, and *O. leucopus*).

Silva-Júnior (2001, 2002) suggested that the tufted capuchins and the untufted capuchins (*sensu* Hershkovitz, 1949, 1955) are sufficiently distinct in their morphology that they should be considered subgenera or even separate genera. *Cebus* Erxleben, 1777, refers to the untufted group and *Sapajus* Kerr, 1792, is the name available for the tufted capuchins. Molecular genetic studies by Lynch Alfaro et al. (2010, 2012a, 2012b) confirmed that the gracile untufted and robust tufted capuchin monkeys should be considered distinct genera, with the divergence being estimated as the Late Miocene, 6.2 mya.

To clarify the evolutionary history of the titi monkeys, Byrne et al. (2016) assembled a large molecular dataset, sequencing 20 nuclear and two mitochondrial loci for 15 species, including

representatives from all the then recognized species groups. The results confirmed four distinct clades, for the most part concordant with previously recognized morphological species-groups—the *torquatus* group, the *personatus* group, the *donacophilus* group, and the *moloch* group (see Hershkovitz, 1990; Kobayashi, 1995; Van Roosmalen et al., 2002). The *cupreus* and *moloch* groups were found to be paraphyletic, and Byrne et al. reassigned all the species of the formerly recognized *cupreus* group to the *moloch* group. Two of the major divergence events are dated to the Miocene. The *torquatus* group, the oldest radiation, diverged about 11 mya; and the Atlantic Forest *personatus* group split from the ancestor of the *donacophilus* and *moloch* species groups about 9–8 mya. Taking into account molecular, morphological and biogeographic evidence, Byrne et al. (2016) proposed a new genus level taxonomy: *Cheracebus* n. gen. in the Orinoco, Negro and upper Amazon basins (*torquatus* group), *Callicebus* Thomas, 1903, in the Atlantic Forest (*personatus* group), and *Plecturocebus* n. gen. in the Amazon basin and Chaco region (*donacophilus* and *moloch* groups).

Groves (2001) placed the Peruvian yellow-tailed woolly monkey in the genus *Oreonax* Thomas, 1929, distinguishing it from the other woolly monkeys, *Lagothrix* Geoffroy St.-Hilaire, 1812. This was resoundingly contested by Matthews and Rosenberger (2008) and more recently by Di Fiore et al. (2015).

Species: Callitrichidae – the marmosets and tamarins

Hershkovitz (1977) recognized no subspecific forms for *Cebuella* but Napier (1976) and Van Roosmalen and Van Roosmalen (1997) argued that the form south of the Rio Solimões-Amazonas, *Cebuella niveiventris* Lönnberg, 1940, was valid. A phylogenetic study by Boubli et al. (2018) showed that the forms *Cebuella pygmaea* Spix (from the north of the Solimões-Amazonas) and *Cebuella niveiventris* Lönnberg (from the south of the Rio Solimões-Amazonas) were distinct species. The type locality for *Cebuella pygmaea*, as given by Spix, was ambiguous but Garbino et al. (2019) and Boubli et al. (2021) concluded that it is the form to the north of the rios Amazonas-Solimões and Napo, with *C. niveiventris* being the correct name for the species south of these rivers. Porter et al. (2021) confirmed the conclusions of Garbino et al. (2019) and Boubli et al. (2021) for Ecuador and Peru.

Garbino (2014) reported that *Mico manicorensis* (Van Roosmalen et al., 2000) was a junior synonym of *Mico marcai* (Alperin, 1993), previously known only from its type locality on the west bank of the Rio Aripuanã, near the mouth of the Rio Roosevelt. The range of *Mico marcai* is now known to be between the rios Aripuanã and Marmelos, including the entire basin of the Rio Manicoré, south bank tributaries of the Rio Madeira, south at least to the mouth of the Rio Roosevelt (Silva et al., 2020). A further two marmosets have been described east of the Rio Tapajós. *Mico munduruku* (Costa-Araújo et al., 2019), occurs in the southwest of the state of Pará, Brazil, from the left margin of the Rio Jamanxim, below the mouth of the Rio Nôvo, possibly up to the right margin of the Tapajós below the mouth of the Rio

Cururú. *Mico schneideri* Costa-Araújo et al. 2021, occurs in the Juruena–Teles Pires interfluvium in the north of the state of Mato Grosso, Brazil.

The *nigricollis* or white-mouthed tamarin group of Hershkovitz (1977, 1982) included just two species, *Saguinus nigricollis* (three subspecies) and *S. fuscicollis* (14 subspecies). Currently, *Leontocebus nigricollis* is composed of the (same) three subspecies, and the saddle-back tamarin of Hershkovitz is now composed of 13 species and one subspecies. A genetic analysis of the Peruvian members of this group by Matauschek (2010; Matauschek et al., 2011) showed that all but *Saguinus fuscicollis melanoleucus* should be considered species. Groves (2001) listed *S. f. melanoleucus* as a species, but Matauschek et al. (2011) found it be genetically very similar to *Saguinus weddelli*. They maintained it as a subspecies of *Saguinus* (now *Leontocebus*) *weddelli* because of its distinct white coloration. Cropp et al. (1999) showed that *Saguinus fuscus*, considered a subspecies of *fuscicollis* by Hershkovitz, was a distinct species. It is the northernmost form of the *nigricollis* tamarin group and its range is otherwise enveloped by *Saguinus nigricollis*, south of the Rio Putumayo-Içã, and *S. nigricollis graellsii* to the west of its range in the Japurá-Caquetá interfluvium (Rylands et al., 2011). It has also been confused with *S. n. nigricollis* (Defler, 1994, 2004; Rylands et al., 2011). *Saguinus fuscus* is quite probably a member of the *nigricollis* clade rather than that of *fuscicollis*.

Of the central Amazonian (Brazilian) forms assigned as subspecies of *fuscicollis* by Hershkovitz (1977), *S. fuscicollis acrensis* was found to be a hybrid *fuscicollis* × *melanoleucus* (see Peres et al., 1996). The form *cruzlimai*, its provenance revealed, was shown to be a species by Sampaio et al. (2015). The taxonomic status of the Brazilian saddle-back tamarins, *Leontocebus fuscicollis avilapiresi*, *L. f. mura* and *L. f. primitivus* was reviewed by Röhe (2021), who placed them as full species. *Saguinus fuscicollis crandalli* Hershkovitz, 1966, known only from a single specimen of unknown provenance, like *acrensis*, may well be a hybrid. Hershkovitz (1977; p.622) indicated that it might have come from the upper reaches of the Purus and Juruá basins, noting that it was intermediate in coloration between *acrensis* and the darker *cruzlimai* from the upper Purus.

Lopes et al. (2023) described the Kulina moustached tamarin, *Tamarinus kulina*, from the interfluvium of the lower rios Juruá and Tefé, Amazonas, Brazil. In a phylogenetic analysis, *Tamarinus mystax* was found to be distinct at the species level from its former subspecies *T. m. pileatus* and *T. m. pluto*. Lopes et al. (2023) placed *pluto* as a subspecies of *pileatus*, providing a new taxonomy for the group: *Tamarinus mystax*, *T. pileatus* and *T. pileatus pluto*. The recognition of *T. kulina* contracts the formerly accepted range of *T. mystax* (extending east to the Rio Tefé). The eastern limit of *T. mystax* is now the left (west) bank of the Rio Juruá. Hershkovitz (1979) reviewed the taxonomy and distribution of *Saguinus imperator* and resurrected *Saguinus imperator subgrisescens* Lönnberg, 1940. Gregorin et al. (2023) determined that it is a species, not a subspecies, on the basis of a study of the pelage, cranial morphometry, and cytochrome-*b* divergence. Hybridization is unknown but sampling in target areas is insufficient to determine a contact zone between the two lineages

(Gregorin et al., 2023). The two forms are placed in the genus *Tamarinus* along with the other mustached tamarins and the mottled-faced tamarin *Tamarinus inustus* that has been shown to belong to the same clade (Buckner et al., 2015; Brcko et al., 2022).

Vallinoto et al. (2006) indicated that the Rio Tocantins may act as a barrier to gene flow for *Saguinus niger*. This was presaged in a molecular genetic analysis by Tagliaro et al. (2005). The form described as *Mystax ursulus umbratus* Thomas, 1922, from Cametá, Rio Tocantins, Pará, listed by Groves (2001, 2005) as a junior synonym of *S. niger*, and by Hershkovitz (1977) as a junior synonym of *S. midas niger*, was, in this case, considered to be a distinct geographical race or species (J. S. Silva-Júnior, pers. comm., April 2007). A study by Gregorin and de Vivo (2013) revalidated *Saguinus ursula* Hoffmannsegg, 1807, the type species of *Saguinus* Hoffmannsegg, 1807, naming a lectotype (one of four syntypes) from the vicinity of Belém, Pará. Its range is delimited in the east by the Rio Tocantins. *Saguinus niger* occurs west of the Rio Tocantins to the Rio Xingu. Differentiation was based on pelage coloration.

Species: *Cebidae* – the squirrel monkeys and capuchin monkeys

The taxonomy of the squirrel monkeys is unclear. Ruiz-García et al. (2014a) carried out a molecular phylogenetic study of the genus *Saimiri*. They argued for just two species – *S. oerstedii* (Central America) and *S. sciureus* (South America) – and found that genetic distances between the populations were small and recent (Pleistocene). They reported on extensive hybridization, and identified five distinct clades within the range that is currently assigned to *S. macrodon* and three within the range of *S. ustus*. They argued that the radiation of South American squirrel monkeys, currently eight species, one with a subspecies (Rylands and Mittermeier, 2024), should be arranged as subspecies of *S. sciureus*, following the Biological Species Concept. A phylogenetic, phylogeographic study by Lynch Alfaro et al. (2015) found that *S. albigena*, *S. cassiquiarensis* and *S. macrodon* formed a clade, and that, like Ruiz-García et al. (2014a), *S. macrodon* was paraphyletic, with three *macrodon* lineages. They termed this group the “*cassiquiarensis* complex” and suggested that *albigena*, and the three lineages of *macrodon* be considered subspecies of *cassiquiarensis*, which they found to be the oldest named taxon. The biogeographical assessment of *Saimiri* by Lynch Alfaro et al. (2015) discussed evidence for the ongoing taxonomic research on this complex group. While Ruiz-García et al. (2014a), following Hershkovitz (1984), limited *S. collinsi* to the island of Marajó in the Amazon estuary, Mercês et al. (2015, 2017) showed that its range extends way south of the Rio Amazonas to the rain forests’ transition to the Cerrado (bush savanna), east to the Maranhão lowlands, and west at least to the Rio Xingu basin.

The capuchin monkeys split into gracile (*Cebus*) and robust (*Sapajus*) forms about 6.2. mya (Lynch Alfaro et al., 2012a). The robust capuchins were confined to the Atlantic Forest and Cerrado (bush savanna) until about 700 ka, and their wide-ranging sympatry across the Amazon Basin is the result of a single explosive late

Pleistocene invasion by *Sapajus apella* about 400 ka (Lynch Alfaro et al., 2012a). The species’ recent occupation explains the lack of differentiation throughout the basin even though the pelage varies considerably, something which severely confounded past attempts to document their taxonomy (Hill, 1960; Torres, 1983, 1988; Silva-Júnior, 2001; Rylands et al., 2005). Although not published by Hershkovitz, a glimpse of his prospective taxonomy for the Peruvian robust capuchins at least can be found in Aquino and Encarnación (1994). Today we accept, tentatively, generously, only *Sapajus apella margaritae*, on the Venezuelan island of Margarita, and *S. apella macrocephalus* of the upper Amazon, as subspecies. All the non-Amazonian robust capuchins are classified as monotypic species, including the southern black-horned capuchin *S. cucullatus* (Spix, 1823), from the Atlantic Forest of southern Brazil and northern Argentina, listed as a subspecies by Groves (2001).

An analysis of the mitochondrial DNA of the genus *Cebus* by Boubli et al. (2012) resulted in the finding that the Venezuelan capuchin, then called *Cebus brunneus*, was a distinct species with affinities to the white-fronted capuchins (the group that includes *Cebus albifrons*) as opposed to the weeper or wedge-capped capuchins (the group that includes *Cebus olivaceus*) as had been thought previously. It was listed in Mittermeier et al. (2013) as such, but examination of the type specimen (the first specimen to which the name had been attributed) revealed that it was in fact *Cebus olivaceus*, rendering the name *brunneus* invalid. Boubli et al. (2012) were not wrong, however, in their finding that there is indeed a distinct capuchin, albeit now lacking a name, of the white-fronted group in Venezuela, and studies are underway to describe it, discover its geographic distribution, and give it a name (B. Urbani, J.W. Lynch, pers. comm.).

Species: *Aotidae* – the night monkeys

There have been no taxonomic changes or new species’ descriptions since the update of Rylands et al. (2012). The most recent review and appraisal maintains 11 species, one of them, *Aotus azarae* comprising three subspecies (Fernandez-Duque et al., 2023). These authors emphasize that it is difficult to distinguish species by phenotypical differences. Ruiz-García et al. (2011) indicated that “*Aotus azarae* and *A. a. boliviensis* are clearly differentiated forms based on the mtCOII gene and they are extremely divergent with regard to other *Aotus*,” and that “if *Aotus azarae* and *A. infulatus* are related, as suggested by Plautz et al. (2009), this would imply that *A. a. azarae* and *A. a. boliviensis* are different species, while *A. a. azarae* and *A. infulatus* represent 2 subspecies of the same species.” (p.1232). We are unaware that this proposal has been confirmed.

Species: *Pitheciidae* – the titi monkeys, sakis, bearded sakis, and uakaris

Six titi monkeys have been described since 2012, five in what is now the genus *Plecturocebus* and one in the genus *Cheracebus*.

Plecturocebus vieirai (Gualda-Barros et al., 2012) occurs in the Brazilian states of Mato Grosso and Pará, in the interfluvium of the rios Xingu and Irirí, south to the upper reaches of the Rio Teles Pires. *Plecturocebus miltoni* (Dalponte et al., 2014) was discovered in the Guariba-Roosevelt Extractivist Reserve, between the rios Roosevelt and Aripuanã in the state of Mato Grosso, Brazil. Formerly confused with *C. brunneus*, *Plecturocebus urubambensis* was described by Vermeer and Tello-Alvarado (2015) from the rios Urubamba and Manu, Peru. *Plecturocebus brunneus* is now confined to the north of the state of Rondônia, Brazil. Vermeer and Tello-Alvarado (2015) also resurrected *Plecturocebus toppini* (Thomas, 1914), described from the Rio Tahuamanu, Peru, and occurring south of the Rio Purus, west from the mouth of its right bank tributary the Rio Ituxí, and south to the north bank of the Rio Madre de Dios, an area formerly thought to have been occupied by *Plecturocebus dubius*. *Plecturocebus grovesi* was described by Boubli et al. (2019) from Alta Floresta, northern Mato Grosso, Brazil. It occurs between the rios Teles-Pires and Jurueña and the Rio Arinos, a right (west) bank tributary of the Jurueña. *Plecturocebus parecis* Gusmão et al., 2019, was described from the central southern part of Brazilian Amazonia in the state of Rondônia and named after the Chapada dos Parecis where it was found. It is closely related to *P. cinerascens*, described by Spix in 1823 that also occurs in the basin of the upper Rio Madeira but further north. Byrne et al. (2024) reviewed the evidence for *P. parecis* being a distinct species and concluded that there was a strong argument for it being considered just a cline of *P. cinerascens*, with gradual variation of pelage coloration from the northern to the southern populations. Gusmão et al. (2019) and Byrne et al. (2024) agree that further study is required.

A collared titi, *Cheracebus aquinoi* was described by Rengifo et al. (2023) using morphological (cranial and pelage) and molecular (mitochondrial DNA) evidence. It occurs between the rios Nanay and Tigre, south of the Rio Napo, in Peru. The distribution of the white-collared titi, *Cheracebus torquatus* (Hoffmannsegg, 1807), had long been a mystery (Hershkovitz, 1990) but Byrne et al. (2020), who reviewed its taxonomic history and studied more than 100 skins across the genus *Cheracebus*, including the holotype of *C. torquatus*, concluded that it was a senior synonym of *Cheracebus purinus* (Thomas, 1927), known from south of the Rio Solimões, between the rios Juruá and Purus in the state of Amazonas, Brazil.

Marsh (2014) revised Hershkovitz's (1987a) taxonomy of the sakis, *Pithecia*. Hershkovitz's (1987a) taxonomy recognized just eight species and subspecies in two species' groups – *Pithecia* (one species) and *P. monachus* (four species). Marsh's revision was based on examination of the morphology of specimens (skins and skulls) in 36 museums and the pelage patterns of hundreds of photographs of captive and wild sakis. Marsh's research resulted in a list of 16 species. They included the eight taxa recognized by Hershkovitz, two that he considered to be synonyms (*Pithecia hirsuta* Spix, 1823, and *inusta* Spix, 1823), one which was evidently overlooked by Hershkovitz (*Pithecia monachus napensis* Lönnberg, 1938), and five newly described species (*P. cazuzai*, *P. isabela*, *P. mittermeieri*, *P. rylandsi*, and *P. pissinattii*). *Pithecia*

isabela is the saki occurring in the Pacaya-Samiria National Reserve between the lower rios Ucayali and Marañón in northern Peru. *Pithecia cazuzai* is found between the lower Rio Japurá and Rio Solimões. Serrano-Villavicencio et al. (2019) reviewed what they referred to as the *P. irrorata* group that included *vanzolinii* and three of the species described by Marsh (2014) – *mittermeieri*, *rylandsi*, and *pissinattii*. They concluded that the three new Marsh species are in fact junior synonyms of *irrorata* Gray, 1843 (not 1842) but that *P. irrorata vanzolinii* of Hershkovitz (1987a) should, as indicated by Marsh, be considered a species. Genetic research underway may well confirm their conclusions (J. P. Boubli, pers. comm.). Serrano-Villavicencio et al. (2019) also made some important observations concerning the date of authorship of *P. irrorata*, its nomenclatural types, and the lack of a precise type locality.

Formerly composed of just two species, *Chiropotes albinasus* (monotypic) and *Chiropotes satanas* (polytypic), as per Hershkovitz (1985), Groves (2001); Silva-Júnior and Figueiredo (2002), and Silva-Júnior et al., 2013) placed all the bearded sakis as species. Silva-Júnior and Figueiredo (2002) concluded that the name for the bearded sakis in Guyana, Suriname, French Guiana, and east of the Rio Branco in Brazil was correctly *Chiropotes sagulatus* (Traill, 1821), and restricted *Chiropotes chiropotes* (Humboldt, 1811) to the west of the Rio Branco and north of the Rio Negro in Brazil, north into Venezuela to the Rio Orinoco.

Silva-Júnior and Martins (1999) reported the occurrence of a white uakari along the Rio Jurupari, affluent of the Rio Envira, in the state of Acre, Brazil, that was distinct from *Cacajao calvus novaesi* of Hershkovitz (1987b) from the Rio Juruá. In 2022, Silva et al. (2022) described it as a new species, the Kanamari white uakari, *Cacajao amuna*, which occurs along the right bank of the Rio Tarauacá, a south-bank tributary of the Rio Juruá extending to the upper reaches of the Rio Pauini, an affluent of the Rio Purus. Silva et al. (2022) argued that all the bald uakaris, formerly subspecies of *Cacajao calvus*, should be considered species.

Species: Atelidae – howler monkeys, spider monkey, woolly monkeys and muriquis

The current count for howler monkeys is 16 taxa, 11 of them monotypic species (Rylands and Mittermeier, 2024) but some of the subspecies are of doubtful validity. The mantled howler monkey, *Alouatta palliata*, has five listed subspecies. A review by Ruiz-García et al. (2017, p.421) concluded that *A. palliata mexicana* is the most differentiated taxon but that the remaining four – *A. p. palliata* (Guatemala, Nicaragua, Honduras, and Costa Rica), *A. p. aequatorialis* (Colombia and Ecuador, west of the Andes), *A. p. coibensis* (island of Coiba, Panama), and *A. p. trabeata* (Azuer Peninsula, Panama) – showed no relevant differences among individuals of the different putative taxa (p.421). They suggested just a single subspecies, *mexicana*, besides the nominate *palliata*. Rylands et al. (2006) listed *coibensis* and *trabeata* as species, which is clearly incorrect. Cortés-Ortiz et al. (2003) found no evidence to justify the validity of *coibensis* and *trabeata* as species or subspecies

but those concerned with their conservation maintain *coibensis* as a species with *trabeata* as its subspecies (for example, Díaz-Ferguson et al., 2024). Cortés-Ortiz et al. (2015) reported on a phylogenetic analysis based on nuclear markers that supported a phylogeographic break between *A. p. palliata* and *A. p. aequatorialis* and, like Ruiz-García et al. (2017), a proximity of *coibensis* and *trabeata* to *aequatorialis*. Cortés-Ortiz et al. (2015) indicated the need for further studies of these taxa to better delineate their subspecific taxonomy.

The taxonomic arrangement for the widespread red howler, *Alouatta seniculus*, currently comprising eight species and subspecies, is also still undecided. In a morphological study, Gregorin (2006) validated two red howler species from western Amazonia, *Alouatta juara* Elliot, 1910, and *Alouatta puruensis* Lönnberg, 1941. Their distributions are poorly known and whether they are valid species or subspecies is still undecided. Cortés-Ortiz et al. (2015) maintained them as subspecies until phylogenomic analyses underway can confirm their validity and taxonomic status. The taxonomy of the black *belzebul* group seems settled with three species – *belzebul*, *ululata* and *discolor* – but genomic analyses may well change that. Research on the long-standing conundrum of whether the Atlantic Forest brown howler, *Alouatta guariba* Humboldt, 1812, is a monotypic species or comprises two subspecies is underway (L. Oklander, pers. comm).

As pointed out by Morales-Jimenez et al. (2015a), the taxonomy of the spider monkeys is complicated because pelage color patterns are so variable, especially in the Mesoamerican forms, and proposed taxonomies for the genus are very mixed, even using molecular genetics, recognizing from 1–7 species. Ruiz-García et al. (2016), for example, proposed two or three species – *Ateles paniscus*, *A. belzebuth* and perhaps *A. geoffroyi*. Morales-Jimenez et al. (2015a) argued that the taxonomy of Groves' (2001) reflects the best phylogeny that they had found and confirmed the arrangement of seven species of spider monkeys. They discovered that *A. marginatus* is basal in the *Ateles* radiation. *Ateles geoffroyi* of Mexico and Central America is polytypic. Kellogg and Goldman, 1944, described nine subspecies, but three have been synonymized. Silva-López et al. (1996) argued that *Ateles geoffroyi pan* Schlegel, 1876, was not valid. *Ateles geoffroyi panamensis* Kellogg and Goldman, 1944, was considered to be a junior synonym of *A. g. ornatus* by Napier (1976), Groves (2001) and Morales-Jimenez et al. (2015b). Morales-Jimenez et al. (2015b) concluded that *Ateles geoffroyi yucatanensis* Kellogg and Goldman, 1944, should be considered a junior synonym of *Ateles geoffroyi vellerosus* Gray, 1865, but believed that the spider monkeys of the Azuero peninsula, Panama, should continue to be distinguished as *A. g. azuerensis* (Bole, 1937) until specimens of *A. g. ornatus* (Gray, 1870) from other locations are available for analysis. Specimens from El Salvador were shown to be distinct from *A. g. vellerosus* and possibly a new subspecies. Spider monkeys from southwestern Nicaragua and northwestern Costa Rica are aligned with *A. g. frontatus*, but whether individuals from Nicaragua, currently considered to be *A. g. geoffroyi* are distinct from those from southwestern Nicaragua and northwestern Costa Rica has yet to be determined, and the phylogenetic identity of individuals from

Honduras, central and western Panama, and eastern Costa Rica is still unknown (Morales-Jiménez et al., 2015b).

The Grizzled Spider Monkey, *Ateles geoffroyi griseus* Sclater in Gray, 1866, was described in a manuscript that catalogued the mammals in the London Zoological Gardens in 1865. The type locality, however, is unknown. Kellogg and Goldman (1944) suggested that it might hail from the Río Tuyra (Tuira) basin, Panama, probably extending south-eastward through the Serranía del Sapo in extreme south-eastern Panama and perhaps the Cordillera de Baudó of north-western Colombia (Hernández-Camacho and Cooper, 1976). Méndez-Carvajal and Cortés-Ortiz (2020) affirmed that it had never yet been seen in the wild. Méndez-Carvajal (2021) reported, however, that a group of black spider monkeys with a fringe of whitish hairs on the chin and cheeks had been found on the Pacific side of eastern Panama and believed it to be the spider monkey that Sclater had described. Whitish hairs around the chin and mouth are, however, a diagnostic feature of the Colombian Black Spider Monkey, *Ateles rufiventris*, the range of which extends into southern Panama (Kellogg and Goldman, 1944 (Hernández-Camacho and Cooper, 1976).

A number of phylogenetic studies have confirmed the taxonomy of the woolly monkeys, *Lagothrix*, as proposed by Fooden (1963). Although Groves (2001, 2005) classified *Lagothrix cana*, *L. lugens*, and *L. poeppigii* as full species rather than subspecies of *Lagothrix lagothricha* (Humboldt, 1812), Botero et al. (2011, 2015), Botero and Stevenson (2014), Defler (2014) and Ruiz-García et al. (2014b) argued that they diverged only in the Pleistocene, and that there was much overlap and interbreeding between neighboring taxa, and considerable phenotypic plasticity amongst them. They argued in favor of the classification of Fooden (1963) that has just two species, *Lagothrix flavicauda* (monotypic) and *L. lagothricha* (polytypic with four subspecies). Groves (2001, 2005) recognized the form *Lagothrix tschudii* Pucheran, 1857, from southern Peru and Bolivia as a subspecies *L. cana*. Fooden (1963) had considered it a junior synonym of *L. lagothricha cana*. Ruiz-García et al. (2019) tentatively validated Groves' (2001) recognition of it as a distinct subspecies but of *L. lagothricha*, not *cana*.

Groves (2001) listed *Lagothrix poeppigii* Schinz, 1844 as a species, with *Lagothrix castelenau* I. Geoffroy St.-Hilaire and Deville, 1848, a junior synonym because its type locality, as restricted by Fooden (1963) (not by Groves), was in the high altitudes of the western edge of the species' range, as is that of *L. poeppigii*. Groves (2001) suggested that there might be an undescribed subspecies in the most easterly, mainly lowland parts of the species' range. There was evidently a misunderstanding on the part of Ruiz-García et al. (2020) in that they believed that Groves had indicated that *L. castelnaui* might be a valid subspecies. He had not, so they merely (but importantly) confirmed Groves' placement of *L. castelnaui* as a synonym. To what extent they would be able to exclude the possibility of an undescribed western, lowland taxon in the range of *poeppigii* is unclear.

Vieira (1944) recognized two subspecies of the miquiri, *Brachyteles*: the southern *B. arachnoides* (É Geoffroy Saint-Hilaire, 1806) and the northern *B. hypoxanthus* (Wied, 1829). Groves (2001,

2005) listed them as species, and this arrangement was confirmed by Chaves et al. (2019).

Conclusion

With the extraordinary advances in genetics in recent decades it is now possible to identify evolutionary lineages – which are what we need to conserve. The taxonomies of the younger “explosive”, late Pliocene and Pleistocene radiations, evident in such as *Sapajus*, *Cebus*, *Saimiri* and *Aotus*, are more difficult to “pin-down”, but hardly indecipherable, and understanding their blurrier lineages, their hybrid zones, is vital. We call them species or subspecies to allow for a descriptive orderliness in understanding diversity. Having the capacity to identify evolutionary lineages, clinging to the BSC – the identification of species and subspecies based on a fixed notion of reproductive isolation and often unfounded opinion of the degree of difference in internal and external morphology – is a sunk-cost fallacy. Groves’ (2004, 2012, 2014) has provided lucid explanations of the importance of the Phylogenetic Species Concept as a scientific proposition for our capacity to identify primate species. Groves’ “diagnosability criterion for species delimitation” is now the key refinement to distinguish evolutionary lineages, providing the insights needed to comprehend, describe, and name biodiversity for its conservation. Even assuming a classification based on the BSC, all taxa with evolutionary or morphologically evident elements, i.e. clear and evident subspecies, must absolutely be taken into consideration from a conservation point of view to safeguard global biodiversity.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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