

AN ASSESSMENT OF THE DIVERSITY OF NEW WORLD PRIMATES

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Abstract

An understanding of the full diversity of the primates is vital for priority-setting for conservation purposes, both for captive breeding and *in situ* conservation measures. Here we provide a full, annotated listing of the Neotropical primate species and subspecies resulting from a workshop, "Primate Taxonomy for the New Millennium", which brought together experts in primate taxonomy and biogeography, morphologists and geneticists. It was organized by the IUCN/SSC Primate Specialist Group (PSG) and held at the Disney Institute, Orlando, Florida, in February 2000. The list separates the Platyrrhini into five families (Callitrichidae, Cebidae, Aotidae, Pitheciidae and Atelidae), 18 genera (*Cebuella*, *Mico*, *Callithrix*, *Saguinus*, *Leontopithecus*, *Callimico*, *Saimiri*, *Cebus*, *Aotus*, *Callicebus*, *Pithecia*, *Chiropotes*, *Cacajao*, *Alouatta*, *Ateles*, *Lagothrix*, *Oreonax* and *Brachyteles*), 110 species, and 205 species and subspecies.

Key Words – Primates, taxonomy, Platyrrhini.

Introduction

"Taxonomy precedes conservation... Without the formal structure of names and an agreed system of usage, there can be no understanding of what exists to be conserved." (Collar, 1997).

The aims of this assessment of the diversity of the New World primates are to have at hand a listing of primates as a basis for conservation measures, both *ex situ* and *in situ*, and to stimulate further research into the systematics and taxonomy of the group. For each genus we have attempted to provide a summary of the different views regarding their systematics, based on the diverse disciplines which identify characteristics that contribute to the recognition of different forms: Morphology, Genetics, Physiology and Behavior. Conservation measures and the assessment of the conservation status, as well as the taxonomic status, of any particular primate are complicated when geographic distributions are poorly known. They are poorly known for the majority. Many new taxa have been discovered in the last two decades (see Table 1), and much research is still required. For some, habitat destruction on a grand scale has already denied us the possibility of ever understanding their original distribution patterns.

The taxonomic listing that we publish here is of course not definitive, but will serve as a working basis for the action of

the IUCN/SSC Primate Specialist Group (PSG). It resulted from a workshop "Primate Taxonomy for the New Millennium", held at the Disney Institute, Orlando, Florida, 25-29 February 2000. It was organized by the PSG Chair Russell A. Mittermeier in collaboration with Don Melnick, Executive Director of the Center for Environmental Research and Conservation, Columbia University, NY, and John F. Oates, Professor at Hunter College, City University of New York, NY, and was sponsored by the Margot Marsh Biodiversity Foundation, Virginia, and the Disney Institute, Orlando, Florida, which kindly provided the venue and accommodation.¹

The Workshop involved the collective brainstorming of approximately 25 field primatologists, taxonomists, biogeographers, morphologists and geneticists in discussions of two major questions: 1) the identification of taxa for which little is known or for which there is conflicting evidence and opinions from the different disciplines regarding their systematics and the validity or otherwise of described forms; and 2) the establishment of a single taxonomic listing for the primates, based on the evidence available today, most particularly from morphological and genetic research. Those who contributed to the group for the Neotropical primates included: Russell A. Mittermeier (Conservation International, Washington, DC), Colin P. Groves (Australian National University,

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Canberra), Horacio Schneider (Universidade Federal do Pará, Belém, Brazil), Douglas Brandon-Jones (British Museum of Natural History, London), Ernesto Rodríguez-Luna (Universidad Veracruzana, Xalapa, Mexico), Alfredo Langguth (Universidade Federal do Pará, João Pessoa, Brazil), Peter Grubb (London, UK), and Anthony B. Rylands, (Center for Applied Biodiversity Science, Conservation International, Washington, DC). Particularly important was the contribution of Colin Groves, whose book on primate taxonomy is soon to be published by the Smithsonian Institution Press, Washington, DC.

Taxonomy - Families and Subfamilies

The taxonomy of the New World primates has undergone considerable change over the last two decades, stimulated in large part by the extensive revision of the callitrichids by Professor Philip Hershkovitz (1977, 1979a, 1982), and his subsequent reviews of the cebid genera, *Aotus*, *Saimiri*, *Chiropotes*, *Pithecia*, *Cacajao* and *Callicebus* (1979b, 1983, 1984, 1985, 1987a, 1987b, 1990). Considerable attention has also been given to the phylogeny and taxonomy at the family and subfamily level, principally through morphological studies (Rosenberger, 1980, 1981; Rosenberger and Coimbra-Filho, 1984; Rosenberger and Strier 1989; Rosenberger *et al.* 1990), but also more recently using chromosome and molecular genetics (Dutrillaux, 1988; Schneider *et al.*, 1993, 1995, 1996). Cytotaxonomy is also becoming increasingly important for systematics at the species and subspecies level (see, for example the revisions of *Aotus* by Hershkovitz 1983; Nagamachi *et al.* 1995, 1996, 1997, 1999).

Platyrrhine systematics at the family and subfamily level was reviewed by Rosenberger (1981). The predominant classification during this century has involved the use of just two families, the Callitrichidae (or, formerly, Hapalidae), with *Cebuella*, *Callithrix*, *Saguinus* and *Leontopithecus*, and Cebidae (including the remaining genera), with *Callimico* being placed in either of the two, or in its own family (Hill, 1957; Dollman, 1933; Hershkovitz, 1977). This system was maintained in all of the major syntheses published over the last 75 years (for example, Simpson, 1945; Hill, 1957, 1960, 1962; Cabrera, 1958; Napier and Napier, 1967; Simons, 1972; and Hershkovitz, 1977). Hershkovitz (1977) placed the extant cebids in seven subfamilies: Saimiriinae, Aotinae, Callicebinae, Pitheciinae, Cebinae, Alouattinae and Atelinae (Table 2). Groves (1989) divided the Cebidae into five families (Cebidae, Aotidae, Atelidae, Callicebidae, and Pitheciidae), although he subsequently (1993) modified this arrangement, defining the following subfamilies: Alouattinae, Aotinae, Atelinae (*Ateles*, *Brachyteles*, and *Lagothrix*), Callicebinae, Cebinae (including *Cebus* and *Saimiri*, following Rosenberger 1981, see below), and Pitheciinae (*Cacajao*, *Chiropotes* and *Pithecia*).

Rosenberger (1981) proposed an alternative classification (Table 2), based on hypotheses concerning phylogenetic relationships and a proposal for the scenario of their adaptive radiation (see also, Rosenberger, 1980; Rosenberger and Coimbra-Filho, 1984; Rosenberger and Strier, 1989; Rosenberger *et al.*, 1990). Rosenberger's (1981) scheme included the use of tribes and subtribes (Table 2). It maintained but redefined the use of the family name Cebidae to include two subfamilies; the Cebinae (extant genera *Cebus* and *Saimiri*) (see Harada *et al.*, 1995) and Callitrichinae (extant genera

Table 1. New World primates described since 1980.

Species name	Common name
1. <i>Callithrix nigriceps</i> Ferrari & Lopes, 1992	Black-headed marmoset
2. <i>Callithrix argentata marcai</i> Alperin, 1993	Marca's marmoset
3. <i>Callithrix mauesi</i> Mittermeier, Schwarz & Ayres, 1992	Maués marmoset
4. <i>Callithrix saterei</i> Silva, Jr. & Noronha, 1998	Sateré marmoset
5. <i>Callithrix humilis</i> Van Roosmalen, Van Roosmalen, Mittermeier & Fonseca, 1998	Black-crowned dwarf marmoset
6. <i>Callithrix manicorensis</i> Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000	Manicoré marmoset
7. <i>Callithrix acariensis</i> Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000	Rio Acari marmoset
8. <i>Callithrix kuhlii</i> Coimbra-Filho, 1985	Wied's black-tufted-ear marmoset
9. <i>Saguinus nigricollis bernandezii</i> Hershkovitz, 1982	Hernández-Camacho's black mantle tamarin
10. <i>Leontopithecus caissara</i> Lorini & Persson, 1990	Black-faced lion tamarin
11. <i>Saimiri boliviensis peruviensis</i> Hershkovitz, 1984	Peruvian squirrel monkey
12. <i>Saimiri vanzolinii</i> Ayres, 1981	Black-crowned squirrel monkey
13. <i>Cebus olivaceus kaapori</i> Queiroz, 1992	Kakapo capuchin
14. <i>Aotus lemurinus brumbacki</i> Hershkovitz, 1983	Brumback's night monkey
15. <i>Aotus herskovitzi</i> Ramirez-Cerquera, 1983	Hershkovitz's night monkey
16. <i>Aotus nancymae</i> Hershkovitz, 1983	Ma's night monkey
17. <i>Callicebus barbarabrownae</i> Hershkovitz, 1990	Northern Bahian blond titi
18. <i>Callicebus coimbrai</i> Kobayashi & Langguth, 1999	Coimbra's titi
19. <i>Pithecia irrorata vanzolinii</i> Hershkovitz, 1987	Vanzolini's bald-faced saki
20. <i>Pithecia aequatorialis</i> Hershkovitz, 1987	Equatorial saki
21. <i>Chiropotes satanas utahicki</i> Hershkovitz, 1985	Uta Hick's bearded saki
22. <i>Cacajao calvus novaesi</i> Hershkovitz, 1987	Novaes' bald-headed uacari

Table 2. Some classifications of the extant genera of Platyrrhini. Differences between Schneider and Rosenberger in Schneider and Rosenberger (1996) are highlighted.

Hershkovitz (1977)	Rosenberger (1981)	Schneider <i>et al.</i> (1993, 1995, 1996)	Schneider in Schneider & Rosenberger (1996)	Rosenberger in Schneider & Rosenberger (1996)	Groves
Infraorder Platyrrhini	Infraorder Platyrrhini	Infraorder Platyrrhini	Infraorder Platyrrhini	Infraorder Platyrrhini	Infraorder Platyrrhini
Family Callitrichidae	Family Cebidae	Family Cebidae	Family Cebidae	Family Cebidae	Family Cebidae
<i>Cebus</i> Gray, 1886	Subfamily Cebinae	Subfamily Cebinae	Subfamily Cebinae	Subfamily Cebinae	Subfamily Cebini
<i>Callithrix</i> Eschleben, 1777	Tribe Cebini	Tribe Cebini	Tribe Cebini	Tribe Cebini	<i>Cebus</i> Eschleb.
<i>Leontopithecus</i> Lesson, 1840	<i>Cebus</i> Eschleben, 1777	<i>Cebus</i> Eschleben, 1777	<i>Cebus</i> Eschleben, 1777	<i>Cebus</i> Eschleben, 1777	Subfamily Chrys
<i>Seiurus Hoffmannsegg</i> , 1807	Tribe Saimirini	Tribe Saimirini	Tribe Saimirini	Tribe Saimirini	<i>Saimiri</i> Vog.
Family Callimiconidae	<i>Saimiri</i> Voëg, 1831	<i>Saimiri</i> Voëg, 1831	<i>Saimiri</i> Voëg, 1831	<i>Saimiri</i> Voëg, 1831	Subfamily Callit
<i>Callinico</i> Thomas, 1913	Subfamily Callinichinae	Subfamily Aotinae	Subfamily Aotinae	Subfamily Callinichinae	<i>Callithrix</i> Eschleb.
Family Cebidae	Tribe Callinichini	<i>Aotus</i> Illiger, 1811	<i>Aotus</i> Illiger, 1811	Tribe Callinichini	<i>Seiurus</i> Hoffmannsegg
Subfamily Saimirinae	Subtribe Callinichina	Subfamily Callinichinae	Subfamily Callinichinae	Subfamily Callinichinae	<i>Leontopithecus</i>
<i>Saimiri</i> Voëg, 1831	<i>Callithrix</i> Eschleben, 1777	Tribe Callinichini	Tribe Callinichini	<i>Callithrix</i> Eschleben, 1777	<i>Callinico</i> T.
Subfamily Callitrichinae	<i>Cebus</i> Gray, 1886	Subtribe Callinichina	<i>Callithrix</i> Eschleben, 1777	<i>Callithrix</i> Eschleben, 1777	Family Nicotipithec
<i>Aotus</i> Illiger, 1811	<i>Leontopithecus</i> Lesson, 1840	<i>Callithrix</i> Eschleben, 1777	<i>Callithrix</i> Eschleben, 1777	<i>Seiurus</i> Hoffmannsegg, 1807	<i>Aotus</i> Illiger,
Subfamily Aotinae	Subtribe Leontocbina	<i>Cebus</i> Gray, 1886	<i>Cebus</i> Gray, 1886	<i>Seiurus</i> Hoffmannsegg, 1807	Family Pitheciidae
<i>Callitrichus</i> Thomas, 1903	<i>Seiurus</i> Hoffmannsegg, 1807	<i>Seiurus</i> Hoffmannsegg, 1807	<i>Seiurus</i> Hoffmannsegg, 1807	<i>Leontopithecus</i> Lesson, 1840	Subfamily Pitheci
Subfamily Aotinae	Tribe Callimiconini	Subtribe Saguira	Subtribe Saguira	<i>Leontopithecus</i> Lesson, 1840	<i>Pithecia</i> Des
<i>Alouatta</i> Lacépède, 1799	<i>Callinico</i> Thomas, 1913	<i>Seiurus</i> Hoffmannsegg, 1807	<i>Seiurus</i> Hoffmannsegg, 1807	<i>Callinico</i> Thomas, 1913	<i>Chiropotes</i> L.
Subfamily Pitheciinae	Family Aetideae	Subtribe Leontopithecina	Family Aetideae	Family Aetideae	<i>Cacajao</i> Less
<i>Pithecia</i> Desmarest, 1820	Subfamily Aetinae	<i>Leontopithecus</i> Lesson, 1840	Subfamily Aetinae	<i>Aotus</i> E. Geoffroy, 1806	Subfamily Callic
<i>Chiropotes</i> Lesson, 1840	Tribe Aetini	Subtribe Calliniconina	Tribe Aetini	<i>Brachydes</i> Spix, 1831	<i>Callitrichus</i> T.
<i>Cacajao</i> Lesson, 1840	Tribe Aetini	<i>Callinico</i> Thomas, 1913	<i>Aotus</i> E. Geoffroy, 1806	<i>Leontopithecus</i> E. Geoffroy, 1812	Family Aetidae
Subfamily Cebinae	Subtribe Aetina	Family Aetidae	<i>Brachydes</i> Spix, 1831	Tribe Aotaurini	Subfamily Myco
<i>Cebus</i> Eschleben, 1777	<i>Aotus</i> E. Geoffroy, 1806	Subfamily Aetinae	<i>Leontopithecus</i> E. Geoffroy, 1812	<i>Alouatta</i> Lacépède, 1799	<i>Alouatta</i> Lacé
Subfamily Aetinae	<i>Brachydes</i> Spix, 1831	Tribe Aetini	Tribe Aotaurini	Subfamily Pitheciinae	Subfamily Aeti
<i>Aotus</i> E. Geoffroy, 1806	Subtribe Lagoichina	Subtribe Aetina	<i>Alouatta</i> Lacépède, 1799	Tribe Pitheciini	Tribe Aetini
<i>Leontopithecus</i> E. Geoffroy, 1812	<i>Leontopithecus</i> E. Geoffroy, 1812	<i>Aotus</i> E. Geoffroy, 1806	Family Pitheciidae	<i>Pithecia</i> Desmarest, 1820	<i>Aotus</i> E. Ge
<i>Brachydes</i> Spix, 1831	Tribe Aotaurini	Subtribe Brachydrina	Tribe Pitheciini	<i>Chiropotes</i> Lesson, 1840	<i>Brachydes</i> S.
Subfamily Pitheciinae	Subfamily Pitheciinae	<i>Brachydes</i> Spix, 1831	<i>Pithecia</i> Desmarest, 1820	<i>Cacajao</i> Lesson, 1840	<i>Leontopithecus</i> E.
<i>Pithecia</i> Desmarest, 1820	Tribe Pitheciini	<i>Leontopithecus</i> E. Geoffroy, 1812	<i>Chiropotes</i> Lesson, 1840	<i>Chiropotes</i> Lesson, 1840	<i>Callitrichus</i> Thomas, 1903
<i>Chiropotes</i> Lesson, 1840	Subfamily Pitheciinae	Tribe Aotaurini	<i>Alouatta</i> Lacépède, 1799	<i>Callitrichus</i> Thomas, 1903	
<i>Cacajao</i> Lesson, 1840	Tribe Pitheciini	Subtribe Pitheciina	<i>Pithecia</i> Desmarest, 1820	<i>Alouatta</i> Lacépède, 1799	
<i>Aotus</i> Illiger, 1811	Subtribe Aotina	<i>Pithecia</i> Desmarest, 1820	<i>Chiropotes</i> Lesson, 1840	Tribe Pitheciini	
<i>Callitrichus</i> Thomas, 1903	Subtribe Chiropotina	<i>Chiropotes</i> Lesson, 1840	<i>Callitrichus</i> Thomas, 1903	Subtribe Pitheciina	
	Tribe Callicebini	<i>Callitrichus</i> Thomas, 1903	<i>Callitrichus</i> Thomas, 1903	<i>Pithecia</i> Desmarest, 1820	
				<i>Chiropotes</i> Lesson, 1840	
				<i>Cacajao</i> Lesson, 1840	
				<i>Callitrichus</i> Thomas, 1903	
				Tribe Callicebini	
				<i>Callitrichus</i> Thomas, 1903	

Callithrix [includes *Cebuella*], *Saguinus*, *Leontopithecus*, and *Callimico*), and placed all other platyrrhines into a second family, the Atelidae, which included two subfamilies: Atelinae (*Alouatta*, *Ateles*, *Brachyteles*, *Lagothrix*) and Pitheciinae (*Pithecia*, *Chiropotes*, *Cacajao*, *Callicebus*, *Aotus*). This classification was adopted by Kinzey (1997) in his review of the evolution, ecology and behavior of the New World primates.

A molecular phylogeny, elaborated by Schneider *et al.* (1993, 1995, Schneider *et al.*, 1993, 1995, 1996) (see below for a summary of the molecular data), agreed in large part with the classification of Rosenberger (1981), having only one major difference; the alignment of *Aotus* with the Cebidae (subfamily Aotinae) rather than the Pitheciinae. Tyler (1991) argued that there are three well-defined clades among the extant platyrrhines: atelines, pitheciines, and callitrichids, but that evolutionary relationships of the remaining genera (*Aotus*, *Callicebus*, *Cebus* and *Saimiri*) was uncertain. Like Schneider *et al.* (1993), Tyler (1991) argued that *Aotus* and *Callicebus* are not closely related, but went even further, and, reviewing morphological characters of the former, concluded that "*Aotus* must be removed from other ceboids and made a sister group of the entire Anthropeidea". Dutrillaux (1988) also argued for the primitiveness of *Aotus* on the basis of its karyotype. There is general consensus regarding the affinity of *Callicebus* with the pitheciines (or pitheciids) (see Porter *et al.*, 1999) but the position of *Aotus* remains problematic. Tejedor (1998) recently reviewed the morphological evidence for the phylogenetic placements of *Callicebus* and *Aotus*. He pointed out that two Miocene genera from Patagonia, *Homunculus* and *Carlocebus* show many primitive characters shared by both *Aotus* and *Callicebus* (see also Kay, 1980; Rosenberger, 1981; Ford, 1986, 1988; but see Rose and Fleagle, 1981; Hershkovitz, 1970 who placed *Homunculus* in its own family Homunculidae), and suggest they have a close common ancestor. Rosenberger in Schneider and Rosenberger (1996) placed *Callicebus* and *Aotus* in the subtribe Homunculini with the Pitheciinae. Gregory (1922), Miranda Ribeiro (1940), Cabrera (1958), Simons (1972) and Fleagle (1988) placed them in the same subfamily Aotinae. Fleagle (1999), however, taking note of Schneider *et al.* (1993) placed them in separate subfamilies, as did Pocock (1925), Hill (1960), Hershkovitz (1977) and Thorington and Anderson (1984). Tejedor (1998) concluded that *Aotus* and *Callicebus* are ancient taxa and placed them in separate subfamilies within the Atelidae but did not discount the possibility that *Callicebus* belongs correctly in the subfamily Pitheciinae. In summary the placements of *Callicebus* have included the subfamilies Callicebinae, Cebinae and Pitheciinae. *Aotus* has been placed in its own family Aotidae, in Atelidae and in Cebidae (*sensu* Rosenberger, 1981), and in the subfamilies Aotinae and Pitheciinae.

The other differences between the schemes of Rosenberger *et al.* (1990) and Schneider *et al.* (1993, 1995, 1996) are as follows: 1) Schneider *et al.* place *Saguinus* in the Subtribe Saguina rather than Leontocebina; 2) Schneider *et al.* separate *Leontopithecus* from *Callithrix* and *Cebuella* and place it

in its own Subtribe Leontopithecina; 3) Schneider *et al.* align *Callimico* more closely with *Callithrix* and *Cebuella* and place it in the Subtribe Callimiconina; 4) Schneider *et al.* align *Lagothrix* with *Brachyteles* in the Subtribe Brachytelina, whereas Rosenberger *et al.* place *Lagothrix* in the Subtribe Atelina 5) Schneider *et al.* place *Cacajao* and *Chiropotes* in the Subtribe Chiropotina separate from *Pithecia*; and 5) place *Callicebus* in a separate Tribe rather than Subtribe of the Pitheciinae.

Hershkovitz (1977) placed *Callimico* in its own family; Callimiconidae. Rosenberger (1981) argued for its alignment as the subfamily Callimiconinae within the family Cebidae, redefined as including also the subfamilies Cebinae (*Cebus*, *Saimiri*) and Callitrichinae (*Cebuella*, *Callithrix*, *Mico*, *Saguinus*, *Leontopithecus*) (see also Martin, 1992; Barroso, 1995; Pastorini *et al.*, 1998; Canavez *et al.*, 1999). Cronin and Sarich (1978), Schneider *et al.* (1993, 1996), Pastorini *et al.* (1998), Chaves *et al.* (1999) and Canavez *et al.* (1999a) demonstrated that *Callimico* is more closely related to *Callithrix* than it is to the tamarins.

Groves (in press) pointed out that the correct family name for the night monkeys is Nictipithecidae Gray, 1870; Aotidae Poche, 1908 being a junior synonym. Aotidae perhaps could be maintained due its common usage, but this will require clarification with the International Commission on Zoological Nomenclature. Likewise, the correct name of the squirrel monkey subfamily is Chrysotrichinae Cabrera, 1900; a senior synonym of Saimirinae Miller, 1924 (Groves, in press). As in the case of the night monkeys, we continue with the use of Saimirinae for the squirrel monkeys because of its familiarity.

The placing of the seed-eating *Cacajao*, *Pithecia* and *Chiropotes*, either as a subfamily of the Atelidae or in a separate family is still under discussion. Although Schneider (in Schneider and Rosenberger, 1996) argued for family status, whereas Rosenberger in the same publication agreed to differ, placing it as a subfamily, Porter *et al.* (1999), with Schneider as co-author, also argued for its subfamily status following their study of the epsilon-globin gene.

We believe that the scheme of Schneider (in Schneider and Rosenberger, 1996) represents the state of the art in Platyrrhini classification since it is based on phylogenetic analyses of morphological as well as molecular data. The precise position of certain genera may need more information not yet available but we can trust the general structure of that proposal, and the species lists we present in the next section follows the suprageneric classification of the above mentioned authors (Table 2).

Genera

There are sixteen genera currently recognized for the Platyrrhini. There is general consensus as to the validity of all except for two. Since 1980, studies on the phylogenetic affinity of the pygmy marmoset, *Cebuella pygmaea*, to the Ama-

zonian marmosets (*Callithrix*) have indicated that it could be considered congeneric (for example, Rosenberger, 1981; Barroso *et al.*, 1997; Tagliaro *et al.*, 1997; Porter *et al.*, 1997a). Here we maintain, however, the genus *Cebuella*, while separating the Amazonian marmosets from the Atlantic forest marmosets, using *Callithrix* Erxleben, 1777 for the latter and *Mico* Lesson, 1840 for the former (see section on *Cebuella*, below).

C. P. Groves (in press) has indicated that the yellow-tailed woolly monkey, *Lagothrix flavicauda*, is sufficiently divergent from other woolly monkeys as to warrant its own genus: *Oreonax* Thomas, 1927. However, no DNA studies have yet been carried out to support this view.

Species and Subspecies

The taxonomy within most of the platyrrhine genera is still controversial, with discrepancies arising due to differing species and subspecies concepts and to the characters used in differentiating the forms. Tables 4-8 give a listing of the species and subspecies. The lists do not reflect a taxonomic study of our own, but an appraisal of the evidence available in the literature mentioned in the text. We have taken, however, the side of the "splitters" rather than the "lumpers". This is most evident in cases such as that of *Saimiri*, where current evaluations have demonstrated the existence of five species and 12 subspecies on the one hand (Hershkovitz, 1984, 1987b), and just two (or even one) species, on the other (Costello *et al.*, 1993). *Alouatta* is another case in point, where new information is continuously being published and the taxonomy research is still in a state of flux (see Rylands and Brandon-Jones, 1998). Our aim is to provide an estimate of the diversity of Neotropical primates, and while there is still discussion as to the validity or otherwise of numerous forms, we prefer to maintain them since genetic evidence has confirmed many formerly dubious forms and is demonstrating a large hidden diversity. For conservation purposes it would be a serious mistake to ignore the genetic and morphological diversity of such wide-ranging genera as *Saimiri*. Even while splitting, it is highly probable that the list understates the diversity of most Neotropical primate genera, most particularly in such genera as *Ateles*, *Alouatta*, *Cebus*, and *Lagothrix*, which have yet to receive modern systematic revisions, but also in, for example *Callithrix*, for which new species have been described recently, and more will undoubtedly be described in the near future. Possible new forms of *Lagothrix*, *Chiropotes*, *Cacajao*, *Saguinus* and *Callithrix* have been informally announced.

The listings in Appendix 1 provide a total of five genera and 39 species with 61 species and subspecies of Callitrichidae, 11 species with 44 species and subspecies of Cebidae, 10 species with 12 species and subspecies of Aotidae, 26 species with 44 species and subspecies of Pitheciidae, and 20 species with 45 species and subspecies of Atelidae. In all, we list 16 genera, 107 species and 204 species and subspecies of Neotropical monkeys ranging from southern Mexico through to north-

ern Argentina and Paraguay, and possibly the northeastern most tip of Uruguay (Villalba *et al.*, 1995). Mittermeier (1987), in his analysis of the diversity of Neotropical primates and their distributions by country and the major phyto-geographic regions of Gentry (1982), worked on the basis of "some 65 species". The increase in species listed here comes from both taxonomic revisions, which have raised subspecific forms to full species and the descriptions of entirely new species. The taxonomic revision of *Callicebus* by Hershkovitz (1990) increased the number of species from just three to 13. All *Callithrix* forms are here listed as species (Rylands *et al.*, 1993), and such as *Alouatta sara*, *Ateles chamek*, *A. marginatus*, and *Brachyteles hypoxanthus* are considered valid species. Entirely new forms described recently include *Callithrix nigriceps*, *C. mauesi*, *C. marcai*, *C. saterei*, *C. humilis*, *C. manicorensis* and *C. acariensis*, *Leontopithecus caissara*, *Aotus hershkovitzi*, *Callicebus coimbrai* and *Cebus kaapori*.

The Molecular Data

Molecular data suitable for cladistic analysis of the New World monkeys were first obtained at the beginning of the 90's. Their contribution to understanding the systematics at supraspecific level and the phylogeny of New World primates has been profound. Here we present a brief summary.

The first DNA dataset of aligned sequences of the nuclear epsilon globin gene involving all 16 platyrrhine genera was published by Schneider *et al.* (1993). Subsequently, a series of datasets was generated, some including all extant New World primate genera (Schneider *et al.*, 1996; Canavez *et al.*, 1999a; von Dorman *et al.*, 1999; Goodman *et al.*, 1998), while others concentrated on particular clades (Canavez *et al.*, 1999b; Chaves *et al.*, 1999; Meireles *et al.*, 1999; Porter *et al.*, 1997a, 1997b; Porter *et al.*, 1999; Pastorini *et al.*, 1998; Tagliaro *et al.*, 1999).

Table 3 summarizes the results involving four nuclear datasets (IRBP, EPSILON, G6PD, and β -2M) for all extant New World primates, and additional molecular data (vWF, upstream region EPSILON, γ -Globin, ND4, and tRNA) including specific clades. The four DNA datasets (EPSILON, IRBP, G6PD and β -2M) were combined in tandem to perform a total analysis using Maximum parsimony (MP) and Neighbor-Joining (NJ) approaches using PAUP version 4.0b3a (Swofford, 1998). MP and NJ trees (not shown) were almost identical, differing only in the placement of *Aotus*. The MP tree placed *Aotus* as the basal lineage of the callitrichine clade, while NJ showed *Aotus* to occur in an unresolved trichotomy with the *Cebus-Saimiri* clade and the callitrichines.

The four nuclear genes (β -2M, EPSILON, G6PD, and IRBP) analyzed separately are not congruent with regard to the close relationship among the three major clades (pitheciine, ateline, callitrichine). EPSILON and β -2M support a pitheciine-ateline clade, whereas G6PD groups the ateline with the callitrichine clade, and IRBP shows the pitheciine clade to be closer to the callitrichine clade. The topology resulting from

Table 3. DNA studies that elucidate the phylogeny of New World primates.

GENES	Kb	AUTHORS	Pitheciine-Ateline-Cebid relationship	<i>Aotus, Cebus</i> and <i>Saimiri</i> as closely linked to callitrichines	<i>Callicebus</i> as basal genus of the pitheciine clade	<i>Lagothrix</i> and <i>Brachyteles</i> as sister group in the ateline clade	Callitrichine clade	
							<i>Saguinus</i> as basal genus	<i>Callimico</i> and <i>Callithrix</i> as sister group
			BS%	BS%	BS %	BS %	BS %	BS %
EPSILON	1,8	Schneider <i>et al.</i> , 1993	PA=79	94	99	86	77*	69
IRBP	1,9	Schneider <i>et al.</i> 1996	PC=96	99	100	77	100	84**
G6PD	1,2	Von Dornum & Ruvolo, 1999	AC=40	83	78	72	100	80
β -2M	1,7	Canavez <i>et al.</i> , 1999a	PA=72	56	87	96	100	92
VWF	0,7	Chaves <i>et al.</i> , 1999					98	84
EPSILON and 5' region	1.8 to 4.3	Porter <i>et al.</i> , 1997a	PAC=100	100				
EPSILON 5' region	1.2 – 1.4	Porter <i>et al.</i> , 1999			100			
ND4, tRNAs	0,8	Pastorini <i>et al.</i> , 1998					81*	80
Gamma-Globin	9,6	Meireles <i>et al.</i> , 1999				100		

BS: Bootstrap Support. Bootstrapping involves creating a new data set by sampling N characters randomly with replacement, so that the resulting data set has the same size as the original, but some characters have been left out and others are duplicated. The random variation of the results from analyzing these bootstrapped data sets can be shown statistically to be typical of the variation that you would get from collecting new data sets (Felsenstein, 1985).

PA= Pitheciines x Atelines; PC= Pitheciines x Cebids; AC= Atelines x Cebids; PAC=unresolved trichotomy

**Saguinus* and *Leontopithecus* as sister group

** *Callimico* and *Leontopithecus* as sister group of *Callithrix*

the total analysis, favors the ateline-pitheciine clade, but the bootstrap support is not strong (78%) in the MP tree. In addition, the analysis of Porter *et al.* (1997b) using 5' upstream region of epsilon gene in selected primate taxa showed the three major clades in an unresolved trichotomy. The poor resolution of the phylogenetic reconstruction of the three major platyrrhine lineages, resulting from the most robust molecular data set so far available for the New World monkeys strongly suggests that the pitheciines, atelines and cebids emerged at almost the same time in the platyrrhine radiation. These lineages are named by Schneider *et al.* (1996), Schneider and Rosenberger (1996) and Goodman *et al.* (1998), as the Families Atelidae, Pitheciidae and Cebidae.

In the Pitheciidae the four nuclear genes and the joint DNA analysis significantly placed *Callicebus* as a sister group of the traditional pitheciines, *Pithecia*, *Chiropotes* and *Cacajao* (bootstrap values ranging from 78 to 100%). These results were reinforced by the complementary study of Porter *et al.* (1999) encompassing more than 4 Kb of the epsilon globin gene and its upstream region.

The joint analysis strongly supports the monophyly of the Cebidae, grouping *Aotus*, *Cebus*, and *Saimiri* with the small callitrichines (bootstrap values from 83 to 100%). Additionally, three of the four nuclear genes (IRBP, G6PD, β -2M), and the epsilon upstream region of Porter *et al.* (1997a, 1999) also indicate a close relationship between *Cebus* and *Saimiri*. Among the callitrichines, additional molecular data of Pastorini *et al.*, (1998) using mitochondrial DNA and Chaves *et al.* (1999), Canavez *et al.* (1999a, 1999b), using nuclear DNA (intron 11 of von Willebrand, β -2-microglobulin genes), strongly supported the reclassification of *Cebuella* as belonging to the genus *Callithrix* (See also Porter *et al.*, 1997b), and also significantly placed *Callimico* as a sister group of *Callithrix*, contrary to the traditional view of *Callimico* as being basal to the callitrichines. Five of the six genes, and the joint analysis placed *Saguinus* as the basal genus of the callitrichine tree with significant bootstrap values

(98-100%). Finally, four nuclear genes and the joint analysis showed a congruent branching pattern in the atelid clade, placing *Alouatta* as the most basal lineage and *Brachyteles* from the Atlantic forest) and *Lagothrix* (from the Amazonian forest), as sharing the last common ancestor (bootstrap values ranging from 78 to 100%), contrasting to the widely disseminated view that *Ateles* and *Brachyteles* share the last common ancestor in the ateline clade. Furthermore, as shown in Table 3, the investigation by Meireles *et al.* (1999), encompassing more than 9 Kb of the gamma globin gene complex strongly supports the *Lagothrix-Brachyteles* clade (bootstrap value of 100%).

In summary, three evolutionary lineages are strongly established for the New World monkeys: atelines, pitheciines, and cebids. However, two major points regarding the branching patterns of the most ancient lineages remain to be clarified: (i) what is the exact branching pattern of *Aotus*, *Cebus*, *Saimiri* and the small callitrichines? and (ii) which two of these three lineages, pitheciines, atelines or cebids, are more closely related?

All the platyrrhine genera require further investigation at the subgeneric level. Preliminary estimates indicate that, in the majority, speciation seems to have occurred in the Pliocene-Pleistocene scenario (5 Ma or less). However, because the internodes are usually very small when species and populations are compared, even using highly variable mitochondrial DNA, a "all-evidence" approach, using geomorphology, biogeography, traditional morphology, behavior and cytogenetics, in association with DNA sequencing, is required to better understand the recent evolutionary processes which have resulted in the species diversity of New World monkeys existing today (see, for example, Boinski and Cropp [1999], who used this approach to examine the systematics of squirrel monkeys).

Table 4. Species and subspecies of the Family Callitrichidae.

Family Callitrichidae	Common name (following Hershkovitz, 1977)
1. <i>Cebuella pygmaea pygmaea</i> (Spix, 1823)	Pygmy marmoset
2. <i>C. pygmaea niveiventris</i> Lönnberg, 1940	
3. <i>Mico argentatus</i> (Linnaeus, 1766)	Silvery marmoset
4. <i>M. leucippe</i> (Thomas, 1922)	Golden-white bare-ear marmoset
5. <i>M. melanurus</i> (É. Geoffroy in Humboldt, 1812)	Black-tailed marmoset
6. <i>M. intermedius</i> (Hershkovitz, 1977)	Aripuanã marmoset
7. <i>M. emiliae</i> (Thomas, 1920)	Snethlage's marmoset
8. <i>M. nigriceps</i> (Ferrari & Lopes, 1992)	Black-headed marmoset
9. <i>M. marcai</i> (Alperin, 1993)	Marca's marmoset
10. <i>M. humeralifer</i> (É. Geoffroy in Humboldt, 1812)	Black and white tassel-ear marmoset
11. <i>M. chrysoleucus</i> (Wagner, 1842)	Golden-white tassel-ear marmoset
12. <i>M. mauesi</i> (Mittermeier, Schwarz & Ayres, 1992)	Maués marmoset
13. <i>M. humilis</i> (Van Roosmalen, Van Roosmalen, Mittermeier & Fonseca, 1998)	Black-crowned dwarf marmoset
14. <i>M. saterei</i> (Silva, Jr. & Noronha, 1998)	Sateré marmoset
15. <i>M. manicorensis</i> (Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000)	Manicoré marmoset
16. <i>M. acariensis</i> . (Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000)	Rio Acarí marmoset
17. <i>Callithrix jacchus</i> (Linnaeus, 1758)	Common marmoset
18. <i>C. penicillata</i> (É. Geoffroy, 1812)	Black-tufted-ear marmoset
19. <i>C. kublii</i> Coimbra-Filho, 1985	Wied's black-tufted-ear marmoset
20. <i>C. geoffroyi</i> (É. Geoffroy in Humboldt, 1812)	Geoffroy's tufted-ear marmoset
21. <i>C. aurita</i> (É. Geoffroy in Humboldt, 1812)	Buffy-tufted-ear marmoset
22. <i>C. flaviceps</i> (Thomas, 1903)	Buffy-headed marmoset
23. <i>Saguinus nigricollis nigricollis</i> (Spix, 1823)	Spix's black mantle tamarin
24. <i>S. nigricollis hernandezii</i> Hershkovitz, 1982	Hernández-Camacho's black mantle tamarin
25. <i>S. graellsii</i> (Jiménez de la Espada, 1870)	Graell's black-mantle tamarin
26. <i>S. fuscicollis fuscicollis</i> (Spix, 1823)	Spix's saddle-back tamarin
27. <i>S. fuscicollis fuscus</i> (Lesson, 1840)	Lesson's saddle-back tamarin
28. <i>S. fuscicollis avilapiresi</i> Hershkovitz, 1966	Ávila Pires' saddle-back tamarin
29. <i>S. fuscicollis cruzlimai</i> Hershkovitz, 1966	Cruz Lima's saddle-back tamarin
30. <i>S. fuscicollis leucogenys</i> (Gray, 1866)	Andean saddle-back tamarin
31. <i>S. fuscicollis lagonotus</i> (Jiménez de la Espada, 1870)	Red-mantle saddle-back tamarin
32. <i>S. fuscicollis primitivus</i> Hershkovitz, 1977	Saddle-back tamarin
33. <i>S. fuscicollis illigeri</i> (Pucheran, 1845)	Illiger's saddle-back tamarin
34. <i>S. fuscicollis nigrifrons</i> (I. Geoffroy, 1850)	Geoffroy's saddle-back tamarin
35. <i>S. fuscicollis weddelli</i> (Deville, 1849)	Weddell's saddle-back tamarin
36. <i>S. fuscicollis melanoleucus</i> (Miranda Ribeiro, 1912)	White saddle-back tamarin
37. <i>S. fuscicollis crandalli</i> Hershkovitz, 1966	Crandall's saddle-back tamarin
38. <i>S. tripartitus</i> (Milne-Edwards, 1878)	Golden-mantle saddle-back tamarin
39. <i>S. mystax mystax</i> (Spix, 1823)	Spix's mustached tamarin
40. <i>S. mystax pileatus</i> (I. Geoffroy & Deville, 1848)	Red-cap mustached tamarin
41. <i>S. mystax pluto</i> (Lönnberg, 1926)	White-rump mustached tamarin
42. <i>S. labiatus labiatus</i> (É. Geoffroy in Humboldt, 1812)	Red-bellied tamarin
43. <i>S. labiatus thomasi</i> (Goeldi, 1907)	Thomas' mustached tamarin
44. <i>S. labiatus rufiventer</i> (Gray, 1843)	
45. <i>S. imperator imperator</i> (Goeldi, 1907)	Black-chinned emperor tamarin
46. <i>S. imperator subgrisescens</i> (Lönnberg, 1940)	Bearded emperor tamarin
47. <i>S. midas</i> (Linnaeus, 1758)	Golden-handed tamarin
48. <i>S. niger</i> (É. Geoffroy, 1803)	Black-handed tamarin
49. <i>S. inustus</i> (Schwarz, 1951)	Mottled-face tamarin
50. <i>S. bicolor</i> (Spix, 1823)	Pied bare-face tamarin
51. <i>S. martinsi martinsi</i> (Thomas, 1912)	Martin's bare-face tamarin
52. <i>S. martinsi ochraceus</i> Hershkovitz, 1966	Ochraceous bare-face tamarin
53. <i>S. leucopus</i> (Günther, 1877)	Silvery-brown bare-face tamarin
54. <i>S. oedipus</i> (Linnaeus, 1758)	Cotton-top tamarin
55. <i>S. geoffroyi</i> (Pucheran, 1845)	Geoffroy's tamarin
56. <i>Leontopithecus rosalia</i> (Linnaeus, 1766)	Golden lion tamarin
57. <i>L. chrysomelas</i> (Kuhl, 1820)	Golden-headed lion tamarin
58. <i>L. chrysopygus</i> (Mikan, 1823)	Black lion tamarin
59. <i>L. caissara</i> Lorini & Persson, 1990	Black-faced lion tamarin
60. <i>Callimico goeldii</i> (Thomas, 1904)	Goeldi's monkey

Table 5. Species and subspecies of the Family Cebidae.

Family Cebidae	Common name
1. <i>S. oerstedii oerstedii</i> (Reinhardt, 1872)	Black-crowned Central American squirrel monkey
2. <i>S. oerstedii citrinellus</i> Thomas, 1904	Grey-crowned Central American squirrel monkey
3. <i>Saimiri boliviensis boliviensis</i> (I. Geoffroy & de Blainville, 1834)	Bolivian squirrel monkey
4. <i>S. boliviensis peruviensis</i> Hershkovitz, 1984	Peruvian squirrel monkey
5. <i>S. boliviensis pluvialis</i> Lönnberg, 1940	
6. <i>S. boliviensis jaburuensis</i> Lönnberg, 1940	
7. <i>S. vanzolinii</i> Ayres, 1981	Black-headed squirrel monkey
8. <i>S. sciureus sciureus</i> (Linnaeus, 1758)	Common squirrel monkey
9. <i>S. sciureus albigena</i> (Von Pusch, 1941)	
10. <i>S. sciureus cassiquiarensis</i> (Lesson, 1840)	Humboldt's squirrel monkey
11. <i>S. sciureus macrodon</i> (Elliot, 1907)	Ecuadorian squirrel monkey
12. <i>S. ustus</i> I. Geoffroy, 1843	Golden-backed squirrel monkey
13. <i>Cebus apella apella</i> (Linnaeus, 1758)	Guianan brown capuchin
14. <i>C. apella fatuellus</i> (Linnaeus, 1766)	
15. <i>C. apella macrocephalus</i> Spix, 1823	Large-headed capuchin
16. <i>C. apella peruanus</i> Thomas, 1901	Peruvian tufted capuchin
17. <i>C. apella tocantinus</i> Lönnberg, 1939	
18. <i>C. apella margaritae</i> Hollister, 1914	Margarita Island capuchin
19. <i>C. libidinosus libidinosus</i> Spix, 1823	Bearded capuchin
20. <i>C. libidinosus pallidus</i> (Gray, 1866)	Tambopata tufted capuchin, pale capuchin
21. <i>C. libidinosus paraguayanus</i> Fischer, 1829	Paraguayan tufted capuchin
22. <i>C. libidinosus juruanus</i> Lönnberg, 1939	
23. <i>C. nigrurus nigrurus</i> (Goldfuss, 1809)	Black-horned capuchin
24. <i>C. nigrurus robustus</i> Kuhl, 1820	Crested capuchin
25. <i>C. nigrurus cucullatus</i> Spix, 1823	
26. <i>C. xanthosternus</i> Wied-Neuwied, 1826	Yellow-breasted capuchin
27. <i>C. albifrons albifrons</i> (Humboldt, 1812)	White-fronted capuchin
28. <i>C. albifrons adustus</i> Hershkovitz, 1949	Brown-faced capuchin
29. <i>C. albifrons aequatorialis</i> Allen, 1914	Ecuadorian capuchin
30. <i>C. albifrons cesarae</i> Hershkovitz, 1949	
31. <i>C. albifrons cuscinus</i> Thomas, 1901	Shock-headed capuchin
32. <i>C. albifrons malitiosus</i> Elliot, 1909	
33. <i>C. albifrons trinitatis</i> Von Pusch, 1941	Trinidad white-fronted capuchin
34. <i>C. albifrons versicolor</i> Pucheran, 1845	Varied capuchin
35. <i>C. albifrons yuracus</i> Hershkovitz, 1949	Andean white-fronted capuchin
36. <i>C. albifrons leucocephalus</i> Gray, 1865	
37. <i>C. capucinus capucinus</i> (Linnaeus, 1758)	White-faced capuchin
38. <i>C. capucinus limitaneus</i> Hollister, 1914	
39. <i>C. capucinus imitator</i> Thomas, 1903	Panamanian white-throated capuchin
40. <i>C. capucinus curtus</i> Bangs, 1905	Gorgona white-fronted capuchin
41. <i>C. olivaceus olivaceus</i> Schomburgk, 1848	Wedge-capped capuchin
42. <i>C. olivaceus apiculatus</i> Hershkovitz, 1949	
43. <i>C. olivaceus brunneus</i> Allen, 1914	Brown weeper capuchin
44. <i>C. olivaceus castaneus</i> I. Geoffroy, 1851	Chestnut capuchin
45. <i>C. olivaceus kaapori</i> Queiroz, 1992	Ka'apor capuchin

Table 6. Species and subspecies of the Family Aotidae.

Family Aotidae	Common name
1. <i>Aotus lemurinus lemurinus</i> I. Geoffroy, 1846	Colombian or lemurine night monkey
2. <i>A. lemurinus griseimembra</i> Elliot, 1912	Grey-legged night monkey
3. <i>A. lemurinus zonalis</i> Goldman, 1914	
4. <i>A. lemurinus brumbacki</i> Hershkovitz, 1983	Brumback's night monkey
5. <i>A. hershkovitzii</i> Ramirez-Cerquera, 1983	Hershkovitz's night monkey
6. <i>A. trivirgatus</i> (Humboldt, 1812)	Douroucouli, owl monkey, night monkey
7. <i>A. vociferans</i> (Spix, 1823)	
8. <i>A. miconax</i> Thomas, 1927	Andean night monkey
9. <i>A. nancymae</i> Hershkovitz, 1983	Ma's night monkey
10. <i>A. nigriceps</i> Dollman, 1909	Black-headed or Peruvian night monkey
11. <i>A. azarai azarai</i> (Humboldt, 1812)	Azara's night monkey
12. <i>A. azarai boliviensis</i> Elliot, 1907	Bolivian night monkey
13. <i>A. azarai infulatus</i> (Kuhl, 1820)	Feline night monkey

Table 7. Species and subspecies of the Family Pitheciidae.

Family Pitheciidae	Common name
1. <i>Callicebus modestus</i> Lönnberg, 1939	
2. <i>C. donacophilus</i> (D'Orbigny, 1836)	
3. <i>C. pallescens</i> Thomas, 1907	
4. <i>C. olallae</i> Lönnberg, 1939	Beni titi monkey
5. <i>C. oenanthe</i> Thomas, 1924	Andean titi monkey
6. <i>C. cinerascens</i> (Spix, 1823)	
7. <i>C. hoffmannsi</i> Thomas, 1908	Hoffmann's titi monkey
8. <i>C. baptista</i> Lönnberg, 1939	
9. <i>C. moloch</i> (Hoffmannsegg, 1807)	
10. <i>C. brunneus</i> (Wagner, 1842)	
11. <i>C. cupreus</i> (Spix, 1823)	
12. <i>C. ornatus</i> (Gray, 1866)	Ornate titi monkey
13. <i>C. medemi</i> Hershkovitz, 1963	
14. <i>C. torquatus torquatus</i> (Hoffmannsegg, 1807)	Collared titi, widow monkey
15. <i>C. torquatus lugens</i> (Humboldt, 1811)	
16. <i>C. torquatus lucifer</i> Thomas, 1914	Widow monkey
17. <i>C. torquatus purinus</i> Thomas, 1927	
18. <i>C. torquatus regulus</i> Thomas, 1927	
19. <i>C. personatus</i> (É. Geoffroy, 1812)	Northern masked titi
20. <i>C. nigrifrons</i> (Spix, 1823)	Black-fronted titi
21. <i>C. melanochir</i> Wied-Neuwied, 1820	Southern Bahian masked titi
22. <i>C. barbarabrownae</i> Hershkovitz, 1990	Northern Bahian blond titi
23. <i>C. coimbrai</i> Kobayashi and Langguth, 1999	Coimbra's titi
24. <i>Pithecia pithecia pithecia</i> (Linnaeus, 1758)	White-faced saki
25. <i>P. pithecia chrysocephala</i> I. Geoffroy, 1850	Golden-faced saki
26. <i>P. monachus monachus</i> (É. Geoffroy, 1812)	Geoffroy's monk saki
27. <i>P. monachus milleri</i> Allen, 1914	Miller's monk saki
28. <i>P. monachus napensis</i> Lönnberg, 1938	Napo monk saki
29. <i>P. irrorata irrorata</i> Gray, 1842	Gray's bald faced saki
30. <i>P. irrorata vanzolinii</i> Hershkovitz, 1987	Vanzolini's bald-faced saki
31. <i>P. albicans</i> Gray, 1860	White saki, buffy saki
32. <i>P. aequatorialis</i> Hershkovitz, 1987	Equatorial saki
33. <i>Chiropotes albinus</i> (I. Geoffroy & Deville, 1848)	White-nosed bearded saki
34. <i>C. satanas satanas</i> (Hoffmannsegg, 1807)	Bearded saki
35. <i>C. satanas chiropotes</i> (Humboldt, 1811)	Black saki
36. <i>C. satanas utahicki</i> Hershkovitz, 1985	Uta Hick's bearded saki
37. <i>Cacajao calvus calvus</i> (I. Geoffroy, 1847)	White bald-headed uacari
38. <i>C. calvus ucayalii</i> (Thomas, 1928)	Ucayali bald-headed uacari
39. <i>C. calvus novaesi</i> Hershkovitz, 1987	Novaes' bald-headed uacari
40. <i>C. calvus rubicundus</i> (I. Geoffroy and Deville, 1848)	Red bald-headed uacari
41. <i>C. melanocephalus melanocephalus</i> (Humboldt, 1811)	Humboldt's black-headed uacari
42. <i>C. melanocephalus ouakary</i> (Spix, 1823)	Spix's black-headed uacari

Table 8. Species and subspecies of the Family Atelidae.

Family Atelidae	Common name
1. <i>Alouatta seniculus seniculus</i> (Linnaeus, 1766)	Red howling monkey
2. <i>A. seniculus insulanus</i> Elliot, 1910	Trinidad howling monkey
3. <i>A. seniculus</i> ssp. (formerly <i>straminea</i> ¹)	Guianan red howling monkey
4. <i>A. seniculus amazonica</i> Lönnberg, 1941	
5. <i>A. seniculus juara</i> Elliot 1910	
6. <i>A. seniculus puruensis</i> Lönnberg, 1941	
7. <i>A. seniculus arctoidea</i> Cabrera, 1940	Ursine howling monkey
8. <i>A. sara</i> Elliot, 1910	Bolivian red howling monkey
9. <i>A. nigerrima</i> Lönnberg, 1941	Black howling monkey
10. <i>A. belzebul belzebul</i> (Linnaeus, 1766)	Red-handed howling monkey
11. <i>A. belzebul discolor</i> (Spix, 1823)	
12. <i>A. belzebul ululata</i> Elliot, 1912	
13. <i>A. guariba guariba</i> (Humboldt, 1812)	Northern brown howling monkey
14. <i>A. guariba clamitans</i> Cabrera, 1940	Southern brown howling monkey
15. <i>A. palliata palliata</i> (Gray, 1849)	Golden-mantled howling monkey
16. <i>A. palliata mexicana</i> (Merriam 1902)	Mexican howling monkey
17. <i>A. palliata aequatorialis</i> (Festa, 1903)	South Pacific blackish howling monkey, Ecuadorian mantled howling monkey
18. <i>A. coibensis coibensis</i> Thomas, 1902	Coiba Island howling monkey
19. <i>A. coibensis trabeata</i> Lawrence, 1933	Azuero howling monkey
20. <i>A. caraya</i> (Humboldt, 1812)	Black howling monkey
21. <i>A. pigra</i> Lawrence, 1933	Black howling monkey
22. <i>Ateles geoffroyi geoffroyi</i> Kuhl, 1820	Geoffroy's spider monkey
23. <i>A. geoffroyi azuerensis</i> (Bole, 1937)	Azuero spider monkey
24. <i>A. geoffroyi frontatus</i> (Gray, 1842)	Black-browed spider monkey
25. <i>A. geoffroyi grisescens</i> Gray, 1866	Hooded spider monkey
26. <i>A. geoffroyi panamensis</i> Kellogg & Goldman, 1944	Red spider monkey
27. <i>A. geoffroyi ornatus</i> (Gray, 1870)	Ornate spider monkey
28. <i>A. geoffroyi vellerosus</i> (Gray, 1866)	Mexican spider monkey
29. <i>A. geoffroyi yucatanensis</i> Kellogg & Goldman, 1944	Yucatán spider monkey
30. <i>A. geoffroyi fusciceps</i> Gray, 1866	Brown-headed spider monkey
31. <i>A. geoffroyi rufiventris</i> Allen, 1914	Colombian black spider monkey
32. <i>A. chamek</i> (Humboldt, 1812)	Black-faced black spider monkey
33. <i>A. paniscus</i> (Linnaeus, 1758)	Red-faced black spider monkey
34. <i>A. marginatus</i> (É. Geoffroy, 1809)	White-whiskered spider monkey
35. <i>A. belzebuth</i> (É. Geoffroy, 1806)	White-bellied spider monkey
36. <i>A. hybridus hybridus</i> (I. Geoffroy, 1829)	Variiegated spider monkey
37. <i>A. hybridus brunneus</i> Gray, 1872	Brown spider monkey
38. <i>Lagothrix lagothricha</i> (Humboldt, 1812)	Humboldt's woolly monkey
39. <i>L. cana cana</i> (É. Geoffroy in Humboldt, 1812)	Geoffroy's woolly monkey
40. <i>L. cana tschudii</i> Pucheran, 1857	
41. <i>L. poeppigii</i> Schinz, 1844	Poeppig's woolly monkey
42. <i>L. lugens</i> Elliot, 1907	Colombian woolly monkey
43. <i>Oreonax flavicauda</i> (Humboldt, 1812)	Yellow-tailed woolly monkey
44. <i>Brachyteles arachnoides</i> (É. Geoffroy, 1806)	Southern muriqui
45. <i>B. hypoxanthus</i> (Kuhl, 1820)	Northern muriqui

Table 9. A summary table of the New World primates by genus.

Family	Species	Taxa
Family Callitrichidae		
<i>Cebuella</i>	1	2
<i>Mico</i>	14	14
<i>Callithrix</i>	6	6
<i>Saguinus</i>	15	33
<i>Leontopithecus</i>	4	4
<i>Callimico</i>	1	1
Subtotal	41	60
Family Cebidae		
<i>Saimiri</i>	5	12
<i>Cebus</i>	7	33
Subtotal	12	45
Family Aotidae		
<i>Aotus</i>	8	13
Family Pitheciidae		
<i>Callicebus</i>	19	23
<i>Pithecia</i>	5	9
<i>Chiropotes</i>	2	4
<i>Cacajao</i>	2	6
Subtotal	28	42
Family Atelidae		
<i>Alouatta</i>	8	21
<i>Ateles</i>	6	16
<i>Lagothrix</i>	4	5
<i>Oreonax</i>	1	1
<i>Brachyteles</i>	2	2
Subtotal	21	45
Total – Neotropical	110	205

CEBUELLA Gray, 1886

Cebuella pygmaea pygmaea (Spix, 1823)
C. pygmaea niveiventris Lönnberg, 1940

Cebuella was proposed by Gray (1866) as a subgenus of *Hapale* (later *Callithrix*), and soon after as a distinct genus (Gray, 1870). Rosenberger (1981), Rosenberger and Coimbra-Filho (1984), and Natori (1994) argued, on morphological terms, that the pygmy marmoset should correctly be included in the genus *Callithrix*. This was not maintained in Rosenberger *et al.* (1990), although Barroso (1995), Barroso *et al.* (1997), Moreira (1996), Schneider *et al.* (1996), Schneider and Rosenberger (1996), Tagliaro *et al.* (1997), Porter *et al.* (1997a), and Canavez *et al.* (1999a) also argued for this arrangement on the basis of molecular genetics. The 1997 AZA studbook for the pygmy marmoset placed it in the genus *Callithrix* (Arden, 1998). The argument that *Cebuella* should be included in the genus *Callithrix* centers on the conclusion, from both morphological and genetic studies, that the pygmy marmoset is more closely related to the Amazonian marmosets (the *argentata* group of Hershkovitz [1977]) than the latter are to the Atlantic forest marmosets (the *jacchus* group of Hershkovitz [1977]). Schneider *et al.* (1993) and Schneider and Rosenberger (1996), however, also concluded that their molecular genetic data are compatible with *jacchus* and *pygmaea* being congeneric. Although closely related to the Amazonian marmosets, we believe that *Cebuella pygmaea* deserves generic status. The species shows very distinct fea-

tures, unique among the callitrichids, involving not only its diminutive size but also the tree-gouging specialization not observed to nearly the same extent in its Amazonian sister group.

If *Cebuella* is maintained as a separate genus, then the group would be paraphyletic unless the *argentata* group marmosets and the *jacchus* group marmosets are placed in different genera. This was the option adopted, with the Amazonian marmosets being placed in the genus *Mico* Lesson, 1840 (see below). This decision was also based on the clear identity of the three genera shown in all morphological and molecular studies available.

In 1940, Lönnberg described the subspecies *Cebuella pygmaea niveiventris* from Lago Ipixuna, south bank of the Rio Solimões, based on its sharply contrasting whitish chest, belly, and inner surface of arms and legs. The ventral surface of *C. p. pygmaea* is ochraceous. Cruz Lima (1945) and Napier (1976) also recognized and described the two subspecies. *Cebuella pygmaea pygmaea* (Spix, 1823) occurs in the state of Amazonas, Brazil, north of the Rio Solimões and south of the Rio Japurá, southern Colombia north of the Ríos Marañón and Putumayo and south of the Río Caquetá (Japurá), eastern Ecuador, and eastern Peru south of Río Putumayo, north of the Río Marañón and east of the Río Pastaza, whereas *Cebuella pygmaea niveiventris* Lönnberg, 1940 occurs in eastern Peru south of the Río Marañón and east of the Río Huallaga, and in the state of Amazonas, Brazil, south of the Rio Solimões and west of the Rio Purus. It occurs as far south as the Río Muyumanu in the Pando of northern Bolivia (Buchanan-Smith *et al.*, 2000). Hershkovitz (1977) argued that the color of the underparts is individually and locally variable and not justifying the subspecific status of *niveiventris*. Van Roosmalen and Van Roosmalen (1997), however, recently presented evidence for the validity of the two subspecies based on field observations and captive specimens of *C. p. niveiventris*, and confirmed its presence in the interfluvium of the Rios Purus and Madeira.

CALLITHRIX Erxleben, 1777

1. *Callithrix jacchus* (Linnaeus, 1758)
2. *C. penicillata* (É. Geoffroy, 1812)
3. *C. kuhlii* Coimbra-Filho, 1985
4. *C. geoffroyi* (É. Geoffroy in Humboldt, 1812)
5. *C. aurita* (É. Geoffroy in Humboldt, 1812)
6. *C. flaviceps* (Thomas, 1903)

Mittermeier and Coimbra-Filho (1981) maintained that the marmosets comprising Hershkovitz's (1975) "Jacchus" group, should be considered good species rather than subspecies of *C. jacchus*, even though fertile hybrids had been produced in captivity (Hill, 1957; Coimbra-Filho, 1970, 1971, 1973, 1974, 1978; Mallinson, 1971; Hampton *et al.*, 1971; Coimbra-Filho and Mittermeier, 1973b; Coimbra-Filho *et al.*, 1993b), and Hershkovitz (1975, 1977) and Alonso *et al.* (1987) had provided evidence of intergradation in the wild.

However, Mittermeier and Coimbra-Filho (1981) argued that the issue of species or subspecies designations for the non-Amazonian marmosets was controversial and depended on the resolution of three questions: 1) Do the forms naturally overlap in their ranges without interbreeding? 2) What is the correct taxonomic interpretation of the intergrades reported by Hershkovitz (1975, 1977), considering they might be merely individual or ontogenetic variants rather than hybrids? and 3) Presuming natural zones of intergradation do exist, are they regions of broad clinal variation or narrow contact zones? Mittermeier *et al.* (1988, p.21) provided answers to these questions, which reinforced the argument that at least the forms *aurita*, *geoffroyi*, *penicillata*, *jacchus* and *kublui* should be considered valid species (*flaviceps* may be subspecific to *aurita*, see below), even though it would seem that none of the "Jacchus" group marmosets overlap in their geographic distributions without interbreeding. Evidence is now available for a number of natural hybrid zones either at the distributional limits of the various forms or due to introductions. They are reviewed by Coimbra-Filho *et al.* (1993b), who considered hybridization at natural distributional limits (*C. penicillata* x *C. geoffroyi*, *C. penicillata* x *C. kublui*, *C. geoffroyi* x *C. flaviceps*, *C. aurita* x *C. flaviceps*) and where one (or both) forms had been introduced (*C. jacchus* x *C. penicillata*).

The important feature is that, in all cases, the documented contact zones are narrow or confined and clinal variation is not evident (Vivo, 1991; Coimbra-Filho *et al.*, 1993b). Vivo (1991) classified all the "Jacchus" group marmosets as species (except for *kublui* which he did not recognize as distinct from *C. penicillata*), arguing that allopatry or parapatry alone cannot be used to determine subspecific or specific status and that there is no evidence for widespread intergradation or clinal variation, and protesting that the use of subspecific classifications based not on spatial distribution of characters but merely on the degree of similarity in pelage between forms is inadequate. On the basis of pelage color and patterns alone, Rosenberger (1984) also argued that they should be considered species rather than subspecies, but that more information is needed from other systems, genetic and morphological.

The authorship of the name *Callithrix kublui* is the subject of some debate. Hershkovitz (1975, p.142) was the first to indicate that Wied-Neuwied (1826) had referred to the marmoset of south-east Bahia as "*Hapale penicillata Kuhlui*" (sic). However, Hershkovitz (1975, 1977) argued at length that *kublui* was not a valid taxon, being merely an intergrade between *C. j. penicillata* and *C. j. geoffroyi*. Vivo (1991, pp.80-81), on the other hand, argued that Wied-Neuwied (1826) had not intentionally given it this name, merely, and incorrectly, ascribing the authorship of the name *penicillata* to Kuhl. The first person to intentionally use the name *kublui* to describe the marmosets from south-east Bahia was Hershkovitz (1975), but his argument that it was not a valid taxonomic entity disqualifies the possibility of him being attributed authorship. This is therefore given to Coimbra-Filho (1985).

Groves (1989, 1993) listed the "Jacchus" group marmosets as separate species (see also Marroig, 1995). Natori (1986, 1990) and Natori and Shigehara (1992) in their studies of the dental morphology, and Natori (1994) in his craniometrical study, also argued for their ranking as species, based however on compliance with the separation of *C. argentata* and *C. humeralifer* as distinct species. Natori (1986) examined six dental characters and tooth size in *Callithrix*. On the basis of molar tooth size alone, he found that the difference between the "Jacchus" group marmosets was greater than between the Amazonian *C. argentata* and *C. humeralifer*. He argued that if the latter are to be considered separate species, then so should the "Jacchus" group marmosets. The same conclusion was drawn by Natori (1994) in his study of 19 cranial measures. On the basis of Q-mode correlation of these measures, the distances between the "Jacchus" group members were greater than those between the Amazonian *argentata* and *humeralifer*, and, excepting *C. jacchus* and *C. penicillata*, were greater than between *Cebuella pygmaea* and *argentata* and between *Cebuella* and *humeralifer*.

Cytogenetics and molecular genetics have to date been incisive in their contribution to the debate concerning the taxonomic status of the "Jacchus" group marmosets. Peixoto (1976) and Peixoto and Pedreira (1982) compared the chromosomes of *C. jacchus*, *C. penicillata* and *C. geoffroyi* and recorded clear differences in G-banding indicating paracentric inversions not found in later studies by Seuánez *et al.* (1988) and Nagamachi (1995). Nagamachi (1995) and Nagamachi *et al.* (1997) carried out a study of the chromosome morphology of *C. kublui* and the other "Jacchus" group marmosets except *C. flaviceps*. All of the eastern Brazilian marmosets have a diploid chromosome number of 46, with 30 two-armed and 14 acrocentric autosomes, a conservative submetacentric X chromosome, and a Y chromosome which is highly variable in size and morphology. In *C. kublui* the Y chromosome is small and two-armed (metacentric). An analysis of the G-banding patterns demonstrated a lack of any chromosomal rearrangements to differentiate their karyotypes. C-banding, likewise, demonstrated no differences between the species. Heterochromatin was found to occur in small quantities in the centromeric regions of all the chromosomes, in the telomeric region of the short arm of pair 6 and the telomeric region of the long arm of chromosome 22. Ag-NOR staining marked secondary constrictions of the small arms of the acrocentric chromosomes. Nagamachi (1995) and Nagamachi *et al.* (1997) concluded that the five species they studied were extremely homogeneous in their karyotypes, except for the size and morphology of the Y chromosome, which in the case of *C. jacchus* was variable even between populations. They concluded that nothing can be said as a result concerning the taxonomic status of each species.

Tagliaro *et al.* (1997) analyzed mitochondrial DNA control region sequences in all the "Jacchus" group marmosets, except for *C. flaviceps*. In reconstructing the phylogeny of these marmosets from their findings, they concluded that "Our trees

certainly do not come down in strong support of a monophyletic *C. kublii*, although their paraphyly is also only weakly supported (i.e. a monophyletic *C. kublii* adds only one substitution to the MP tree)" (p.682), and later (p.683): "our data do not support a clear taxonomic distinction between *C. kublii*, *C. penicillata*, and possibly *C. jacchus*, which [...] we regard as a tentative proposal but one that needs to be further explored..." They found, on the contrary, strong support that both *C. aurita* and *C. geoffroyi* are "distinct evolutionary entities". Genetic studies by Meireles *et al.* (1992) concluded that *M. humeralifer* and *M. emiliae* are subspecies of *M. argentatus*; and that *C. jacchus*, *C. penicillata*, and *C. geoffroyi* are subspecies; but that *C. geoffroyi* is the most primitive of the "jacchus" Group (most similar genetically to *M. argentatus*), which should, therefore, be referred to as the "geoffroyi" Group, with *C. jacchus* and *C. penicillata* as subspecific to *C. geoffroyi*. Meireles *et al.* (1998) concluded that the forms *kublii* and *penicillata* are conspecific.

The primitiveness (Hershkovitz, 1977) of *C. geoffroyi* was also advocated by Natori (1986, 1994) and Natori and Shigehara (1992), and agrees with the low degree of morphological adaptation for tree-gouging observed in this species. Dental and behavioral adaptations for tree-gouging are most advanced in *C. jacchus* and *C. penicillata*.

Coimbra-Filho (1984, 1985, 1990), Rylands (1989b), Mittermeier *et al.* (1988), Natori (1990), Rylands *et al.* (1993), and Groves (1993, in press) recognize as a valid form. Hershkovitz (1977) regarded *Callithrix kublii* from southern Bahia to be a hybrid between *C. j. geoffroyi* and *C. j. penicillata*. Vivo (1991) considered it to be indistinguishable from *C. penicillata* from northern Minas Gerais. Coimbra-Filho (1984, 1985, 1990), Rylands (1989b), Mittermeier *et al.* (1988), Natori (1990), Rylands *et al.* (1993), and Groves (1993, in press) recognize it as a valid species. Groves (1993) and Eisenberg and Redford (1999) gave the distribution as Bolivia - evidently a typographic error.

Coimbra-Filho (1986a, 1986b, 1990) and Coimbra-Filho *et al.* (1991) argued that *Callithrix flaviceps* should be considered subspecific to *C. aurita*. The similarities between *C. flaviceps* and *C. aurita* in pelage patterns such as the ear tufts and the skull-like facial mask, ecological adaptations, ontogeny, (the infants are extremely similar), vocalizations and clinal variation in overall pelage color, indicate to us that *flaviceps* might well be best considered a subspecies of *aurita* (Coimbra-Filho, 1986a, 1986b; Coimbra-Filho *et al.*, 1993b).

The following publications list *all* marmosets as species: Mittermeier *et al.* (1992a), Vivo (1985, 1991), and Groves (1993, in press).

MICO Lesson, 1840

1. *Mico argentatus* (Linnaeus, 1766)
2. *M. leucippe* (Thomas, 1922)

3. *M. melanurus* (É. Geoffroy in Humboldt, 1812)
4. *M. intermedius* (Hershkovitz, 1977)
5. *M. emiliae* (Thomas, 1920)
6. *M. nigriceps* (Ferrari & Lopes, 1992)
7. *M. marcai* (Alperin, 1993)
8. *M. humeralifer* (É. Geoffroy in Humboldt, 1812)
9. *M. chrysoleucus* (Wagner, 1842)
10. *M. mauesi* (Mittermeier, Schwarz & Ayres, 1992)
11. *M. humilis* (Van Roosmalen, Van Roosmalen, Mittermeier & Fonseca, 1998)
12. *M. saterei* (Silva, Jr. & Noronha, 1998)
13. *M. manicorensis* (Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000)
14. *M. acariensis* (Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000)

As discussed in the section dealing with *Cebuella*, the phylogenetic closeness of the pygmy marmoset to the other Amazonian marmosets has indicated that they could be considered to be of the same genus. The alternative, to recognize the distinctiveness of *pygmaea* and avoid paraphyletic genera, is to place the Amazonian and Atlantic forest marmosets into separate genera. The oldest generic name applicable to the Amazonian marmosets alone is *Mico* Lesson, 1840 (type species *Mico argentatus*). The name *Mico* is used as a subgenus for the Amazonian marmosets by Groves (in press).

Coimbra-Filho (1990) argued that the three subspecies of *Mico humeralifer* listed by Hershkovitz (1977) (*Callithrix h. humeralifer*, *C. h. chrysoleuca*, and *C. h. intermedius*) should be considered species, following De Boer (1974) and Vivo (1991). *Mico intermedius* was described as an intermediate color form of *M. h. humeralifer* and *M. h. chrysoleuca* by Hershkovitz (1977). Pelage color and pattern, and its geographic distribution, however, would place it as a subspecies of *M. argentatus* if, following Hershkovitz (1977), the Amazonian marmosets are considered subspecies of just two species, *M. argentatus* and *M. humeralifer* (see Rylands *et al.*, 1993). Meireles *et al.* (1992) indicated that *M. humeralifer* and *M. "emiliae"* from Rondônia are subspecific to *M. argentatus* (see below).

Hapale emiliae was first described by Thomas (1904) from the Rio Iriri, southern Pará. It was not recognized by Hershkovitz (1977) who regarded it as a dark form of *Callithrix argentata*. Vivo (1985, 1991) revalidated this form on the basis of specimens from the state of Rondônia. However, Rylands *et al.* (1993) indicated that the Rondônia marmosets described by Vivo should be considered a distinct form based on the fact that its distribution and that of the *Hapale emiliae* Thomas, 1904 from Maloca on the Rio Curuá (see Vivo 1985; Ávila Pires 1986) are disjunct, and separated by *M. melanurus*. *M. emiliae* was not listed by Groves (1993). That the Rondônia "emiliae" is a distinct form from *emiliae* Thomas 1904 was confirmed by Sena (1998) and Ferrari *et al.* (1999), who found *M. emiliae* to be more similar to *M. argentatus* than the "emiliae" from Rondônia. These authors argue that the Rio Tapajós separates two distinct, if very re-

cent, radiations of *Mico*. Alperin (1995) argued that *Mico nigricaps* (Ferrari and Lopes, 1992) and “*emiliae*” from Rondônia belong to the same species.

Callithrix argentata marcai was described by Alperin 1993. It is listed here as a species to conform with the view that all Amazonian marmosets should be considered species (Vivo, 1985, 1991; Mittermeier *et al.*, 1992a). It is known only from the type locality, “Foz do Rio Castanho (= Rio Roosevelt), afluenta esquerda do Rio Aripuanã. Estado do Amazonas, Brasil” (Alperin 1993). The type locality as described by Alperin is confused in that the Rio Castanho is not a synonym of the Rio Roosevelt, and is a left bank affluent of the Rio Roosevelt, not the Rio Aripuanã. Confused also is the map and gazetteer of localities provided in Alperin (1993) which do not correspond.

The karyotype of *M. saterei* (Sousa e Silva Jr. & Noronha, 1998) was studied by Barros *et al.* (1996) and found to be typical of the “*argentata*” marmoset group and very similar to that of *M. chrysoleuca*.

SAGUINUS Hoffmannsegg, 1807

1. *Saguinus nigricollis nigricollis* (Spix, 1823)
2. *S. nigricollis hernandezii* Hershkovitz, 1982
3. *S. graellsii* (Jiménez de la Espada, 1870)
4. *S. fuscicollis fuscicollis* (Spix, 1823)
5. *S. fuscicollis fuscus* (Lesson, 1840)
6. *S. fuscicollis avilapirensi* Hershkovitz, 1966
7. *S. fuscicollis cruzlimai* Hershkovitz, 1966
8. *S. fuscicollis leucogenys* (Gray, 1866)
9. *S. fuscicollis lagonotus* (Jiménez de la Espada, 1870)
10. *S. fuscicollis primitivus* Hershkovitz, 1977
11. *S. fuscicollis illigeri* (Pucheran, 1845)
12. *S. fuscicollis nigrifrons* (I. Geoffroy, 1850)
13. *S. fuscicollis weddelli* (Deville, 1849)
14. *S. fuscicollis melanoleucus* (Miranda Ribeiro, 1912)
15. *S. fuscicollis crandalli* Hershkovitz, 1966
16. *S. tripartitus* (Milne-Edwards, 1878)
17. *S. mystax mystax* (Spix, 1823)
18. *S. mystax pileatus* (I. Geoffroy & Deville, 1848)
19. *S. mystax pluto* (Lönnerberg, 1926)
20. *S. labiatus labiatus* (É. Geoffroy in Humboldt, 1812)
21. *S. labiatus rufiventer* (Gray, 1843)
22. *S. labiatus thomasi* (Goeldi, 1907)
23. *S. imperator imperator* (Goeldi, 1907)
24. *S. imperator subgrisescens* (Lönnerberg, 1940)
25. *S. midas* (Linnaeus, 1758)
26. *S. niger* (É. Geoffroy, 1803)
27. *S. inustus* (Schwarz, 1951)
28. *S. bicolor* (Spix, 1823)
29. *S. martinsi martinsi* (Thomas, 1912)
30. *S. martinsi ochraceus* Hershkovitz, 1966
31. *S. leucopus* (Günther, 1877)
32. *S. oedipus* (Linnaeus, 1758)
33. *S. geoffroyi* (Pucheran, 1845)

The taxonomy of *Saguinus nigricollis* follows Hershkovitz (1982). *S. n. graellsii* is listed as a full species by Hernández-Camacho and Cooper (1976) and Defler (1994), on the basis that it is sympatric with a population of *S. nigricollis* in the region of Puerto Leguizamo in southern Colombia. Hernández-Camacho and Defler (1991) listed it as a subspecies of *S. nigricollis*, in conformity with Hershkovitz (1977). Although Defler (1994) indicated that further studies are needed to prove the species' status of this form, it was considered a distinct species by Groves (in press).

The taxonomy of *Saguinus fuscicollis* is based on Hershkovitz (1977); see also Cheverud and Moore (1990). *S. f. melanoleucus*, *S. f. acensis*, and *S. f. crandalli* were listed as subspecies of *S. melanoleucus* by Coimbra-Filho (1990). *Saguinus fuscicollis acensis* Carvalho 1957 is not considered a valid form but a hybrid between *S. f. fuscicollis* and *S. f. melanoleucus* on the upper Rio Juruá, following Peres (1993). *S. f. cruzlimai* and *S. f. crandalli* are of unknown provenance (Hershkovitz, 1977), and the latter at least may well also be a hybrid of *S. f. fuscicollis* x *S. f. melanoleucus*. Hernández-Camacho and Cooper (1976) indicated the existence of an undescribed *S. fuscicollis* subspecies in the region of San José de Guaviare, Colombia (also cited by Defler, 1994). In a molecular genetic study, Cropp *et al.* (1999) argued that the form *fuscus* was closer to *S. nigricollis* than to *S. fuscicollis* and gave it species status. Rylands *et al.* (1993) argued that *S. f. melanoleucus* should be considered a species distinct from *S. fuscicollis*. This arrangement was adopted by Groves (in press), with the form *crandalli* (of unknown provenance) as a subspecies.

Hershkovitz (1977) listed *Saguinus tripartitus* as a subspecies of *S. fuscicollis*. Thorington (1988) argued for its species status (see also Albuja, 1994). It was listed as a species by Rylands *et al.* (1993) and Groves (in press).

Saguinus labiatus rufiventer (Gray, 1843) was listed as a junior synonym of *S. l. labiatus* by Hershkovitz (1977). He recognized that red-bellied tamarins in the north of their range were distinct but argued that it was probably a clinal variation. It was considered a valid subspecies, however, by Groves (in press), with a provisional distribution (also indicated by Hershkovitz) which 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 (in press) found that, while *S. m. mystax* and *S. m. pluto* are very similar to each other, the form *pileatus* is quite distinct, and he listed it as a good species, *S. pileatus*.

Hershkovitz (1977) and Eisenberg (1989) listed the black handed tamarin as a subspecies of *S. midas*. On the basis of morphometric studies of the postcanine dentition, Natori and Hanihara (1992) found *S. m. midas* to be more similar to *S. bicolor* than to *S. m. niger* and argued that *S. m. niger* should be raised to species status (Rylands *et al.*, 1993), and also

noted that there was a need to modify the species' group arrangements of Hershkovitz (1977), that is, placing the *S. midas* Group in the Bare-face Tamarin section. Melo *et al.* (1992), on the other hand, examined 20 blood genetic systems in the two subspecies and obtained results compatible with their classification as subspecies, not being sufficiently divergent to warrant species status. Canavez *et al.* (1999a) using molecular data (nuclear DNA) found that *S. midas midas* and *S. bicolor* are more closely related to each other than to *Saguinus midas niger*. Molecular data from mitochondrial DNA, including the two *S. midas* (*S. m. midas*, *S. m. niger*) and the three *S. bicolor* subspecies (*S. b. bicolor*, *S. b. martinsi* and *S. b. ochraceus*), strongly support (Bootstrap values of 98%) *S. midas* (*S. m. midas*, *S. m. niger*) and *S. bicolor* (*S. b. bicolor*, *S. b. martinsi*, and *S. b. ochraceus*) as two distinct clades (Cropp *et al.*, 1999).

Hernández-Camacho and Defler (1991) indicated the probable existence of two subspecies of *S. inustus* in Colombia.

Hershkovitz (1977) considered *Saguinus geoffroyi* to be a subspecies of *S. oedipus*. Comparative morphological studies by Hanihara and Natori (1987), Moore and Cheverud (1992) and Skinner (1991) argued for them being separate species. Eisenberg (1989), Rylands (1993). Hernández-Camacho and Cooper (1976), Mittermeier and Coimbra-Filho (1981), Hernández-Camacho and Defler (1988, 1991), Mittermeier *et al.* (1988), Rylands *et al.* (1993), Groves (1993, in press), Mast *et al.* (1993) and Defler (1994) all list *S. geoffroyi* and *S. oedipus* as separate species.

LEONTOPITHECUS Lesson, 1840

1. *Leontopithecus rosalia* (Linnaeus, 1766)
2. *L. chrysomelas* (Kuhl, 1820)
3. *L. chrysopygus* (Mikan, 1823)
4. *L. caissara* Lorini & Persson, 1990

The lion tamarins, *Leontopithecus*, are given as separate species following Della Serra (1951), Rosenberger and Coimbra-Filho (1984), Mittermeier *et al.* (1988), Natori (1989), and Rylands *et al.* (1993). They have been listed as subspecies of *L. rosalia* by Coimbra-Filho and Mittermeier (1972, 1973a), Hershkovitz (1977), Mittermeier and Coimbra-Filho (1981), Forman *et al.* (1986) and Seuánez *et al.* (1988), the latter two publications on the basis of identical chromosome morphologies. *L. caissara* Lorini and Persson 1990 is regarded as a subspecies of *L. chrysopygus* by Coimbra-Filho (1990). Although some species hybridize in captivity (Coimbra-Filho and Mittermeier, 1976), no contact or hybridization zones are found today in the wild.

CALLIMICO Miranda-Ribeiro, 1912

1. *Callimico goeldii* (Thomas, 1904)

To date, only a single species has been described for this genus, although no evaluation of geographic or population variation has been carried out since the 1977 treatise by

Hershkovitz.

AOTUS Illiger, 1811

1. *Aotus lemurinus lemurinus* (I. Geoffroy, 1846)
2. *A. lemurinus griseimembra* (Elliot, 1912)
3. *A. lemurinus zonalis* Goldman, 1914
4. *A. lemurinus brumbacki* Hershkovitz, 1983
5. *A. hershkovitzi* Ramirez-Cerquera, 1983
6. *A. trivirgatus* (Humboldt, 1812)
7. *A. vociferans* (Spix, 1823)
8. *A. miconax* Thomas, 1927
9. *A. nancymae* Hershkovitz, 1983
10. *A. nigriceps* Dollman, 1909
11. *A. azarai azarai* (Humboldt, 1812)
12. *A. azarai boliviensis* Elliot, 1907
13. *A. azarai infulatus* (Kuhl, 1820)

The taxonomy of *Aotus* follows Hershkovitz (1983), modified by Groves (in press). *A. hershkovitzi* was described by Ramirez-Cerquera in 1983 (*Abstracts. IX Cong. Latinoamericano de Zoología*, Arequipa, Peru, p.148) (see also Defler 1994). Mentioned only in an abstract, this form requires a proper description.

Hernández-Camacho and Cooper (1976) referred to *A. trivirgatus zonalis* (Goldman 1914) in Panama and Colombia, which is considered a synonym of *A. t. griseimembra* by Hershkovitz (1949) and Hill (1960), but as a synonym of *A. l. lemurinus* by Hershkovitz (1983), and a synonym of *A. lemurinus* by Groves (1993). The status recommended by Hershkovitz (1983) was accepted by Hernández-Camacho and Defler (1991), but Groves (in press) listed it as a valid subspecies of *A. lemurinus*. Further modifications by Groves (in press) of Hershkovitz's (1983) appraisal of *Aotus* taxonomy are as follows: the form *brumbacki* Hershkovitz, 1983 is subspecific to *A. lemurinus*, and the form *infulatus* (Kuhl, 1820) is subspecific to *A. azarai* (see below). The name *azarae* was changed by Groves to *azarai* to conform to the *International Code of Zoological Nomenclature*.

Pieczarka and Nagamachi (1988) found that the karyotypes of *A. infulatus* and *A. azarai boliviensis* are closer to each other than to the karyotype of *A. a. azarai*, and argue for the need to further revise the systematic classification of the genus. Recent cytogenetic studies by Pieczarka *et al.* (1992) have reinforced the validity of the species *A. vociferans* and *A. nancymae*. A phylogeny based on karyotypes is provided by Galbreath (1983).

Groves (1993) suggested that *A. nancymae* rather than *A. nancymai* (see Hershkovitz 1983) is the correct name in accordance with Article 31 (a(ii)) of the *International Code of Zoological Nomenclature* (International Trust for on Zoological Nomenclature, 1985). D. Brandon-Jones (in litt., 2000) argues, however, that surnames have no intrinsic gender, and by default, when latinized should have a masculine ending. When there is doubt, the spelling used in the original description (*nancymai* Hershkovitz, 1983 and *azarai* Humboldt,

1812, in this case) should be maintained, also following the directive of the *International Code of Zoological Nomenclature*. A detailed review of *Aotus* taxonomy is given by Ford (1994).

SAIMIRI Voigt, 1831

1. *Saimiri boliviensis boliviensis* (I. Geoffroy & de Blainville, 1834)
2. *S. boliviensis peruviansis* Hershkovitz, 1984
3. *S. boliviensis pluvialis* Lönnberg, 1940
4. *S. boliviensis jaburuensis* Lönnberg, 1940
5. *S. vanzolinii* Ayres, 1985
6. *S. sciureus sciureus* (Linnaeus, 1758)
7. *S. sciureus macrodon* (Elliot, 1907)
8. *S. sciureus cassiquiarensis* (Lesson, 1840)
9. *S. sciureus albigena* (von Pusch, 1941)
10. *S. oerstedii oerstedii* (Reinhardt, 1872)
11. *S. oerstedii citrinellus* Thomas, 1904
12. *S. ustus* I. Geoffroy, 1843

Saimiri taxonomy follows Hershkovitz (1984) and Groves (in press). Hershkovitz (1987b, footnote page 22) also recognized *Saimiri boliviensis jaburuensis* and *S. b. pluvialis* (given as junior synonyms of *S. b. boliviensis* in Hershkovitz 1984) as valid subspecies. They are not listed by Groves (in press). Hershkovitz (1987b) referred to *S. vanzolinii* Ayres, 1985 as a subspecies of *S. boliviensis*.

An alternative taxonomy is presented by Thorington (1985) as follows: *S. sciureus sciureus* (includes the forms *albigena*, *macrodon*, and *ustus* recognized by Hershkovitz, [1984]), *S. sciureus boliviensis* (includes the forms *pluvialis* Lönnberg, 1940 and *jaburuensis* Lönnberg, 1940 recognized by Hershkovitz [1987a]), *S. sciureus cassiquiarensis*, *S. sciureus oerstedii* (includes the form *citrinellus* recognized by Hershkovitz [1984]), and *S. madeirae* (given as a junior synonym of *S. ustus* by Hershkovitz [1984]). Hernández-Camacho and Defler (1991) recognize *S. sciureus caquetensis* Allen 1916, given as a junior synonym of *S. sciureus macrodon* by Hershkovitz (1984). Groves (1993) recognized just five species of *Saimiri* (*S. boliviensis*, *S. oerstedii*, *S. sciureus*, *S. ustus* and *S. vanzolinii*). He listed *S. b. peruviansis*, *S. b. jaburuensis* and *S. b. pluvialis* as synonyms of *S. boliviensis*, *S. o. citrinellus* as a synonym of *S. oerstedii*, all subspecies of *S. sciureus* listed here as synonyms, and *S. madeirae* recognized by Thorington (1985) as a synonym of *S. ustus*. The most recent review (morphology, genetics and behavior) of squirrel monkey taxonomy by Costello *et al.* (1993) argued for the recognition of just two species: *S. sciureus* in South America, and *S. oerstedii* in Panama and Costa Rica. Silva *et al.* (1993) also gave evidence for just one large polytypic South American species, *Saimiri sciureus*. On the other hand, recent studies of Boinski and Cropp (1999) using mtDNA, behavioral and morphological data, and Cropp and Boinski (1999) using two nuclear genes (IRBP and ZFX) and one mitochondrial (D-Loop) strongly support the Hershkovitz (1984) taxonomy, advocating four distinct species: *Saimiri sciureus*, *S. boliviensis*, *S. oerstedii* and

S. ustus.

CEBUS Erxleben, 1777

1. *Cebus apella apella* (Linnaeus, 1758)
2. *C. apella fatuellus* (Linnaeus, 1766)
3. *C. apella macrocephalus* Spix, 1823
4. *C. apella peruanus* Thomas, 1901
5. *C. apella tocantinus* Lönnberg, 1939
6. *C. apella margaritae* Hollister, 1914
7. *C. libidinosus libidinosus* Spix, 1823
8. *C. libidinosus pallidus* Gray, 1866)
9. *C. libidinosus paraguayanus* Fischer, 1829
10. *C. libidinosus juruanus* Lönnberg, 1939
11. *C. nigritus nigritus* (Goldfuss, 1809)
12. *C. nigritus robustus* Kuhl, 1820
13. *C. nigritus cucullatus* Spix, 1823
14. *C. xanthosternos* Wied-Neuwied, 1826
15. *C. albifrons albifrons* (Humboldt, 1812)
16. *C. albifrons adustus* Hershkovitz, 1949
17. *C. albifrons aequatorialis* Allen, 1914
18. *C. albifrons cesariae* Hershkovitz, 1949
19. *C. albifrons cuscinus* Thomas, 1901
20. *C. albifrons malitiosus* Elliot, 1909
21. *C. albifrons trinitatis* Von Pusch, 1941
22. *C. albifrons versicolor* Pucheran, 1845
23. *C. albifrons yuracus* Hershkovitz, 1949
24. *C. albifrons leucocephalus* Gray, 1865
25. *C. capucinus capucinus* (Linnaeus, 1758)
26. *C. capucinus limitaneus* Hollister, 1914
27. *C. capucinus imitator* Thomas, 1903
28. *C. capucinus curtus* Bangs, 1905
29. *C. olivaceus olivaceus* Schomburgk, 1848
30. *C. olivaceus apiculatus* Hershkovitz, 1949
31. *C. olivaceus brunneus* Allen, 1914
32. *C. olivaceus castaneus* I. Geoffroy, 1851
33. *C. olivaceus kaapori* Queiroz, 1992

As recorded by Hill (1960, pp.405-6) "The classification of the numerous forms of the present genus [*Cebus*] is one of the most vexatious problems in Primate taxonomy and has been so since early times. The fact has been commented on by every student of the group, including particularly F. Cuvier (1819-24), I. Geoffroy Saint-Hilaire (1851), Burmeister (1854), Gray (1870) and Cabrera (1917). The main cause of the confusion is undoubtedly the proneness of *Cebus* monkeys to individual variation, more particularly in certain populations. This is so much so that scarcely any two individuals are alike. Some of the variations are due to changes with age; a few are sexual differences; some may be due to hybridization between adjacent populations, but by far the majority are purely individual and appear quite fortuitously in members of the same stock brought up under identical environmental conditions..."

Hill's (1960) lamentations are as valid today as they were over 30 years ago, with natural variability exacerbated by hybridization caused by the transportation of animals as pets, and the subsequent release of many in locations outside their natural

ranges. This process began with Indians even before European colonization, and continues today due to casual releases and illegal commerce, and even, paradoxically, with environmental authorities releasing confiscated animals without consideration of their origin.

At species level there is not much disagreement, the difficulty is in understanding regional variation in order to establish subspecies. The current taxonomy of the capuchin monkeys has followed the division established by Hershkovitz (1949, 1955) of three "untufted" species, the white-throated or white-faced capuchin *Cebus capucinus* (Linnaeus, 1758) of Colombia and Central America, the weeper or wedge-capped capuchin, *Cebus nigrivittatus* Wagner, 1848 (referred to as *Cebus griseus* F. Cuvier, 1819 by Hill [1960]); and *Cebus olivaceus* Schomburgk, 1848 by Husson [1978], and Robinson [1986]; see also Hershkovitz [1958]) of the Brazilian Amazon, the Guianas, and Venezuela, and the white-fronted capuchin, *Cebus albifrons* (Humboldt, 1812) of the Amazonian regions of Colombia, Ecuador, Peru, Bolivia, and Brazil, and a single "tufted" species, the brown or tufted capuchin, *Cebus apella* (Linnaeus, 1758), occurring throughout the Amazon and Brazil, as well as northern Venezuela, northern Argentina and eastern Paraguay, and the Yungas region of southern Bolivia.

The taxonomy of the tufted capuchins adopted here is that of the most recent revision by Colin P. Groves (in press). He did not, however, list any subspecies of *C. capucinus* nor *C. olivaceus*, and only *albifrons*, *unicolor*, *cuscinus*, *trinitatis*, *aequatorialis*, and *versicolor* for *C. albifrons*. Those listed by Rylands *et al.* (1995) are however maintained here pending a detailed systematic revision these forms.

The *C. apella* taxonomy of Hill (1960) was based on personal communications from Kellogg, who was revising the taxonomy but died before completing it. Apart from those listed above, Hill (1960) gives the following subspecies: *Cebus apella fatuellus* Colombian brown capuchin, from northern Colombia, type locality unknown; *Cebus apella tocaninus* from type locality Rio Tocantins - no clear difference from *peruanus*; *Cebus apella magnus* from the Río Putumayo; *Cebus apella juruanus* from

the Rio Juruá; *Cebus apella cay* Azara's capuchin from Paraguay; *Cebus apella frontatus* the white-cheeked capuchin, no type locality, but argued by Vieira (1955) to occur in the Serra da Paranapiacaba, Alto da Serra, Cananéia, Santa Catarina, and Rio Grande do Sul; *Cebus apella vellerosus* from Argentina is given by Hill (1960) as a synonym of *C. a. nigritus*.

Hernández-Camacho and Cooper (1976) argued that *C. apella* north of the Amazon in Colombia exhibit no phenotypic distinctions sufficient to warrant subspecies. They give the subspecies as *C. a. apella* (see also Hernández-Camacho and Defler, 1991; Defler, 1994). Hershkovitz in his studies of *Cebus* taxonomy was apparently maintaining as valid the subspecies *C. a. maranonis*, *C. a. macrocephalus*, *C. a. pallidus*, and *C. a. peruanus* (*apud* Encarnación, 1993). All these subspecies were listed by Aquino and Encarnación (1994).

The subspecies in the Pando Department of Bolivia is uncertain (Buchanan-Smith *et al.* 2000). According to Hill (1960), *C. apella pallidus* Gray, 1865 occurs south of the Río Madre de Dios, indicating a distribution in north and central Bolivia and adjacent Brazil in the north-west of the Mato Grosso (as described by Cabrera, 1958). Aquino and Encarnación (1994) placed *C. a. pallidus* south of the Río Madre de Dios in the basin of the Río Tambopata in Peru. According to Cabrera (1958) and Hill (1960), *macrocephalus* Spix, 1823 occurs from the north of Bolivia through the upper Amazon south of the Rio Amazonas-Solimões in Brazil, west as far as the Río Ucayali and along the left (west) bank of the Purus (see Aquino and Encarnación, 1994); this may also be the form in the Pando. A third candidate is *C. a. peruanus* Thomas, 1901. Cabrera (1958) listed this form as a junior synonym of *C. a. macrocephalus*. Hill (1960) indicated it was restricted to the upper Rio Juruá and the basin of the Río Inambari, and Aquino and Encarnación (1994) include the Tambopata basin and both sides of the Río Madre de Dios in Peru, west as far as the border with Bolivia. Groves (in press) listed the form *pallidus* as a subspecies of *C. libidinosus*. Anderson (1997) listed *C. apella pallidus* for northern and central Bolivia, with *C. a. paraguayanus* occurring in the south east of the Andes.

Table 10. A comparison of the classifications of *Cebus apella* by Vieira (1955), Cabrera (1958) and Hill (1960).

Vieira (1955) (Brazil)	Cabrera (1958)	Hill (1960)
<i>C. nigritus</i> (Goldfuss, 1809)	<i>C. apella apella</i> (Linnaeus, 1758)	<i>C. apella apella</i> (Linnaeus, 1758)
<i>C. libidinosus pallidus</i> Gray, 1865	<i>C. apella libidinosus</i> Spix, 1823	<i>C. apella margaritae</i> (Goldfuss, 1809)
<i>C. frontatus</i> Kuhl, 1820	<i>C. apella macrocephalus</i> Spix 1823	<i>C. apella fatuellus</i> (Linnaeus, 1766)
<i>C. vellerosus</i> I. Geoffroy, 1851	<i>C. apella margaritae</i> (Goldfuss, 1809)	<i>C. apella tocaninus</i> Lönnberg, 1939
<i>C. robustus</i> Kuhl, 1820	<i>C. apella nigritus</i> (Goldfuss, 1809)	<i>C. apella macrocephalus</i> Spix 1823
<i>C. variegatus</i> É. Geoffroy, 1812	<i>C. apella pallidus</i> Gray, 1865	<i>C. apella magnus</i> von Pusch, 1941
<i>C. libidinosus libidinosus</i> Spix, 1823	<i>C. apella paraguayanus</i> Fischer, 1829	<i>C. apella juruanus</i> Lönnberg, 1939
<i>C. libidinosus versutus</i> Elliot, 1910	<i>C. apella robustus</i> Kuhl, 1820	<i>C. apella maranonis</i> von Pusch, 1941
<i>C. libidinosus paraguayanus</i> Fischer, 1829	<i>C. apella vellerosus</i> I. Geoffroy, 1851	<i>C. apella peruanus</i> Thomas, 1901
<i>C. libidinosus pallidus</i> Gray, 1865	<i>C. apella versutus</i> Elliot, 1910	<i>C. apella pallidus</i> Gray 1865
<i>C. libidinosus juruanus</i> Lönnberg, 1941	<i>C. apella xanthosternos</i> Wied, 1820	<i>C. apella cay</i> Illiger, 1815
<i>C. apella apella</i> (Linnaeus, 1758)		<i>C. apella libidinosus</i> Spix, 1823
<i>C. fatuellus macrocephalus</i> Spix, 1823		<i>C. apella xanthosternos</i> Wied-Neuwied, 1820
<i>C. fatuellus tocaninus</i> Lönnberg, 1939		<i>C. apella robustus</i> Kuhl, 1820
<i>C. fatuellus peruanus</i> Thomas 1901		<i>C. apella frontatus</i> Kuhl, 1820
<i>C. fatuellus trepidus</i> (Linnaeus, 1766)		<i>C. apella nigritus</i> (Goldfuss, 1809)

Kinzey (1982) reviewed the southern forms of *C. apella*, and did not recognize *C. a. paraguayanus* Fischer, 1829 from Argentina and Paraguay, considered by him to be a junior synonym of *C. a. libidinosus*. Bodini and Pérez-Hernández (1987) and Bodini (1989) list only two subspecies for Venezuela: *C. a. margaritae* (an outlier and probably introduced to the Island of Margarita) and *C. a. apella* (Federal Territory of Amazonas) (see also Sanz and Márquez, 1994).

C. xanthosternos, formerly considered a subspecies of *Cebus apella*, is genetically quite distinct (Seuáñez *et al.*, 1986), and is, therefore, listed as a separate species (Mittermeier *et al.*, 1988; see also Coimbra-Filho *et al.*, 1991).

Torres (1988) carried out an incomplete revision. She identified different forms either side of the Rio São Francisco, Rio Doce, and Rio Paraná, and six core areas, five of which have easily distinguished phenotypes. She indicated that *C. a. macrocephalus* from the upper Amazon may be a valid form, that *C. a. apella* occurs in the lower Amazon basin and Guianas, and that *C. a. xanthosternos* may be a valid species with the Rio São Francisco separating *C. a. xanthosternos* and *C. a. libidinosus* in the past. José de Sousa e Silva Jr. (a graduate student at the Museu Nacional, Rio de Janeiro) is currently carrying out a systematic revision of the species. The classification of the tufted capuchins adopted by Groves (in press) is based on the studies of Torres (1988).

Ten subspecies are listed for *Cebus albifrons*. The taxonomy and distributions of the white-fronted capuchins are confused and require revision. Groves (in press) listed only six subspecies, not recognizing the forms *adustus*, *cesarae*, *pleei*, *malitiosus*

and *leucocephalus* recognized by Hershkovitz (1949). The subspecies listed here are based on Hershkovitz (1949) and Hernández-Camacho and Cooper (1976) (see also Hernández-Camacho and Defler, 1985, 1991). Hernández-Camacho and Defler (1991) mentioned six subspecies in Colombia and listed five: *C. a. malitiosus*, *C. a. cesarae*, *C. a. versicolor*, *C. a. albifrons*, and *C. a. yuracus*. They regarded *C. a. unicolor* as possibly a junior synonym of *C. a. albifrons*, although, later, Defler (1994) also included this subspecies for Colombia. Defler and Hernández-Camacho (in press) discussed the taxonomy and nomenclature of *C. a. albifrons* and *C. a. unicolor* and concluded that *C. a. unicolor* is a junior synonym. Defler (1994) listed six subspecies for Colombia, three endemic: *C. a. albifrons*, *C. a. cesarae* (endemic), *C. a. versicolor* (endemic), *C. a. malitiosus* (endemic), *C. a. unicolor*, and *C. a. yuracus*. *C. a. pleei* Hershkovitz, 1949 and *C. a. leucocephalus* Gray, 1865 (listed by Hershkovitz 1949) are regarded by Hernández-Camacho and Cooper (1976), Hernández Camacho and Defler (1991), and Defler (1994) as junior synonyms of *C. a. versicolor*. Bodini and Pérez-Hernández (1987) listed three subspecies for Venezuela: *C. a. adustus*, *C. a. leucocephalus* (regarded a junior synonym of *C. a. versicolor* by Hernández-Camacho and Cooper [1976]), and *C. a. unicolor*. Bodini (1989) pointed out that Hill (1960) gives four subspecies for Venezuela, *C. a. cesarae*, *C. a. adustus*, *C. a. albifrons* and *C. a. unicolor*. Bodini and Pérez-Hernández (1987) give the form in the Federal Territory of Amazonas as *C. a. unicolor*, in agreement with Hershkovitz (1949), although Hershkovitz was uncertain of the limits of both this subspecies and *C. a. unicolor*. Hernández-Camacho and Cooper (1976) indicated that the Amazonian form in Venezuela was *C. a. albifrons* based on their belief that *C. a. unicolor* is a junior synonym. Defler and Hernández-Camacho (in prep.)

Table 11. A comparison of the classifications of the untufted capuchins, *Cebus*, by Cabrera (1958), Hill (1960) and Groves (in press).

Cabrera (1958)	Hill (1960)	Groves (in press)
<i>C. albifrons adustus</i> Hershkovitz, 1949	<i>C. albifrons hypoleucus</i> (Humboldt, 1812)	<i>C. albifrons albifrons</i> (Humboldt, 1812)
<i>C. albifrons aequatorialis</i> Allen, 1914	<i>C. albifrons malitiosus</i> Elliot, 1909	<i>C. albifrons unicolor</i> Spix, 1823
<i>C. albifrons albifrons</i> (Humboldt, 1812)	<i>C. albifrons cesarae</i> Hershkovitz, 1949	<i>C. albifrons cuscinus</i> Thomas, 1901
<i>C. albifrons cesarae</i> Hershkovitz, 1949	<i>C. albifrons pleei</i> Hershkovitz, 1949	<i>C. albifrons trinitatis</i> Von Pusch, 1942
<i>C. albifrons cuscinus</i> Thomas, 1901	<i>C. albifrons versicolor</i> Pucheran, 1845	<i>C. albifrons aequatorialis</i> Allen, 1914
<i>C. albifrons hypoleucus</i> (Humboldt, 1812)	<i>C. albifrons leucocephalus</i> Gray, 1865	<i>C. albifrons versicolor</i> Pucheran, 1845
<i>C. albifrons leucocephalus</i> Gray, 1865	<i>C. albifrons adustus</i> Hershkovitz, 1949	
<i>C. albifrons pleei</i> Hershkovitz, 1949	<i>C. albifrons albifrons</i> (Humboldt, 1812)	<i>C. olivaceus</i> Schomburgk, 1848
<i>C. albifrons unicolor</i> Spix, 1823	<i>C. albifrons unicolor</i> Spix, 1823	
<i>C. albifrons versicolor</i> Pucheran, 1845	<i>C. albifrons yuracus</i> Hershkovitz, 1949	<i>C. kaapori</i> Queiroz, 1982
<i>C. albifrons yuracus</i> Hershkovitz, 1949	<i>C. albifrons cuscinus</i> Thomas, 1901	
	<i>C. albifrons aequatorialis</i> Allen, 1914	<i>C. capucinus</i> (Linnaeus, 1758)
<i>C. nigrivittatus apiculatus</i> Hershkovitz, 1949	<i>C. albifrons trinitatis</i> Von Pusch, 194	
<i>C. nigrivittatus brunneus</i> Allen, 1914		
<i>C. nigrivittatus castaneus</i> I. Geoffroy, 1851	<i>C. capucinus limitaneus</i> Hollister, 1914	
<i>C. nigrivittatus nigrivittatus</i> Wagner, 1848	<i>C. capucinus imitator</i> Thomas, 1903	
<i>C. nigrivittatus olivaceus</i> Schomburgk, 1848	<i>C. capucinus capucinus</i> (Linnaeus, 1758)	
	<i>C. capucinus nigripectus</i> Elliot, 1909	
	<i>C. capucinus curtus</i> Bangs, 1905	
	<i>C. griseus griseus</i> Cuvier, 1819	
	<i>C. griseus castaneus</i> I. Geoffroy, 1851	
	<i>C. griseus brunneus</i> Allen, 1914	
	<i>C. griseus leporinus</i> Von Pusch, 1941	

in redescribing the type species of *Simia albifrons* Humboldt, 1812, demonstrated finally that the form *C. a. unicolor* (Spix, 1823) is a junior synonym, and is therefore not listed here.

C. a. hypoleucus (Humboldt, 1812) from northern Colombia was not recognized as a valid form by Hershkovitz (1949) who regarded it as a synonym of *C. a. albifrons*, neither by Hernández-Camacho and Cooper (1976), Hernández Camacho and Defler (1991), and Defler (1994).

Hill (1960) listed five subspecies of *Cebus capucinus*. *C. c. nigripectus* from the upper Rio Cauca in Colombia, *C. c. capucinus* (Colombia), *C. c. imitator* (Costa Rica, including Coiba Island, and Panama), *C. c. limitaneus* (Honduras and Nicaragua), and *C. c. curtus* (Colombia). Hernández-Camacho and Cooper (1976) argued that variability in populations of these capuchins on the upper Río Cauca did not support the validity of *C. c. nigripectus*, and Hernández-Camacho and Defler (1991) and Defler (1994) listed just two subspecies of *C. capucinus* for Colombia: *C. c. capucinus* and *C. c. curtus*. Defler (1994) includes *C. c. nigripectus* under the name of *C. c. curtus*. *C. c. curtus* is endemic to the Colombian Island of Gorgona. It was possibly introduced in the 16th or 17th Centuries (Hernández-Camacho and Defler, 1991) and is very similar to Panamanian *C. capucinus* (R. A. Mittermeier, pers. obs.). Groves (in press) found the species to be monotypic.

The correct scientific name for the weeper capuchin, has been the cause for some discussion. Two names in current use are *nigrivittatus* Wagner, 1848 (adopted by Cruz Lima, 1945; Hershkovitz, 1949; Cabrera, 1958) and *olivaceus* Schomburgk 1848 (adopted by Tate, 1939, and Husson, 1957, 1978). A third name, *griseus* F. Cuvier, 1819, was used by Hill (1960).

Hill (1960) argued that the first name properly given to this capuchin monkey is *Cebus griseus* F. Cuvier, 1819, based on a color plate drawn from a live animal. In a footnote, Hill (1960, p.429) explained that different copies of Cuvier's plate vary in the depth of the color of the upper parts of the monkey, and that this may have caused the doubts expressed by Hershkovitz (1949) who said that although the head clearly depicts the distinctive wedge-shaped black patch on the crown, the remainder of the body resembles *Cebus albifrons*, the confusion as such making the identity of the animal uncertain and the name invalid. Hill (1960) insisted that the copy of the plate in his possession depicted the animal which Hershkovitz refers to as *nigrivittatus*. There is no preserved type specimen for *C. griseus*, and the type locality was restricted by Hill to French Guiana (1958a in Hill 1960). However, Hershkovitz (1959) demonstrated that Frédéric Cuvier did not in fact attribute the name of *griseus* to the "sajou mâle" depicted, and that it was only his son in 1842 that referred to it as *griseus*, by which time the same name had been used by Desmarest for Buffon's "sajou gris", a tufted capuchin (Groves, in press).

Hershkovitz (1949) opted for the name of *Cebus nigrivittatus* Wagner, 1848, although recognizing that Schomburgk had described the same animal as *C. olivaceus* in the same year, and

that *nigrivittatus* may be a junior synonym if it can be proved that *olivaceus* predates it. Husson (1957, 1978) argued, however, for the name of *Cebus olivaceus* Schomburgk, 1848, on the basis that the use of the name *nigrivittatus* is not valid according to the International Rules of Zoological Nomenclature. The problem arises from a taxonomic confusion caused by Von Pusch (1941) who combined the genera *Saimiri* (the squirrel monkeys) and *Cebus*, resulting in two species having the same name of *nigrivittatus*, *Chrysothrix nigrivittatus* Wagner, 1846 (now considered a junior synonym of *Saimiri sciureus*) and *Cebus nigrivittatus* Wagner, 1848. Regarding both as belonging to the same genus, Von Pusch (1941), correctly under the circumstances, rejected the name *Cebus nigrivittatus* because it was predated by *Chrysothrix nigrivittatus*, the former then being considered a junior secondary homonym. Von Pusch (1941) renamed the capuchin *Cebus capucinus leporinus*. Although now in separate genera, Husson (1957), citing Follett (1955), argued that the International Rules of Zoological Nomenclature do not permit the revalidation of the name, having been, as it was, invalidated before 1951. The International Rules published in 1985 state "A junior secondary homonym replaced before 1961 is permanently invalid" (Article 59b). Hershkovitz (1955), on the other hand, merely referred to *Cebus capucinus leporinus* Von Pusch as a junior synonym of *nigrivittatus*, and argued that the ephemeral, and now discarded, homonymy between the squirrel monkey and the capuchin was unworthy of consideration (Hershkovitz, 1958).

In summary, *C. griseus* is the earliest name, the validity of which depends on the interpretation of a color plate, while *C. nigrivittatus* and *C. olivaceus* were names published by separate authors in the same year, with controversy concerning the fact that the former, even if it was published earlier, was invalidated by Von Pusch (1941), and such an invalidation is deemed permanent according to the International Trust for Zoological Nomenclature (1985).

Husson (1957, 1978), Eisenberg (1989), Groves (1993, in press) and Emmons and Feer (1997), and a number of recent authors who have studied this animal in the wild (for example, Fragaszy, 1986; Robinson, 1986, 1988; Miller, 1996, 1998) refer to the Guiana wedge-capped capuchin as *Cebus olivaceus*. A recent study of the chromosomes of a Venezuelan form of this species refers to it as *C. nigrivittatus* (see Martinez *et al.*, 1999). It would seem likely, however, that the correct name is *C. griseus*. Under any circumstances, a modern taxonomic revision is urgently needed for this species (Bodini, 1989). Hershkovitz (1949), Cabrera (1958) and Hill (1960) are still the best sources of reference for the subspecific variation. Hershkovitz (1949) listed five subspecies which he conditionally regarded as valid: *nigrivittatus* Wagner, 1848, from the upper Rio Branco Brazil (given as a junior synonym of *Cebus apella* by Elliot [1913], and as a junior synonym of *C. griseus leporinus* Von Pusch, 1941 by Hill, [1960]); *olivaceus* Schomburgk, 1848, from the southern foot of Monte Roraima, Brazil (given as a junior synonym of *Cebus apella* by Elliot [1913], and as a junior synonym of *C. griseus griseus* by Hill [1960]); *castaneus* I. Geoffroy, 1851 described from Cayenne, French

Guiana (listed as a full species by Elliot [1913]; listed by Hill [1960], but considered of doubtful validity); *apiculatus* Elliot, 1907 (listed as a subspecies of *Cebus apella* by Tate [1939], and listed as a junior synonym of *C. griseus griseus* by Hill [1960]), from La Unión, Río Cuara, Venezuela; and *brunneus* Allen, 1914 from northern Venezuela (listed by Hill [1960], but also considered of doubtful validity). Hershkovitz (1949) gave the type localities for each of the forms, but unfortunately not the distributional limits.

A sixth, undescribed form was mentioned by Bodini and Pérez-Hernández (1987) from central Venezuela, north of the Río Orinoco, and a seventh weeper capuchin, described as a species but probably only subspecifically different (Harada and Ferrari, 1996), was described from the eastern Amazon in the state of Maranhão and eastern part of the state of Pará in 1992: *C. kaapori* Queiroz, 1992. The distribution of this form is now quite well known, occurring east of the lower Rio Tocantins to the right bank of the Rio Pindaré and the lower Rio Mearim (Queiroz, 1992; Ferrari and Lopes, 1996; Silva, Jr. and Cerqueira, 1998; Carvalho, Jr. *et al.*, 1999).

Bodini and Pérez-Hernández (1987) listed five subspecies for Venezuela: *C. n. brunneus*, *C. n. apiculatus*, *C. n. nigrivittatus* (Amazonian), *C. n. olivaceus* and a fifth form which has yet to be classified (widely distributed throughout central and northern Venezuela, to the north of Río Orinoco). Bodini (1989) pointed out that the subspecies of *C. nigrivittatus* are not well defined.

Groves (in press) listed no subspecific forms of *C. olivaceus*, although he noted a "differentiation between paler, more buffy colors in Venezuela and the Demerara region of Guyana, and dark brown in the hinterland of Guyana", but he had not seen sufficient specimens from Brazil to allocate subspecific names to them. The type of *apiculatus* is pale and that of *castaneus* dark.

CALLICEBUS Thomas, 1903

1. *Callicebus modestus* Lönnberg, 1939
2. *C. donacophilus* (D'Orbigny, 1836)
3. *C. pallelescens* Thomas, 1907
4. *C. olallae* Lönnberg 1939
5. *C. oenanthe* Thomas, 1924
6. *C. cinerascens* (Spix, 1823)
7. *C. hoffmannsi* Thomas, 1908
8. *C. baptista* Lönnberg, 1939
9. *C. moloch* (Hoffmannsegg, 1807)
10. *C. brunneus* (Wagner, 1842)
11. *C. cupreus* (Spix, 1823)
12. *C. ornatus* (Gray, 1866)
13. *C. medemi* Hershkovitz, 1963
14. *C. torquatus torquatus* (Hoffmannsegg, 1807)
15. *C. torquatus lugens* (Humboldt, 1811)
16. *C. torquatus lucifer* Thomas, 1914
17. *C. torquatus purinus* Thomas, 1927
18. *C. torquatus regulus* Thomas, 1927
19. *C. personatus* (É. Geoffroy, 1812)

20. *C. nigrifrons* (Spix, 1823)

21. *C. melanochir* Wied-Neuwied, 1820

22. *C. barbarabrownae* Hershkovitz, 1990

23. *C. coimbrai* Kobayashi and Langguth, 1999

Callicebus taxonomy according to Hershkovitz (1988, 1990), modified by Kobayashi and Langguth (1999) and Groves (in press). Hershkovitz (1990) placed the *Callicebus* species into four groupings: 1) *C. modestus* (*C. modestus*); 2) *C. donacophilus* (*C. olallae*, *C. donacophilus*, *C. oenanthe*); 3) *C. moloch* (*C. brunneus*, *C. caligatus*, *C. cupreus*, *C. dubius*, *C. hoffmannsi*, *C. moloch*, *C. cinerascens* and *C. personatus*); and 4) *C. torquatus* (*C. torquatus*). A recent phylogenetic study, based on cranial measurements, by Kobayashi (1995) resulted in the following five groupings: 1) *C. donacophilus* (*C. modestus*, *C. ollalae*, *C. donacophilus*); 2) *C. cupreus* (*C. caligatus*, *C. cupreus*); *C. moloch* (*C. brunneus*, *C. hoffmannsi*, *C. moloch*, *C. cinerascens*); 4) *C. personatus* (*C. personatus*); and 5) *C. torquatus* (*C. torquatus*). Kobayashi (1995) did not evaluate *C. oenanthe* and *C. p. barbarabrownae*, and the position of *C. dubius* was uncertain. Kobayashi (1995) indicated that *C. caligatus* is a synonym of *C. cupreus*. Groves (1992, 1993) indicated that *C. brunneus* and *C. hoffmannsi* may be subspecies of *C. moloch* (*C. h. baptista* is a synonym of *C. hoffmannsi*), that *C. caligatus* and *C. dubius* may be synonyms of *C. cupreus*, that *C. cupreus discolor* and *C. c. ornatus* are synonyms of *C. cupreus*, that *C. donacophilus pallelescens* is a synonym of *C. donacophilus*, and that all subspecies of *C. torquatus* and *C. personatus* listed here are synonyms of their respective species. However, in a later publication and following further study of museum specimens, Groves (in press) advocated the taxonomy adopted here. The changes from the Hershkovitz (1990) taxonomy are as follows: The form *pallelescens* Thomas, 1907 is considered a separate species rather than subspecific to *C. donacophilus*; the form *baptista* Lönnberg, 1939 is considered a separate species rather than subspecific to *C. hoffmannsi*; the forms *discolor* (I. Geoffroy & Deville, 1848), *dubius* Hershkovitz, 1990, and *caligatus* are not valid; the forms *ornatus* (Gray, 1866) and *medemi* Hershkovitz, 1963, are considered separate species rather than subspecific to *C. cupreus* and *C. torquatus*, respectively; all the *personatus* subspecies listed by Hershkovitz (1990) are considered distinct species, following Kobayashi and Langguth (1999).

Kobayashi and Langguth (1994a, 1994b, 1999) described *Callicebus coimbrai* from the coast of the state of Sergipe, Brazil. On the basis of their study of this new species, along with previous craniometric studies by Kobayashi (1995), Kobayashi and Langguth (1999a, 1999b) argued that the titis of the Atlantic forest should be considered species rather than subspecies of *C. personatus*. They listed *C. nigrifrons*, *C. personatus*, *C. melanochir*, and *C. barbarabrownae* besides *C. coimbrai*.

PITHECIA Desmarest, 1804

1. *Pithecia pithecia pithecia* Linnaeus, 1766

2. *P. pithecia chrysocephala* I. Geoffroy, 1850
3. *P. monachus monachus* (É. Geoffroy, 1812)
4. *P. monachus milleri* Allen, 1914
5. *P. monachus napensis* Lönnberg, 1938
6. *P. irrorata irrorata* Gray, 1842
7. *P. irrorata vanzolinii* Hershkovitz, 1987
8. *P. albicans* Gray, 1860
9. *P. aequatorialis* Hershkovitz, 1987

Taxonomy and distributions of *Pithecia* follow those of Hershkovitz (1987a) and Eisenberg (1989) except in the recognition of *P. monachus napensis* Lönnberg, 1939. A phylogeny at the generic level was recently proposed by Schneider *et al.* (1995).

Hershkovitz carried out two revisions of *Pithecia*, the first he published in 1979(b) that recognized only four species (*P. pithecia*, *P. hirsuta*, *P. monachus* and *P. albicans*) was superseded by a second in 1987(a). Hershkovitz (1987a) placed *hirsuta* Wagner, 1840, as a junior synonym of *monachus* É. Geoffroy, 1812. The form *napensis* Lönnberg, 1939 was considered by Hershkovitz to be a local population of *hirsuta* in 1979(b), and then also junior synonym of *monachus* in 1987(a). However, P. Grubb (pers. comm. 2000) pointed out that the forms *napensis* and possibly *hirsuta* are distinct, and have defined geographical distributions. *P. monachus napensis* from the Río Napo, Ecuador, is listed here and, pending further revision, it is quite possible that *hirsuta* should also be considered a valid subspecies of *P. monachus*.

CHIROPOTES Lesson, 1840

1. *Chiropotes albinus* (I. Geoffroy & Deville, 1848)
2. *C. satanas satanas* (Hoffmannsegg, 1807)
3. *C. satanas chiropotes* (Humboldt, 1811)
4. *C. satanas utahicki* Hershkovitz, 1985

The taxonomy of *Chiropotes* follows Hershkovitz (1985). J. P. Boubli (pers. comm.) observed an undescribed bearded saki from the upper Rio Negro, in Brazil, which was also confirmed by Marc G. M. van Roosmalen (pers. comm., 1999).

CACAJAO Lesson, 1840

1. *Cacajao calvus calvus* (I. Geoffroy, 1847)
2. *C. calvus ucayalii* Thomas, 1928
3. *C. calvus novaesi* Hershkovitz, 1987
4. *C. calvus rubicundus* (I. Geoffroy and Deville, 1848)
5. *C. melanocephalus melanocephalus* (Humboldt, 1811)
6. *C. melanocephalus ouakary* (Spix, 1823)

The taxonomy of *Cacajao* follows Hernández-Camacho and Cooper (1976), Hershkovitz (1987b), Eisenberg (1989) and Boubli (1994). Szalay and Delson (1979) gave *C. c. rubicundus* full species status. The geographic range of *C. c. novaesi* is broader than was previously

thought, and a new population of white uakaris has been recorded from the Rio Jurupari, a tributary of the Rio Envira, well to the south of *C. c. calvus*, and separated by the red *C. c. novaesi*, which may indicate the need for a reappraisal of the taxonomy and systematics of the species (Silva, Jr. and Martins, 1999). In a full review of the ecology and biogeography of the genus, Barnett and Brandon-Jones (1997) argued that *Cacajao* may be congeneric with *Chiropotes*. Morphologically they are separated by the smaller skull and longer tail of the latter, differences considered by them to be insufficient to separate them at any more than the subgeneric level.

ALOUATTA Lacépède, 1799

1. *Alouatta seniculus seniculus* (Linnaeus, 1766)
2. *A. seniculus insulanus* Elliot, 1910
3. *A. seniculus* (formerly *stramineus*)
4. *A. seniculus amazonica* Lönnberg, 1941
5. *A. seniculus juara* Elliot, 1910
6. *A. seniculus puruensis* Lönnberg, 1941
7. *A. seniculus arctoidea* Cabrera, 1940
8. *A. sara* Elliot, 1910
9. *A. nigerrima* Lönnberg, 1941
10. *A. belzebul belzebul* (Linnaeus, 1766)
11. *A. belzebul discolor* (Spix, 1823)
12. *A. belzebul ululata* Elliot, 1912
13. *A. guariba guariba* (Humboldt, 1812)
14. *A. guariba clamitans* Cabrera, 1940
15. *A. palliata palliata* (Gray, 1849)
16. *A. palliata mexicana* (Merriam, 1902)
17. *A. palliata aequatorialis* (Festa, 1903)
18. *A. coibensis coibensis* Thomas, 1902
19. *A. coibensis trabeata* Lawrence, 1933
20. *A. caraya* (Humboldt, 1812)
21. *A. pigra* Lawrence, 1933

Hill (1962) and Stanyon *et al.* (1995) list nine subspecies of *A. seniculus*: *A. s. seniculus*, *A. s. arctoidea*, *A. s. stramineus*, *A. s. macconnelli*, *A. s. insulanus*, *A. s. amazonica*, *A. s. juara*, *A. s. puruensis*, *A. s. sara*. Cytogenetic studies have been carried out on; *A. s. seniculus* by Chu and Bender (1961), Bender and Chu (1963), and Yunis *et al.* (1976); *A. s. stramineus* by Lima and Seuánez (1991); *A. s. macconnelli* by Lima *et al.* (1990); *A. s. sara* by Minezawa *et al.* (1985) and Stanyon *et al.* (1995); and *A. s. arctoidea* by Stanyon *et al.* (1995). *A. sara* is recognized as a full species here following Minezawa *et al.* (1985; see also Groves, 1993; Stanyon *et al.* 1995). Stanyon *et al.* (1995) concluded that the number of chromosomal differences between *A. s. sara* and *A. s. arctoidea* was on a similar scale to those found between *A. s. sara* and *A. s. seniculus* by Minezawa *et al.* (1985). Stanyon *et al.* (1995) noted that "as for other organisms in tropical forest regions, it is probable the biological diversity and number of species have been underestimated". Hill (1962) argued that the description of *A. s. juara* by Elliot (1910) confused the name and type locality. Hill (1962) demonstrated that it came in fact from the Rio Juruá in Brazil, whereas Elliot

Table 12. A comparison of the classifications of the spider monkeys, *Ateles*, by Kellogg and Goldman (1944), Cruz Lima (1945), Froehlich *et al.* (1991), Collins (1999a, 1999b) and Collins and Dubach (2000a, 2000b).

200 Kellogg & Goldman (1944)	Froehlich <i>et al.</i> (1991)
<i>A. paniscus paniscus</i> (Linnaeus, 1758)	<i>A. paniscus</i> (Linnaeus, 1758)
<i>A. paniscus chamek</i> (Humboldt, 1812)	<i>A. belzebuth belzebuth</i> É. Geoffroy, 1806
<i>A. belzebuth belzebuth</i> É. Geoffroy, 1806	<i>A. belzebuth marginatus</i> É. Geoffroy, 1809
<i>A. belzebuth marginatus</i> É. Geoffroy, 1809	<i>A. belzebuth chamek</i> (Humboldt, 1812)
<i>A. belzebuth hybridus</i> I. Geoffroy, 1829	<i>A. geoffroyi hybridus</i> I. Geoffroy, 1829
<i>A. fusciceps fusciceps</i> Gray, 1866	<i>A. geoffroyi robustus</i> Allen, 1914
<i>A. fusciceps robustus</i> Allen, 1914 ²	<i>A. geoffroyi fusciceps</i> Gray, 1866
<i>A. geoffroyi geoffroyi</i> Kuhl, 1820	<i>A. geoffroyi</i> (subspecies of Kellogg & Goldman, 1944)
<i>A. geoffroyi vellerosus</i> Gray 1866	Collins (1999a, 1999b; Collins and Dubach, 2000a, 2000b)
<i>A. geoffroyi yucatanensis</i> Kellogg & Goldman, 1944	
<i>A. geoffroyi pan</i> Schlegel, 1876	<i>A. paniscus</i> (Linnaeus, 1758)
<i>A. geoffroyi frontatus</i> (Gray, 1842)	<i>A. hybridus</i> I. Geoffroy, 1829
<i>A. geoffroyi ornatus</i> Gray, 1870	<i>A. belzebuth belzebuth</i> É. Geoffroy, 1806
<i>A. geoffroyi panamensis</i> Kellogg & Goldman, 1944	<i>A. belzebuth marginatus</i> É. Geoffroy, 1809
<i>A. geoffroyi azuerensis</i> Bole, 1937	<i>A. belzebuth chamek</i> (Humboldt, 1812)
<i>A. geoffroyi grisescens</i> Gray, 1866	<i>A. geoffroyi</i> (subspecies of Kellogg & Goldman, 1944,
? <i>A. rufiventris</i> Sclater, 1871	but including the forms <i>fusciceps</i> and <i>robustus</i>)
Cruz Lima (1945) (Brazilian Amazon)	
<i>A. paniscus paniscus</i> (Linnaeus, 1758)	
<i>A. paniscus longimembris</i> Allen, 1914	
<i>A. marginatus</i> É. Geoffroy, 1809	
<i>A. geoffroyi</i> von Hasselt & Kuhl in Kuhl 1820 ¹	
<i>A. belzebuth</i> E. Geoffroy, 1806	
<i>A. variegatus</i> Wagner, 1840	

gave the Rio Juara in the Peruvian Amazon. Three years later, Elliot (1913) referred to the Rio Juara in the Brazilian, not Peruvian, Amazon. Hill (1962) indicated that *A. s. juara* is probably a junior synonym of *A. s. seniculus*.

The holotype of the form *straminea* Humboldt, 1812 is a female *A. caraya*, and is, therefore, a junior synonym, and not available for the red howlers. Further research into the systematics of the red howlers from northern South America is necessary to establish the true name for those in the north-eastern Amazon and Venezuela. A number of names will need to be considered, including such as *Mycetes auratus* Gray, 1845 and *M. laniger* Gray, 1845 (Rylands and Brandon-Jones, 1998). Bonvicino *et al.* (1996) argued that red howlers east of the Rio Trombetas are distinct from those to the west, and gave them the name of *macconnelli* (see, however, Rylands and Brandon-Jones, 1998). Groves (in press) listed the Guiana red howler as *A. macconnelli* Elliot, 1910.

An undescribed subspecies of *A. seniculus* north of the Río Orinoco was reported by Bodini and Pérez-Hernández (1987). This may be one of the forms described by Gray (1845).

The taxonomy and distributions of *A. belzebul* follow Hill (1962), Langguth *et al.* (1987), and Bonvicino *et al.* (1989). Cruz Lima (1945) listed the form *nigerrima* Lönnberg 1941 as a full species. Cytogenetic studies have indicated the probability that *A. b. nigerrima* is sufficiently distinct as to warrant species status (Armada *et al.*, 1987; see also Lima and Seuánez

1989), and more closely related to *seniculus* than to *belzebul* (see Oliveira, 1996). The possibility remains it may in fact be a subspecies of *A. seniculus*.

Hershkovitz (1963, p.397) claimed that, although pre-dating *Stentor fuscus* É. Geoffroy, 1812 by two months (as related by Thomas, 1913), *Simia guariba* Humboldt, 1812 is a primary homonym of É. Geoffroy's (1806) *guariba*, which Hershkovitz (1963), therefore, regarded as a junior objective synonym of *Alouatta belzebul* (Linnaeus, 1766). However, unlike "*simia belzebuth*" and "*simia seniculus*", the name "*guariba*" is not mentioned binominally by É. Geoffroy (1806), who was evidently proposing it only as a vernacular name with which to distinguish the howler, *Alouatta belzebul*, from the spider monkey, *Ateles belzebuth*. *Simia guariba* Humboldt, 1812, therefore, does not have an available senior homonym, and Hill (1962) and Hirsch *et al.* (1991), following Cabrera (1958), were correct in employing it as the species name for the Atlantic forest brown howling monkey. *Stentor fuscus* É. Geoffroy, 1812 is a junior synonym. The correct name for the Atlantic forest brown howling monkey is *Alouatta guariba* (Humboldt, 1812) (Rylands and Brandon-Jones 1998). The occurrence of *A. guariba* in Argentina was reviewed by Bitteti *et al.* (1994). Cytogenetic studies were carried out by Lima and Seuánez (1991) and Oliveira *et al.* (1998).

Villalba *et al.* (1995) have raised the possibility that *A. caraya* extends as far south as northern Uruguay.

Table 13. A comparison of the classifications of the woolly monkeys, *Lagothrix*, by Vieira (1955), Cruz Lima (1945), Hill (1962), Cabrera (1958) and Fooden (1963).

Vieira (1955) (only Brazil) and Cruz Lima (1945) (only Brazilian Amazon)	Cabrera (1958)
<i>L. lagothricha lagothricha</i> (Humboldt, 1812)	<i>L. cana cana</i> É. Geoffroy, 1812
<i>L. lagothricha puruensis</i> Lönnberg, 1940	<i>L. cana lugens</i> Elliot, 1907
<i>L. ubericola</i> Elliot, 1909	<i>L. cana olivacea</i> (Spix, 1823)
<i>L. infumata</i> (Spix, 1823)	<i>L. cana poeppigii</i> Schinz, 1844
<i>L. caroarensis</i> Lönnberg, 1940	<i>L. lagothricha</i> (Humboldt, 1812)
	<i>L. hendeei</i> Thomas, 1927
Hill (1962)	Fooden (1963)
<i>L. cana cana</i> É. Geoffroy, 1812	<i>L. lagothricha cana</i> É. Geoffroy in Humboldt, 1812
<i>L. cana lugens</i> Elliot, 1907	<i>L. lagothricha lugens</i> Elliot, 1907
<i>L. cana olivacea</i> (Spix, 1823)	<i>L. lagothricha poeppigii</i> Schinz, 1844
<i>L. cana poeppigii</i> Schinz, 1844	<i>L. lagothricha lagothricha</i> (Humboldt, 1812)
<i>L. lagothricha</i> (Humboldt, 1812)	<i>L. flavicauda</i> (Humboldt, 1812)
<i>L. (Oreonax) hendeei</i> Thomas, 1927	

The taxonomic status and distribution of *Alouatta pigra* follows Smith (1970), Horwich (1983), Horwich and Johnson (1984). *Alouatta palliata luctuosa* Lawrence, 1933 listed by Hill (1962) for Belize was not recognized by Froehlich and Froehlich (1986). *Alouatta pigra luctuosa* was listed by Dahl (1987) for the primates of Belize.

Rodríguez-Luna *et al.* (in prep.) have found mixed populations of *Alouatta palliata mexicana* and *A. pigra* in reduced habitat fragments in Tabasco, Mexico that are sympatric. Individuals of these populations have been captured for a comparative molecular genetic analysis of *A. palliata* and *A. pigra* to clarify this intergradation of populations and possible hybridization processes (Cortés Ortiz *et al.*, in prep.). Canales-Espinosa *et al.* (in prep.) are also studying evident morphological differences in these populations.

Using mtDNA markers, Cortés-Ortiz *et al.* (in prep.) found that *Alouatta palliata* and *A. coibensis* comprise a very closely related and monophyletic group of mtDNA lineages. The mitochondrial DNA divergence between the nominal species *A. palliata* and *A. coibensis* is very low, showing only 0.1% sequence divergence, more than an order of magnitude fewer nucleotide substitutions than were observed between any other pair of *Alouatta* species. Divergence between *A. palliata* and *A. coibensis* is similar to mitochondrial DNA distances observed between geographically-separated populations within each of these two species.

Groves (1993) lists the following species: *A. belzebul* (*discolor*, *nigerrima*, and *ululata* synonyms), *A. caraya*, *A. coibensis* (*trabeata* synonym), *A. fusca* (*clamitans* synonym), *A. palliata* (*aequatorialis*, *mexicana* synonyms), *A. pigra* (*A. p. luctuosa* synonym), *A. seniculus*, and *A. sara*. Groves (in press) listed the form *nigerrima* as full species.

ATELES E. Geoffroy, 1806

1. *Ateles geoffroyi geoffroyi* Kuhl, 1820

2. *A. geoffroyi azuerensis* (Bole, 1937)
3. *A. geoffroyi frontatus* (Gray, 1842)
4. *A. geoffroyi griseus* Gray, 1866
5. *A. geoffroyi panamensis* Kellogg & Goldman, 1944
6. *A. geoffroyi ornatus* Gray, 1870
7. *A. geoffroyi vellerosus* Gray, 1866
8. *A. geoffroyi yucatanensis* Kellogg & Goldman, 1944
9. *A. geoffroyi fusciceps* Gray, 1866
10. *A. geoffroyi rufiventris* Allen, 1914
11. *A. chamek* (Humboldt, 1812)
12. *A. paniscus* (Linnaeus, 1758)
13. *A. marginatus* É. Geoffroy, 1809
14. *A. belzebuth* É. Geoffroy, 1806
15. *A. hybridus hybridus* I. Geoffroy, 1829
16. *A. hybridus brunneus* Gray, 1872

The taxonomy of the spider monkeys, *Ateles*, follows Kellogg and Goldman (1944) and Konstant *et al.* (1985), except in the recognition of the forms *hybridus*, *chamek* and *marginatus* as distinct species. Hill (1962) followed Kellogg and Goldman (1944). Heltne and Kunkel (1975) argued that *A. fusciceps robustus* Allen, 1914 is a junior synonym of *A. f. rufiventris* Sclater, 1871. De Boer and Bruijn (1990), Froehlich *et al.* (1991), and Medeiros (1994) argued that *A. paniscus* is a distinct form with no subspecies. De Boer and Bruijn (1990) indicated that *chamek* should be considered a full species, and likewise Sampaio *et al.* (1993) argued that the forms *paniscus* and *chamek* should be considered distinct species on the basis of the genetic distance between them. *Ateles chamek* was found to be closer to *belzebuth* than to *paniscus*. Froehlich *et al.* (1991) indicated that the form *chamek* is subspecific to *A. belzebuth* rather than *A. paniscus*. Hernández-Camacho and Cooper (1976), Hernández-Camacho and Defler (1991) refer to all *Ateles* as subspecies of *A. paniscus*, following Hershkovitz (1972). Defler (1994), on the other hand, follows Kellogg and Goldman (1944) and refers to three species in Colombia: *A. belzebuth*, *A. fusciceps*, and *A. geoffroyi*. Groves (1993) recognized the following species: *chamek* Humboldt 1812, *paniscus* (Linnaeus, 1758), *marginatus* É. Geoffroy 1809, *fusciceps* Gray, 1866, *geoffroyi* Kuhl, 1820,

and *belzebuth* É. Geoffroy, 1806. He placed the forms *hybridus* I. Geoffroy, 1829, and *brunneus* Gray, 1870 as synonyms of *A. belzebuth*. Heltne and Kunkel (1975) provided additional taxonomic notes concerning pelage coloration in *A. paniscus* (including *chamek*) and *A. fusciceps*. Kunkel *et al.* (1980), reported on chromosomal variation and zoogeography in the genus.

Hernández-Camacho and Defler (1988, 1991) and Defler (1994, in press) argue for the validity of the form *brunneus* Gray, 1872 from the Departments of Bolívar, Antioquia and Caldas, between the lower Ríos Cauca and Magdalena in Colombia, and it is listed here as a subspecies of *A. hybridus* as recommended by Defler (in press).

A. rufiventris Sclater, 1871, from the Río Atrato, Darien, Colombia, is listed as *incertae sedis* by Kellogg and Goldman (1944).

Silva-López *et al.* (1996) argued against the validity of the subspecies of spider monkey *A. geoffroyi pan.* In their review of the taxonomic status of Guatemalan spider monkeys they concluded that 1) the coloration pattern of *A. g. vellerosus* includes a broader spectrum of color and tones than was previously considered; 2) *A. g. yucatanensis* may be considered a valid taxon, but only after more evidence can be obtained from several localities in the known geographical range of the subspecies; and 3) based on the available evidence (maps, vegetation types, and existing records) and supporting the observations of Konstant *et al.* (1985) that *A. g. pan* is probably merely a variation of the highly variable *A. g. vellerosus*.

Medeiros *et al.* (1997) confirmed the conclusions of Froehlich *et al.* (1991) in indicating that the forms *marginatus* (E. Geoffroy, 1809) and *chamek* (Humboldt, 1812) should be considered subspecific to *A. belzebuth*, and that *hybridus* I. Geoffroy, 1829 is better placed as a subspecies of *A. geoffroyi*. Medeiros *et al.* (1997) indicate, however, that from the cytogenetic viewpoint *rufiventris* Sclater, 1871, may well be reproductively isolated, although a hybrid zone between this form and *A. g. panamensis* was reported by Rossan and Baerg (1977). Collins (1999a, 1999b; Collins and Dubach, 2000a, 2000b) argued strongly for the species status of the form *hybridus* I. Geoffroy, 1829, but otherwise agreeing with the classification proposed by Froehlich *et al.* (1991).

LAGOTHRIX É. Geoffroy in Humboldt, 1812

1. *Lagothrix lagothricha* (Humboldt, 1812)
2. *L. cana cana* (É. Geoffroy in Humboldt, 1812)
3. *L. cana tschudii* Pucheran, 1857
4. *L. poeppigii* (Schinz, 1844)
5. *L. lugens* (Elliot, 1907)

The *Lagothrix* taxonomy follows Fooden (1963), Hernández-Camacho and Cooper (1976), Eisenberg (1989), Hernández-Camacho and Defler (1991) and Aquino and Encarnación

(1994), and Groves (in press). The taxonomy of Groves (in press is adopted here, but the genus is in need of revision. While Fooden (1963) listed all the woolly monkeys except for *L. flavicauda* as subspecies of *L. lagothricha*, Groves gives them species status and lists two subspecies of *cana*, the nominate and *L. c. tschudii* Pucheran, 1857, a dark form from Peru and Bolivia. Although for many years there were no records of woolly monkeys in Bolivia, the recent discovery of a population in Madidi (Wallace and Painter, 1999) may well be referable to this subspecies (see Fooden, 1963) or may represent a new taxon. Fooden (1963) considered the form *olivaceus* (Spix, 1823) to be a junior synonym of *L. l. cana*. The form *infumata* (Spix, 1823) is considered a junior synonym of *L. l. lagothricha* and *L. l. poeppigii*, by Fooden (1963). Vieira (1955) recorded its distribution as eastern Peru, Ecuador, and Amazonas, Brazil from the Rio Juruá. *L. caroarensis* Lönnberg, 1940, known only from its type locality, the Lago Caroaro, lower Rio Iça on the frontier of Brazil and Peru, is considered by Fooden (1963) to be a junior synonym of *L. l. lagothricha*. *L. ubericola* Elliot, 1909 from eastern Peru and Brazil (Igarapé Grande, Rio Juruá) and *L. l. puruensis* from Brazil, (Redenção, Lago Beruri, Arumã, Rio Purus), are considered junior synonyms of *L. l. cana* by Fooden (1963).

The juvenile, orange-colored woolly monkey illustrated by Cruz Lima (1945), of unknown provenance and given merely as *Lagothrix* sp. has recently been located on the upper Rio Jutai by Carlos Peres (pers. comm. 1999).

OREONAX Thomas, 1927

1. *Oreonax flavicauda* (Humboldt, 1812)

As a result of his comparative studies of cranial morphology in the atelines, Groves (in press) concluded that the yellow-tailed woolly monkey should properly be considered a monotypic genus, quite separate from the woolly monkeys, *Lagothrix*.

BRACHYTELES Spix, 1823

1. *Brachyteles arachnoides* (É. Geoffroy, 1806)
2. *Brachyteles hypoxanthus* (Kuhl, 1820)

Vieira (1944) recognized two subspecies of *Brachyteles*. Recent evidence provided by Lemos de Sá *et al.* (1990, 1993), Fonseca *et al.* (1991) and Lemos de Sá and Glander (1993) indicates that Vieira's original (1944) standing was valid, but that differentiation is even more extreme and justifies the classification of the two forms as separate species (see also Coimbra-Filho *et al.*, 1993). Groves (in press) lists the two muriquis as separate species.

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