Chapter 2 The Diversity of the New World Primates (Platyrrhini): An Annotated Taxonomy

Anthony B. Rylands and Russell A. Mittermeier

2.1 Introduction

The modern taxonomy of the Infraorder Platyrrhini is deeply influenced by the numerous publications of the late Philip Hershkovitz (1909–1997). This has meant that in many aspects platyrrhine taxonomy has been extraordinarily stable over the last two decades, while his work has at the same time provided the wherewithal for considerable refinement and adjustments. Hershkovitz laid the foundation for the modern taxonomy of the New World primates first in his monumental treatise on the Families Callitrichidae and Callimiconidae (1977) (supplemented with revisions of the emperor tamarins, Saguinus imperator [1979] and black-mantle tamarins, S. nigricollis [1982]), and subsequently with a number of papers, results of his revisions of the systematics of most of the remaining extant platyrrhines that he lumped in a third family, the Cebidae: the saki monkeys *Pithecia* (1987a); the night monkeys, Aotus (1983); the squirrel monkeys, Saimiri (1984); the bearded sakis, Chiropotes (1985); the uacaris, Cacajao (1987b); and the titi monkeys, Callicebus (1988, 1990). Hershkovitz was working on the remaining genera for the second volume of his treatise, but his findings were never published. The foundations for the modern taxonomies of the capuchin monkeys (*Cebus*), howling monkeys (*Alouatta*), spider monkeys (Ateles), woolly monkeys (Lagothrix) and muriquis (Brachyteles) have had to depend, therefore, on studies such as those Kellogg and Goldman (1944) for the spider monkeys, Hershkovitz (1949) for *Cebus* in particular, Cabrera (1957) and Hill (1960, 1962) who covered all the platyrrhines, and Fooden (1963) for the woolly monkeys.

It may well be that the legacy of Hershkovitz is the cause of there currently being more species and subspecies of primates in the New World than in Africa or Asia, providing as he did the capacity to compare findings with what is known, both in terms of the physiognomy of the primates under scrutiny and their supposed distributions. The latest taxonomies of the non-human primates indicate approximately

Center for Applied Biodiversity Science, Conservation International, Arlington, VA 22202, USA e-mail: a.rylands@conservation.org

A.B. Rylands (⋈)

657 species and subspecies in 71 genera and 16 families. Of these, we list here five families, 19 genera and 199 species and subspecies in the Neotropics—31% of the primates. At present, Africa has 169 species and subspecies, Asia 186 and Madagascar 100 (Grubb et al. 2003, Brandon-Jones et al. 2004, Mittermeier et al. in press).

Two further tendencies deserve mention. The first is associated with the desire to conserve the full diversity of primates, an aspect which drags taxonomy from the realm of cataloguing and academic pursuit into the applied sciences. It is of paramount importance that the full diversity of primates be recognized and mapped. The second is related to our increased knowledge of the geography of the phenotypes we observe in situ that has made it increasingly difficult to accept single definitions or dichotomies of species and subspecies. This and the new insights resulting from molecular genetics and chromosome studies have promoted the adoption of the Phylogenetic Species Concept, and the gradual rejection of the often arbitrary interpretations of variation using the category of subspecies (see Groves 2001, 2004).

The basis for the taxonomy we present here can be found in two recent compilations. The first is that of Rylands et al. (2000); the result of the workshop "Primate Taxonomy for the New Millennium," organized by the IUCN/SSC Primate Specialist Group and held in Orlando, Florida, 25–29 February 2000. The second is the remarkable and timely revision of the taxonomy of the Order Primates by Groves (2001, 2005). Our concern in this chapter is not merely to present a taxonomic list, but to indicate the scientific sources and reasoning upon which it is based, and to indicate, if only summarily, changes or divergences from the hypotheses of other authors, most notably those of Groves (2001), due to new studies and information.

2.2 Families, Subfamilies and Genera

Previously considered to comprise just two families (the Callitrichidae, formerly Hapalidae [marmosets and tamarins], and Cebidae [the rest]), credit is due to Rosenberger (1980, 1981) for breaking with tradition and suggesting an arrangement based on morphological affinity and phylogenetic relationships. While the callitrichines, pitheciines (*Chiropotes, Pithecia, Cacajao*), and atelines (*Alouatta, Ateles, Lagothrix, Brachyteles*) continued as well-defined groupings, revolutionary was his demonstration of the affiliation of the titi monkeys (*Callicebus*) with the pitheciines and, likewise, the capuchin (*Cebus*) and squirrel monkeys (*Saimiri*) with the callitrichines (placed in a redefined, family Cebidae). Confirmed by the genetic evidence, Rosenberger's (1981) proposal provided the basis of platyrrhine systematics at the family and subfamily level as accepted today (Schneider and Rosenberger 1996, Rylands et al. 2000, Groves 2001, 2005).

Groves (2001) argued for the priority of the following family and subfamily names: Hapalinae Gray, 1821 for the marmosets and tamarins; Chrysotrichinae Cabrera, 1900 for the squirrel monkeys; Nyctipithecidae Gray, 1870 for the

Table 2.1 Families, subfamilies and genera of New World primates—the taxonomy of Groves (2001, 2005) and that proposed here

	Rylands and
Groves (2001)	Mittermeier (this paper)
Family Cebidae Gray, 1821	Family Callitrichidae
Subfamily Callitrichinae Gray, 1821	•
Callithrix Erxleben, 1777	Callithrix
(Cebuella) Gray, 1866	Cebuella
(Callibella) Van Roosmalen & Van Roosmalen, 2003	Callibella
(Mico) Lesson, 1840	Mico
Saguinus Hoffmannsegg, 1807	Saguinus
Leontopithecus Lesson, 1840	Leontopithecus
Callimico Miranda-Ribeiro, 1911	Callimico
	Family Cebidae
Subfamily Cebinae Bonaparte, 1821	Subfamily Cebinae
Cebus Erxleben, 1777	Cebus
Subfamily Saimiriinae Miller, 1812	Subfamily Saimiriinae
Saimiri Voigt, 1831	Saimiri
Family Aotidae Elliott, 1913	Family Aotidae
Aotus Illiger, 1811	Aotus
Family Pitheciidae Mivart, 1865	Family Pitheciidae
Subfamily Pitheciinae Mivart, 1965	Subfamily Pitheciinae
Pithecia Desmarest, 1804	Pithecia
Chiropotes Lesson, 1840	Chiropotes
Cacajao Lesson, 1840	Cacajao
Subfamily Callicebinae Pocock, 1925	Subfamily Callicebinae
Callicebus Thomas, 1903	Callicebus
Family Atelidae Gray, 1825	Family Atelidae
Subfamily Alouattinae Trouessart, 1897	Subfamily Alouattinae
Alouatta Lacepede, 1799	Alouatta
Subfamily Atelinae Gray, 1825	Subfamily Atelinae
Ateles É. Geoffroy, 1806	Ateles
Brachyteles Spix, 1823	Brachyteles
Lagothrix É. Geoffroy, 1812	Lagothrix
Oreonax Thomas, 1927	Oreonax

night monkeys, and Mycetinae Gray, 1825 for the howling monkeys. These he later retracted (Brandon-Jones and Groves 2002), and Callitrichinae, Saimiriinae, Aotidae, and Alouattinae were the respective names used by Groves (2005). The taxonomy at the family level that we maintain here (Table 2.1) is that of Groves (2001, 2005), except that we place the marmosets and tamarins in their own family, Callitrichidae, rather than as a subfamily of the Cebidae.

Hershkovitz (1977) placed *Callimico* in its own family, Callimiconidae, and others have since placed it in its own subfamily within the Callitrichidae. Cronin and Sarich (1978), Seuánez et al. (1989), Schneider et al. (1993), Pastorini et al. (1998), Chaves et al. (1999) and Canavez et al. (1999) have demonstrated that *Callimico* is more closely related to *Callithrix* than it is to the tamarins, *Saguinus*. Placing *Callimico* in its own subfamily, therefore, is no longer correct, unless, *Leontopithecus* and *Saguinus* are independently separated from *Callithrix* by their own subfamily.

Regarding genera, there is also concordance between our vision and that of Groves (2001, 2005), except for his use of subgenera for the marmosets. *Cebuella*, *Callibella* and *Mico* he lists as subgenera of *Callithrix* Erxleben, 1777 (see Table 2.1). Silva Jr. (2001, 2002) argued that the tufted capuchins and the untufted capuchins (*sensu* Hershkovitz 1949, 1955) are distinct in their morphology and should be considered separate genera. *Cebus* Erxleben, 1777 is referable to the untufted group, and *Sapajus* Kerr, 1792 is the name available for the tufted capuchins.

2.3 Species and Subspecies

We emphasize that the taxonomic list we present here (Table 2.2) will change considerably, even in the near future, with further discoveries of new forms, genetic and phylogenetic analyses, and the revision of genera and species groups based on morphology and the study of museum specimens. We use the Phylogenetic Species Concept (see Groves 2001, 2004) as the basis for our determination of the taxonomic status of each of the forms we list, but have not changed subspecies to species automatically. We are doing so only when we can take recourse to a recent revision of the group combining a careful review of the taxonomic characters and clear explanations as to why the forms are to be considered "good species" rather than geographic variants or subspecies. Gregorin (2006) recently eliminated subspecies from the taxonomy of the Brazilian howler monkeys (Alouatta), fruit of some years of detailed morphological studies, geographical analyses, and investigation of the taxonomic history, types and type localities. Likewise, Silva Jr. (2001) proposed a taxonomy of Cebus without the use of subspecies. Genetic research on the tamarins (Saguinus) and some major revisions underway for the sakis (Pithecia) and uacaris (Cacajao), combined with genetic research and discoveries of new forms will also result in changes in the taxonomy of these groups in the near future. The taxonomy we present here is certainly not definitive, it is merely a working hypothesis, based on the information we can muster.

Space, unfortunately, does not allow for a detailed analysis of the history and issues concerning the systematic arrangements and the taxonomy of the species and subspecies we recognize here. We present some notes and mention the principal literature we have at hand for each of the genera that justifies or has influenced the taxonomy we present. More details and discussion can be found particularly in Rylands, Coimbra-Filho and Mittermeier (1993, Rylands et al. 2000, 2006, Rylands, Mittermeier and Coimbra-Filho in press) and Groves (2001, 2005), but there can certainly never be any justification for not referring to older literature and past major works such as those of Elliott (1913), Lawrence (1933), Cruz Lima (1945), Kellogg and Goldman (1944), Hershkovitz, Cabrera (1957), and Hill (1957, 1960, 1962).

2.3.1 Pygmy and Dwarf Marmosets, Cebuella and Callibella

Although Hershkovitz (1977) recognized no subspecific forms for *Cebuella*, Napier (1976) and Van Roosmalen and Van Roosmalen (1997) argued that a southerly

Table 2.2 A taxonomy of Neotropical primates

Species	Gen.	Sp.	Common name
Family Callitrichidae			
 Cebuella pygmaea pygmaea (Spix, 1823) Cebuella pygmaea niveiventris (Lönnberg, 1940) 	_	-	Pygmy marmoset
3. Callibella humilis (Van Roosmalen, Van Roosmalen, Mittermeier & Fonseca, 1998)	2	2	Black-crowned dwarf marmoset
4. Mico argentatus (Linnaeus, 1771)	В	3	Silvery marmoset
5. Mico leucippe (Thomas, 1922)		4	Golden-white bare-ear marmoset
6. Mico melanurus (É. Geoffroy, 1812)		5	Black-tailed marmoset
7. Mico intermedius (Hershkovitz, 1977)		9	Aripuanã marmoset
8. Mico emiliae (Thomas, 1920)		7	Snethlage's marmoset
9. Mico cf. emiliae		~	Rondônia marmoset
10. Mico nigriceps (Ferrari & Lopes, 1992)		6	Black-headed marmoset
11. Mico marcai (Alperin, 1993)		10	Marca's marmoset
12. Mico humeralifer (É. Geoffroy, 1812)		11	Black and white tassel-ear marmoset
13. Mico chrysoleucus (Wagner, 1842)		12	Golden-white tassel-ear marmoset
14. Mico mauesi (Mittermeier, Schwarz & Ayres, 1992)		13	Maués marmoset
15. Mico saterei (Silva Jr. & Noronha 1998)		14	Sateré marmoset
16. Mico manicorensis Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000		15	Manicoré marmoset
17. Mico acariensis. Van Roosmalen, Van Roosmalen, Mittermeier & Rylands, 2000		16	Rio Acarí marmoset
18. Callithrix jacchus (Linnaeus, 1758)	4	17	Common marmoset
19. Callithrix penicillata (É. Geoffroy, 1812)		18	Black-tufted-ear marmoset
20. Callithrix kuhlii Coimbra-Filho, 1985		19	Wied's black-tufted-ear marmoset
21. Callithrix geoffroyi (É. Geoffroy, 1812)		20	Geoffroy's tufted-ear marmoset
22. Callithrix aurita (É. Geoffroy, 1812)		21	Buffy-tufted-ear marmoset
23. Callithrix flaviceps (Thomas, 1903)		22	Buffy-headed marmoset
24. Callimico goeldii (Thomas, 1904)	5	23	Goeldi's monkey, callimico

Table 2.2 (continued)

SpeciesGen.25. Saguinus nigricollis nigricollis (Spix, 1823)626. Saguinus nigricollis graellsi (Jiménez de la Espada, 1870)627. Saguinus nigricollis hernandezi Hershkovitz, 1982828. Saguinus fuscicollis fuscus (Lesson, 1840)929. Saguinus fuscicollis fuscus (Espix, 1823)3030. Saguinus fuscicollis avilapiresi Hershkovitz, 19663132. Saguinus fuscicollis leucogenys (Gray, 1866)3333. Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870)	en. Sp. 24	Common name Spix's black-mantle tamarin Graell's black-mantle tamarin
t, 1870) da, 1870)	24	Spix's black-mantle tamarin Graell's black-mantle tamarin
 Saguinus nigricollis graellsi (Jiménez de la Espada, 1870) Saguinus nigricollis hernandezi Hershkovitz, 1982 Saguinus fuscicollis fuscus (Lesson, 1840) Saguinus fuscicollis fuscicollis (Spix, 1823) Saguinus fuscicollis avilapiresi Hershkovitz, 1966 Saguinus fuscicollis leucogenys (Gray, 1866) Saguinus fuscicollis leucogenys (Gray, 1866) Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870) 	25	Graell's black-mantle tamarin
 Saguinus nigricollis hernandezi Hershkovitz, 1982 Saguinus fuscicollis fuscus (Lesson, 1840) Saguinus fuscicollis fuscicollis (Spix, 1823) Saguinus fuscicollis avilapiresi Hershkovitz, 1966 Saguinus fuscicollis cruzlimai Hershkovitz, 1966 Saguinus fuscicollis leucogenys (Gray, 1866) Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870) 	25	
 Saguinus fuscicollis fuscus (Lesson, 1840) Saguinus fuscicollis fuscicollis (Spix, 1823) Saguinus fuscicollis avilapiresi Hershkovitz, 1966 Saguinus fuscicollis cruzlimai Hershkovitz, 1966 Saguinus fuscicollis leucogenys (Gray, 1866) Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870) 	25	Hernández-Camacho's black-mantle tamarin
 29. Saguinus fuscicollis fuscicollis (Spix, 1823) 30. Saguinus fuscicollis avilapiresi Hershkovitz, 1966 31. Saguinus fuscicollis cruzlimai Hershkovitz, 1966 32. Saguinus fuscicollis leucogenys (Gray, 1866) 33. Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870) 		Lesson's saddle-back tamarin
 Saguinus fuscicollis avilapiresi Hershkovitz, 1966 Saguinus fuscicollis cruzlimai Hershkovitz, 1966 Saguinus fuscicollis leucogenys (Gray, 1866) Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870) 		Spix's saddle-back tamarin
 Saguinus fuscicollis cruzlimai Hershkovitz, 1966 Saguinus fuscicollis leucogenys (Gray, 1866) Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870) 		Ávila Pires' saddle-back tamarin
32. Saguinus fuscicollis leucogenys (Gray, 1866) 33. Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870)		Cruz Lima's saddle-back tamarin
33. Saguinus fuscicollis lagonotus (Jiménez de la Espada, 1870)		Andean saddle-back tamarin
		Red-mantle saddle-back tamarin
34. Saguinus fuscicollis primitivus Hershkovitz, 1977		Hershkovitz's saddle-back tamarin
35. Saguinus fuscicollis illigeri (Pucheran, 1845)		Illiger's saddle-back tamarin
36. Saguinus fuscicollis nigrifrons (I. Geoffroy, 1850)		Geoffroy's saddle-back tamarin
37. Saguinus fuscicollis weddelli (Deville, 1849)		Weddell's saddle-back tamarin
38. Saguinus melanoleucus melanoleucus (Miranda Ribeiro, 1912)	26	White saddle-back tamarin
39. Saguinus melanolecus crandalli Hershkovitz, 1966		Crandall's saddle-back tamarin
40. Saguinus tripartitus (Milne-Edwards, 1878)	27	Golden-mantle saddle-back tamarin
41. Saguinus mystax mystax (Spix, 1823)	28	Spix's mustached tamarin
42. Saguinus mystax pileatus (I. Geoffroy, 1848)		Red-cap mustached tamarin
43. Saguinus mystax pluto (Lonnberg, 1926)		White-rump mustached tamarin
44. Saguinus labiatus labiatus (É. Geoffroy, 1812)	29	Southern red-bellied tamarin
45. Saguinus labiatus thomasi (Goeldi, 1907)		Thomas's red-bellied tamarin
46. Saguinus labiatus rufiventer (Gray, 1843)		Northern red-bellied tamarin
47. Saguinus imperator imperator (Goeldi, 1907)	30	Black-chinned emperor tamarin
48. Saguinus imperator subgrisescens (Lönnberg, 1940)		Bearded emperor tamarin
49. Saguinus midas (Linnaeus, 1758)	31	Golden-handed tamarin
50. Saguinus niger (É. Geoffroy, 1803)	32	Black-handed tamarin
51. Saguinus inustus (Schwarz, 1951)	33	Mottled-face tamarin
52. Saguinus bicolor (Spix, 1823)	34	Pied bare-face tamarin
53. Saguinus martinsi martinsi (Thomas, 1912)	35	Martin's bare-face tamarin
54. Saguinus martinsi ochraceus Hershkovitz, 1966		Ochraceous bare-face tamarin
55. Saguinus leucopus (Günther, 1877)	36	Silvery-brown tamarin
56. Saguinus oedipus (Linnaeus, 1758)	37	Cotton-top tamarin

Table 2.2 (continued)

Species	Gen.	Sp.	Common name
57. Saguinus geoffroyi (Pucheran, 1845)		38	Geoffroy's tamarin
58. Leontopithecus rosalia (Linnaeus, 1766)	7	39	Golden lion tamarin
59. Leontopithecus chrysomelas (Kuhl, 1820)		40	Golden-headed lion tamarin
60. Leontopithecus chrysopygus (Mikan, 1823)		41	Black lion tamarin
61. Leontopithecus caissara Lorini & Persson, 1990 Family Cebidae		42	Black-faced lion tamarin
62. Saimiri oerstedii oerstedii (Reinhardt, 1872)	∞	43	Black-crowned Central American squirrel monkey
63. Saimiri oerstedii citrinellus Thomas, 1904			Grey-crowned Central American squirrel monkey
64. Saimiri boliviensis boliviensis (I. Geoffroy & de Blainiulle, 1834)		4	Bolivian squirrel monkey
65. Saimiri boliviensis peruviensis Hershkovitz, 1984			Peruvian squirrel monkey
66. Saimiri vanzolinii Ayres, 1981		45	Vanzolini's squirrel monkey
67. Saimiri sciureus sciureus (Linnaeus, 1758)		46	Common squirrel monkey
68. Saimiri sciureus albigena (Von Pusch, 1941)			Colombian squirrel monkey
69. Saimiri sciureus cassiquiarensis (Lesson, 1840)			Humboldt's squirrel monkey
70. Saimiri sciureus macrodon (Elliot, 1907)			Ecuadorian squirrel monkey
71. Saimiri ustus I. Geoffroy, 1843		47	Golden-backed squirrel monkey
72. Cebus apella apella (Linnaeus, 1758)	6	48	Guianan brown tufted capuchin
73. Cebus apella margaritae Hollister, 1914			Margarita Island tufted capuchin
		49	Large-headed tufted capuchin
75. Cebus libidinosus Spix, 1823		20	Bearded capuchin
76. Cebus nigritus (Goldfuss, 1809)		51	Black-horned capuchin
77. Cebus robustus Kuhl, 1820		52	Crested capuchin
78. Cebus cay Illiger, 1815		53	Hooded capuchin
79. Cebus flavius (Schreber, 1774)		54	Marcgraf's capuchin, blond capuchin
80. Cebus xanthosternos Wied-Neuwied, 1826		55	Yellow-breasted capuchin
81. Cebus albifrons albifrons (Humboldt, 1812)		99	White-fronted capuchin
82. Cebus albifrons cuscinus Thomas, 1901			Shock-headed capuchin
83. Cebus albifrons cesarae Hershkovitz, 1949			César Valley white-fronted capuchin
84. Cebus albifrons malitiosus Elliot, 1909			Brown white-fronted capuchin
85. Cebus albifrons versicolor Pucheran, 1845			Varied capuchin
Cebus albifrons			Trinidad white-fronted capuchin
87. Cebus albifrons aequatorialis Allen, 1914			Ecuadorian white-fronted capuchin

Table 2.2 (continued)

S	(
	Gen.	Sp.	Common name
		57	White-faced capuchin
89. Cebus capucinus limitaneus Hollister, 1914			Honduran white-throated capuchin
90. Cebus capucinus imitator Thomas, 1903			Panamanian white-throated capuchin
91. Cebus capucinus curtus Bangs, 1905			Gorgona Island white-throated capuchin
92. Cebus olivaceus olivaceus Schomburgk, 1848		58	Guianan wedge-capped capuchin
93. Cebus olivaceus nigrivittatus Wagner, 1848			Wedge-capped capuchin
94. Cebus olivaceus apiculatus Hershkovitz, 1949			Pale weeper capuchin
95. Cebus olivaceus brunneus Allen, 1914			Brown weeper capuchin
96. Cebus olivaceus castaneus I. Geoffroy, 1851			Chestnut wedge-capped capuchin
97. Cebus kaapori Queiroz, 1992		59	Ka' apor capuchin
Family Aotidae			
98. Aotus lemurinus (I. Geoffroy, 1843)	10	09	Colombian or lemurine night monkey
99. Aotus griseimembra Elliot, 1912		61	Grey-legged night monkey
100. Aotus zonalis Goldman, 1914		62	Panamanian night monkey
101. Aotus brumbacki Hershkovitz, 1983		63	Brumback's night monkey
102. Aotus trivirgatus (Humboldt, 1811)		49	Douroucouli, owl monkey, night monkey
103. Aotus vociferans (Spix, 1823)		65	Noisy night monkey
104. Aotus miconax Thomas, 1927		99	Andean night monkey
105. Aotus nancymaae Hershkovitz, 1983		29	Nancy Ma's night monkey
106. Aotus nigriceps Dollman, 1909		89	Black-headed or Peruvian night monkey
107. Aotus azarae azarae (Humboldt, 1811)		69	Azara's night monkey
108. Aotus azarae boliviensis Elliot, 1907			Bolivian night monkey
109. Aotus azarae infulatus (Kuhl, 1820)			Feline night monkey
110 C 11: 1 TELLINE	-	1	
110. Callicebus modestus Lonnberg, 1939	П	9	Beni titi
111. Callicebus donacophilus (D'Orbigny, 1836)		71	Reed titi, D'Orbigny's titi
Callicebus pallesce		72	Paraguayan yellow titi
113. Callicebus olallae Lönnberg, 1939		73	Ollala's titi
114. Callicebus oenanthe Thomas, 1924		74	Andean titi, Isabelline titi
115. Callicebus cupreus (Spix, 1823)		75	Red titi, coppery titi
		92	Red-crowned titi
117. Callicebus ornatus (Gray, 1866)		77	Ornate titi

Table 2.2 (continued)

	Chestnut-bellied titi Doubtful titi Stephen Nash's titi
alen, Van Roosmalen & Mittermeier, 2002 8 1807)	Doubtful titi Stephen Nash's titi
Callicebus stephennashi Van Roosmalen, Van Roosmalen & Mittermeier, 2002 Callicebus cinerascens (Spix, 1823) Callicebus hoffmannsi Thomas, 1908 Callicebus baptista Lönnberg, 1939 Callicebus moloch (Hoffmannsegg, 1807) Callicebus brunneus (Wagner, 1842)	Stephen Nash's titi
Callicebus cinerascens (Spix, 1823) Callicebus hoffmannsi Thomas, 1908 Callicebus baptista Lönnberg, 1939 Callicebus moloch (Hoffmannsegg, 1807) Callicebus brunneus (Wagner, 1842)	
Callicebus hoffmannsi Thomas, 1908 Callicebus baptista Lönnberg, 1939 Callicebus moloch (Hoffmannsegg, 1807) Callicebus brunneus (Wagner, 1842)	Ashy titi
Callicebus baptista Lönnberg, 1939 Callicebus moloch (Hoffmannsegg, 1807) Callicebus brunneus (Wagner, 1842)	Hoffmann's titi
Callicebus moloch (Hoffmannsegg, 1807) Callicebus brunneus (Wagner, 1842)	Lago do Baptista titi
Callicebus brunneus (Wagner, 1842)	Orabassu titi
	Brown titi
126. C. bernhardi Van Roosmalen, Van Roosmalen & Mittermeier, 2002	Prince Bernhard's titi
128. Callicebus aureipalatii Wallace, Gómez, A. M. Felton & A. Felton, 2006	Madidi titi
Callicebus medemi Hershkovitz, 1963	Medem's collared titi
128. Callicebus torquatus (Hoffmannsegg, 1807)	White-collared titi
129. Callicebus lugens (Humboldt, 1811) 90	Widow monkey, white-chested titi
	Rufous-tailed collared titi
131. Callicebus purinus Thomas, 1927 92	Red-bellied collared titi
132. Callicebus regulus Thomas, 1927 93	Juruá collared titi
133. Callicebus personatus (É. Geoffroy, 1812)	Northern masked titi
134. Callicebus nigrifrons (Spix, 1823)	Black-fronted masked titi
135. Callicebus melanochir Wied-Neuwied, 1820	Southern Bahian masked titi,
	black-handed masked titi
136. Callicebus barbarabrownae Hershkovitz, 1990	Northern Bahian blond titi
137. Callicebus coimbrai Kobayashi & Langguth, 1999	Coimbra's titi
138. Pithecia pithecia pithecia (Linnaeus, 1758)	White-faced saki
139. Pithecia pithecia chrysocephala I. Geoffroy, 1850	Golden-faced saki
140. Pithecia monachus monachus (É. Geoffroy, 1812)	Geoffroy's monk saki
141. Pithecia monachus milleri Allen, 1914	Miller's monk saki
142. Pithecia monachus napensis Lönnberg, 1938	Napo monk saki
143. Pithecia irrorata irrorata Gray, 1842	Gray's bald faced saki
144. Pithecia irrorata vanzolinii Hershkovitz, 1987	Vanzolini's bald-faced saki
145. Pithecia albicans Gray, 1860	Buffy saki

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Species	Gen.	Sp.	Common name
146. Pithecia aequatorialis Hershkovitz, 1987		103	Equatorial saki
147. Chiropotes albinasus (I. Geoffroy & Deville, 1848)	13	104	White-nosed bearded saki
148. Chiropotes satanas (Hoffmannsegg, 1807)		105	Black bearded saki
149. Chiropotes chiropotes (Humboldt, 1811)		106	Guianan bearded saki
150. Chiropotes utahickae Hershkovitz, 1985		107	Uta Hick's bearded saki
151. Chiropotes israelita (Spix, 1823)		108	Rio Negro bearded saki
152. Cacajao calvus calvus (I. Geoffroy, 1847)	14	109	White bald-headed uacari
153. Cacajao calvus ucayalii (Thomas, 1928)			Ucayali bald-headed uacari
154. Cacajao calvus novaesi Hershkovitz, 1987			Novaes' bald-headed uacaris
155. Cacajao calvus rubicundus (I. Geoffroy and Deville, 1848)			Red bald-headed uacari
156. Cacajao melanocephalus (Humboldt, 1811)		110	Humboldt's black-headed uacari
157. Cacajao ouakary (Spix, 1823)		1111	Spix's black-headed uacari
Family Atelidae			
158. Alouatta seniculus (Linnaeus, 1766)	15	112	Red howler monkey
159. Alouatta arctoidea Cabrera, 1940		113	Ursine howler monkey
160. Alouatta macconnelli Elliot, 1910		114	Guianan red howler monkey
161. Alouatta juara Elliot, 1910		115	Juruá red howler monkey
162. Alouatta puruensis Lönnberg, 1941		116	Purús red howler monkey
163. Alouatta sara Elliot, 1910		117	Bolivian red howler monkey
164. Alouatta nigerrima Lönnberg, 1941		118	Black howler monkey
165. Alouatta belzebul (Linnaeus, 1766)		119	Red-handed howler monkey
166. Alouatta discolor (Spix, 1823)		120	Spix's red-handed howler monkey
167. Alouatta ululata Elliot, 1912		121	Maranhão red-handed howler monkey
168. Alouatta guariba guariba (Humboldt, 1812)		122	Northern brown howler monkey
169. Alouatta guariba clamitans Cabrera, 1940			Southern brown howler monkey
170. Alouatta caraya (Humboldt, 1812)		123	South American black howler monkey
171. Alouatta palliata palliata (Gray, 1849)		124	Golden-mantled howler monkey
172. Alouatta palliata mexicana (Merriam, 1902)			Mexican howler monkey
173. Alouatta palliata aequatorialis (Festa, 1903)			Ecuadorian mantled howler monkey
174. Alouatta palliata coibensis Thomas, 1902			Coiba Island howler monkey

Table 2.2 (continued)

S. C.			
Species	Gen.	Sp.	Common name
175. Alouatta palliata trabeata Lawrence, 1933			Azuero howler monkey
176. Alouatta pigra Lawrence, 1933		125	Central American black howler monkey
177. Ateles geoffroyi geoffroyi Kuhl, 1820	16	126	Geoffroy's spider monkey
178. Ateles geoffroyi azuerensis (Bole, 1937)			Azuero spider monkey
179. Ateles geoffroyi frontatus (Gray, 1842)			Black-browed spider monkey
180. Ateles geoffroyi grisescens Gray, 1866			Hooded spider monkey
181. Ateles geoffroyi ornatus (Gray, 1870)			Ornate spider monkey
182. Ateles geoffroyi vellerosus (Gray, 1866)			Mexican spider monkey
183. Ateles geoffroyi yucatanensis Kellogg & Goldman, 1944			Yucatán spider monkey
184. Ateles fusciceps fusciceps Gray, 1866		127	Brown-headed spider monkey
185. Ateles fusciceps rufiventris Sclater, 1872			Colombian black spider monkey
186. Ateles chamek (Humboldt, 1812)		128	Black-faced black spider monkey
187. Ateles paniscus (Linnaeus, 1758)		129	Red-faced black spider monkey
188. Ateles marginatus (É. Geoffroy, 1809)		130	White-whiskered spider monkey
189. Ateles belzebuth (É. Geoffroy, 1806)		131	White-bellied spider monkey
190. Ateles hybridus hybridus (I. Geoffroy, 1829)		132	Variegated spider monkey
191. Ateles hybridus brunneus Gray, 1872			Brown spider monkey
192. Lagothrix lagotricha (Humboldt, 1812)	17	133	Humboldt's woolly monkey
193. Lagothrix cana cana (É. Geoffroy in Humboldt, 1812)		134	Geoffroy's woolly monkey
194. Lagothrix cana tschudii Pucheran, 1857			Peruvian woolly monkey
195. Lagothrix poeppigii Schinz, 1844		135	Poeppig's woolly monkey
196. Lagothrix lugens Elliot, 1907		136	Colombian woolly monkey
197. Oreonax flavicauda (Humboldt, 1812)	18	137	Peruvian yellow-tailed woolly monkey
198. Brachyteles arachnoides (É. Geoffroy, 1806)	19	138	Southern muriqui
199. Brachyteles hypoxanthus (Kuhl, 1820)		139	Northern muriqui

(south of the Rio Solimões) form *niveiventris* Lönnberg, 1940 was valid (see Groves 2001, Rylands, Mittermeier and Coimbra-Filho in press). A number of studies on the phylogenetic affinity of the pygmy marmoset (*Cebuella pygmaea*) to the Amazonian marmosets (*Callithrix*) (for example, Rosenberger 1981, Barroso et al. 1997, Porter et al. 1997, Tagliaro et al. 1997) have indicated that it could, even should, be considered congeneric. Groves (2001) listed *Cebuella* as a subgenus of *Callithrix* (embracing all of the marmosets).

The black-crowned dwarf marmoset was first described in the genus *Callithrix* by Van Roosmalen et al. (1998) but was subsequently placed in its own genus *Callibella* by Van Roosmalen and Van Roosmalen (2003, see also Aguiar and Lacher 2003). Groves (2001) listed *Callibella* as a subgenus of *Callithrix*. The pygmy and dwarf marmosets are quite distinct in their size, morphology and habits when compared to *Callithrix*, and we maintain them in separate genera.

2.3.2 Marmosets, Callithrix and Mico, and Goeldi's Monkey, Callimico

The Amazonian marmosets were formerly considered to be of the genus *Callithrix* (see Hershkovitz 1977). 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 (non-Amazonian) 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* should be maintained in a separate genus (see Groves 2004; Rylands et al. 2000, Rylands, Mittermeier and Coimbra-Filho in press). The oldest generic name applicable to the Amazonian marmosets alone is *Mico* Lesson, 1840 (type species *Mico argentatus*).

Hapale emiliae was first described by Thomas (1904) from the Rio Irirí, southern Pará. Hershkovitz (1977) regarded it to be a dark form of *Callithrix argentata*. Vivo (1985, 1991) revalidated it on the basis of specimens from the state of Rondônia. The Rondônia marmoset described by Vivo should be considered distinct, however, because its distribution is disjunct—separated from that of *Hapale emiliae* by *M. melanurus* (see Rylands, Coimbra-Filho and Mittermeier 1993). Sena (1998) and Ferrari, Sena and Schneider (1999) found *M. emiliae* to be more similar to *M. argentatus* than the "emiliae" from Rondônia. Alperin (1995) argued that *Mico nigriceps* (Ferrari and Lopes 1992) and "emiliae" from Rondônia belong to the same species.

To date, *Callimico* is a monotypic genus, although speculation persists regarding the possibility of there being more than one species or subspecies. Vàsàrhelyi (2002) examined the genetic structure of the founder stock of captive callimicos, and concluded that more than one cryptic subspecies or species may be represented.

2.3.3 Tamarins and Lion Tamarins, Saguinus and Leontopithcus

The taxonomy of the tamarins and lion tamarins has been quite stable since the assessments of Hershkovitz (1966, 1977, 1979, 1982) with some few modifications we have adopted here. Except for the two subspecies of *Cebuella*, where a clear geographic distinction has yet to be established, all marmosets are now listed as species, and the question remains whether the numerous tamarin subspecies of Hershkovitz (1977, 1979, 1982) should also now be considered species.

Saguinus nigricollis graellsi is listed as a full species by Hernández-Camacho and Cooper (1976) on the basis of supposed sympatry with a population of *S. nigricollis* in the region of Puerto Leguízamo in southern Colombia. Defler (2004) discussed the evidence concerning this and found it to be inconclusive. He listed *graellsi* as a subspecies of *S. nigricollis*, although Groves (2001) listed it as a distinct species following Hernández-Camacho and Cooper (1976).

The taxonomy of Saguinus fuscicollis is based on Hershkovitz (1977; see also Cheverud and Moore, 1990), but there are some suggested modifications. In a molecular genetic study of the phylogeny of the genus, Cropp, Larson and Cheverud (1999) found that the form fuscus was closer to S. nigricollis than to S. fuscicollis and gave it species status. Saguinus f. melanoleucus and S. f. crandalli were listed as subspecies of S. melanoleucus by Coimbra-Filho (1990) and Groves (2001, 2005), although Tagliaro et al. (2005) found that differences between melanoleucus and weddelli were no larger than among the weddelli specimens. Saguinus f. acrensis, listed by Hershkovitz (1977), is not considered a valid form but a hybrid S. f. fuscicollis × S. f. melanoleucus from the upper Rio Juruá, following Peres, Patton and Silva (1996). Saguinus f. crandalli (listed here as a subspecies of melanoleucus) is of unknown provenance (Hershkovitz 1977), and may also be a hybrid. Hershkovitz (1977) listed the form tripartitus as a subspecies of S. fuscicollis, but Thorington (1988) argued for its species' status due to its supposed sympatry with S. f. lagonotus. Rylands, Coimbra-Filho and Mittermeier (1993, Rylands et al. 2000) and Groves (2001) listed it as a species, but a re-evaluation of the evidence for its distribution indicates that both Hershkovitz (1977) and Thorington (1988) may have been wrong (Heymann 2000; Rylands and Heymann in prep.), and sympatry between S. f. lagonotus and S. tripartitus has yet to be confirmed. M. G. M. van Roosmalen recorded a new form of saddleback tamarin in the interfluvium of the rios Madeira and Purus; a subspecies bounded to the south by the Rio Ipixuna and to the north by the várzeas of the Rio Solimões (Van Roosmalen 2003; described 16 August 2003).

Hershkovitz (1977) recognized three subspecies of the mustached tamarin, *S. mystax*. Groves (2001), however, found that while two, *mystax* and *pluto*, were quite similar, the form *pileatus* is quite distinct, and he listed it as a separate species, *S. pileatus*. The problem with this is that *pileatus* is sandwiched between the ranges of *mystax* and *pluto*, separating them geographically, and indicating that if *pileatus* is not a subspecies of *mystax*, then *pluto* too must be a distinct species. Groves (2001) also listed the form *S. labiatus rufiventer*, considered by Hershkovitz (1977) to be a synonym of *S. l. labiatus*.

The black-handed tamarin (*S. niger*) was considered by Hershkovitz (1977) to be a subspecies of *S. midas*. Melo et al. (1992) examined 20 blood genetic systems in *midas* and *niger* and obtained results compatible with their classification as subspecies, but Natori and Hanihara (1992) studying the postcanine dentition found *S. m. midas* to be more similar to *S. bicolor* than to *S. m. niger*, and argued that *niger* and *midas* should be considered distinct species. Tagliaro et al. (2005) came to the same conclusion, showing a grouping of *S. midas – S. bicolor* with the bare-faced tamarins of northwestern Colombia and Panama (*S. oedipus, S. leucopus*, and *S. geoffroyi*). Vallinoto et al. (2006) found that *S. midas* from the Rio Uatumã had a haplotype distinct from *S. midas* from the Rio Trombetas to the east, indicating a possibility of geographical races or distinct species. Vallinoto et al. (2006) also indicated that the Rio Tocantins may act as a barrier to gene flow for *S. niger* and, as such, that there may be two taxa of black-handed tamarins. This was presaged in the molecular genetic analysis by Tagliaro et al. (2005).

Whereas Hershkovitz (1977) placed the bare-faced tamarins *ochraceus* and *martinsi* as subspecies of *S. bicolor*, we here follow Groves (2001, 2005), in considering *martinsi* and *bicolor* as distinct species, with *ochraceus* being a subspecies of the former. Coimbra-Filho, Pissinatti and Rylands (1997) indicated the possibility that *ochraceus* may have arisen as a natural hybrid, intermediate between *bicolor* to its west and *martinsi* to the east. Although only one mottled-face tamarin, *S. inustus*, is recognized, Hernández-Camacho and Defler (1991) and Defler (2004) have indicated the probable existence of two subspecies in Colombia. Hershkovitz (1977) considered *S. geoffroyi* to be a subspecies of *S. oedipus*, but a number of studies have argued for them being separate species (see Rylands 1993, Groves 2001, 2005). Finally, the lion tamarins, *Leontopithecus*, are considered separate species following Rosenberger and Coimbra-Filho (1984) (see Rylands, Coimbra-Filho and Mittermeier, 1993). Coimbra-Filho (1990) considered *L. caissara* Lorini and Persson 1990 to be a subspecies of *L. chrysopygus*.

2.3.4 The Squirrel Monkeys, Saimiri

Saimiri taxonomy follows Hershkovitz (1984) and Groves (2001). An alternative taxonomy was presented by Thorington (1985). This for some reason never "caught on" but, being a solid and carefully considered assessment, should not be ignored in future studies and re-assessments of squirrel monkey systematics. Hernández-Camacho and Defler (1991) recognized S. sciureus caquetensis Allen, 1916, given as a junior synonym of S. sciureus macrodon by Hershkovitz (1984). 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. The findings of Boinski and Cropp (1999), however, strongly supported the Hershkovitz (1984) taxonomy, advocating four species: Saimiri sciureus, S. boliviensis, S. oerstedii and S. ustus. Hershkovitz (1987b, footnote p.22) indicated his recognition of jaburuensis Lönnberg, 1940 and pluvialis Lönnberg, 1940 as subspecies of S. b. boliviensis.

They are listed by Groves (2001) as synonyms. Hershkovitz (1987b) referred to *S. vanzolinii* as a subspecies of *S. boliviensis*. Rylands et al. (2006) discussed the taxonomy of the Central American squirrel monkeys.

2.3.5 The Tufted Capuchin Monkeys, Cebus

The taxonomy of the tufted capuchins (sensu Hershkovitz 1949, 1955) here follows Silva Jr. (2001), who did not recognize any subspecific forms. Groves (2001) presented an alternative taxonomy for the tufted capuchins as follows: C. apella apella; C. a. fatuellus (Linnaeus, 1766); C. a. macrocephalus; C. a. peruanus Thomas, 1901; C. a. tocantinus Lönnberg, 1939; C. a. margaritae?; C. libidinosus libidinosus; C. l. pallidus Gray, 1866; C. l. paraguayanus Fischer, 1829; C. l. juruanus Lönnberg, 1939; C. nigritus nigritus; C. n. robustus; C. n. cucullatus Spix, 1823; and C. xanthosternos (see Fragaszy et al. 2004; Rylands, Kierulff and Mittermeier 2005). Groves (2001) and Silva Jr. (2001) as such differ in their definitions of the forms Cebus apella and C. macrocephalus. Cebus a. fatuellus, C. a. peruanus, and C. libidinosus juruanus recognized by Groves (2001) are considered synonyms of C. macrocephalus by Silva Jr. (2001). Silva Jr. (2001) considered C. apella tocantinus a synonym of C. apella, and C. l. juruanus from the upper Rio Juruá a synonym of C. macrocephalus. C. libidinosus pallidus and C. l. paraguayanus are referred to as Cebus cay by Silva Jr. (2001). Both Groves (2001) and Silva Jr. (2001) were undecided about C. a. margaritae of the Venezuelan Island of Margarita.

Of the three subspecies of *C. nigritus* listed by Groves (2001), Silva Jr. (2001) considered *robustus* to be a separate species, and *cucullatus* a synonym of *C. nigritus*. *Cebus queirozi*, recently described in Pontes, Malta and Asfora (2006) is evidently a junior synonym of *C. flavius*, or, as argued by Oliveira and Langguth (2006), unavailable for lack of a registered type specimen. Distinct genetically (Seuánez et al. 1986), *C. xanthosternos* is considered a distinct species by both Groves (2001) and Silva Jr. (2001).

2.3.6 The Untufted Capuchin Monkeys, Cebus

Hershkovitz (1949) listed 13 subspecies of *C. albifrons*. Many of them were Colombian, and subsequently considered in some detail by Hernández-Camacho and Cooper (1976), Defler and Hernández-Camacho (2002), and Defler (2004). Hernández-Camacho and Cooper (1976) concluded that: 1. *C. a. malitiosus* is a well-defined subspecies of the northern slopes of the Santa Marta Mountains; 2. the light *C. a. cesarae* from the Río Cesar, Magdalena valley is a well-defined subspecies; 3. *C. a. versicolor* is a complex of forms from the Cauca-Magdalena interfluvium, including, besides, *C. a. versicolor* (intermediate phase), *C. a. leucocephalus* Gray, 1865) (dark phase) and *C. a. pleei* Hershkovitz, 1949 (light phase); 4. *C. a. adustus* Hershkovitz, 1949 probably occurs in piedmont forests of western

Arauca, the northern tip of Boyacá and north Santander, as well as the Lake Maracaibo region and upper Apure basin of Venezuela. 5. *C. a. unicolor* Spix, 1823, widespread in the upper Amazon, is very similar to the type species, and a junior synonym of *C. a. albifrons* Humboldt, 1812 (confirmed with further study [Defler and Hernández-Camacho 2002]).

We list here seven forms: *Cebus a. albifrons* and *C. a. versicolor* (recognized by Groves 2001 and Defler 2004); *C. a. cuscinus* (recognized by Groves 2001, and listed as *C. a. yuracus* Hershkovitz, 1949 by Defler 2004); *Cebus a. cesarae* and *C. a. malitiosus* (recognized by Defler 2004, but not Groves 2001); *C. a. trinitatis* (recognized by Groves 2001) and *C. a. aequatorialis* (recognized by Groves 2001).

Of the white-faced capuchins *C. capucinus*, Defler (2004) noted that three subspecies had been recorded for Colombia: *C. c. capucinus*, *C. c. nigripectus* Elliot, 1909; and *C. c. curtus* of the Pacific Island of Gorgona. Neither *nigripectus* nor *curtus* are recognized as valid by Hershkovitz (1949), Hernández-Camacho and Cooper (1976), Groves (2001) or Defler (2004). This listing maintains *C. c. curtus*, however, because it is an island population, and we believe that further studies are necessary. Fragaszy et al. (2004) and Rylands et al. (2006) discussed the taxonomy of the doubtfully valid Central American subspecies: *C. c. limitaneus* and *C. c. imitator*.

Hershkovitz (1949) listed five subspecies of the weeper or wedge-capped capuchin. Their ranges are not known; Hershkovitz plotted only their type localities (see, however, Bodini and Pérez-Hernández [1987] for ranges in Venezuela). Neither Silva Jr. (2001) nor Groves (2001) considered them valid. They continue to be listed here, however, because a detailed, modern, study (genetic/morphological/geographical) of the taxonomy of *Cebus olivaceus* has yet to be carried out. *Cebus o. brunneus* of Venezuela is definitely distinct from *olivaceus* in Suriname, for example. Queiroz (1992) described *Cebus kaapori* from south of the Amazon in Pará and Maranhão. It is of the weeper capuchin group in appearance, but is generally recognized as a distinct species (but see Harada and Ferrari 1996). Fragaszy et al. (2004) provided a more detailed discussion of the taxonomy of this group.

2.3.7 The Night Monkeys, Actus

Reviewing the entire taxonomy and distributions of the night monkeys, *Aotus*, Ford (1994) carried out a multivariate analyses of craniodental measures and pelage patterns and color, and also took into consideration chromosomal data and blood protein variations. Ford (1994) concluded that there was "good support" for just two species north of the Río Amazonas: *A. trivirgatus* east and north of the Rio Negro, and the polymorphic *A. vociferans* to the west of the Rio Negro. *Aotus vociferans*, as such, would include all the forms north of the Río Amazonas/Solimões in Brazil (west of the Rio Negro), Peru, Colombia and Ecuador, and in the Chocó, northern Colombia and Colombian Andes, and Panama: *brumbacki*, *lemurinus*, *griseimembra*, and *zonalis*.

It is doubtful, however, that the current taxonomy provides a true picture of the diversity of the genus *Aotus*. Ruiz-Herrera et al. (2005) reported that cytogenetic studies have characterized 18 different karyotypes with diploid numbers ranging from 46 to 58 chromosomes. The taxonomy of the night monkeys here follows the revision by Hershkovitz (1983), with some modifications for the Colombian and Central American forms.

Hernández-Camacho and Cooper (1976) restricted both lemurinus and griseimembra to Colombia, while recognizing the form zonalis as the night monkey of northwestern Colombia (Chocó) and Panama. Hershkovitz (1983) made no mention of the name zonalis. Groves (2001) followed Hernández-Camacho and Cooper (1976) in recognizing zonalis as the form in Panama, and listed it as a subspecies of lemurinus along with griseimembra and brumbacki. Defler, Bueno and Hernández-Camacho (2001) concluded that the karyotype of Aotus hershkovitzi Ramirez-Cerquera, 1983 (from the upper Río Cusiana, Boyacá, Colombia; 2n = 58) was in fact that of true *lemurinus*, and that the karyotypes which Hershkovitz (1983) had considered to be those of lemurinus were in fact of zonalis. Defler, Bueno and Hernández-Camacho (2001, Defler and Bueno 2003, Defler 2004) concluded that A. *lemurinus* of Hershkovitz (1983) is in fact three karyotypically well-defined species, and that the night monkeys of the lowlands of Panama and the Chocó region of Colombia belong to the species A. zonalis, and those of the Magdalena valley to A. griseimembra, while those above altitudes of 1500 m should correctly be referred to as A. lemurinus (see Rylands et al. 2006). The form infulatus is listed here as a subspecies of *Aotus azarae* following Groves (2001), although Hershkovitz (1983) considered it a distinct species.

2.3.8 The Titi Monkeys, Callicebus

The taxonomy of *Callicebus* follows Hershkovitz (1988, 1990), Groves (2001) and Van Roosmalen, Van Roosmalen and Mittermeier (2002). Groves (2001) listed all the titi monkeys as full species except for those in the *torquatus* group, for which he recognized only two species—*C. torquatus* and *C. medemi*, and the *personatus* group of the Atlantic forest in which he again recognized just two species—*C. personatus* and *C. coimbrai*. Van Roosmalen, Van Roosmalen and Mittermeier (2002) listed all titi monkeys as full species. We continue to recognize *Callicebus dubius*, although Groves (2001) considered it a synonym of *C. cupreus*.

Defler (2004) considered all the Colombian titi monkeys to be subspecies of *torquatus* or *cupreus*, following the taxonomy of Hershkovitz (1990). In their karyological analysis Bueno et al. (2006), however, indicated that the form *ornatus* should be classified a distinct species. T. R Defler is currently investigating the longignored mention by Moynihan (1976) of an apparently undescribed titi between the ríos Orteguaza and Caquetá, in southern Caquetá Department, near Valparaíso, Colombia.

Groves (2001) maintained *C. medemi* of the *C. torquatus* group as a full species because of its geographical isolation. Defler (2004) pointed out that it was not in fact isolated; it is "found in continuous forest which harbors (to the east), *C. torquatus lucifer*" (p. 300). Defler (2004) argued that the members of the *C. torquatus* group should all be considered subspecies, following Hershkovitz (1990). Heymann, Encarnación and Soini (2002) have indicated that the taxonomy of this group requires further study. They reported that the diagnostic features for *C. lucifer* provided by Hershkovitz (1990) and repeated in Van Roosmalen, Van Roosmalen and Mittermeier (2002) (used to distinguish it from *C. medemi*, for example) were inconsistently represented in different localities in northeastern Peru.

Bonvicino et al. (2003b) argued that *Callicebus lugens* is a distinct species on the basis of its morphology and karyological and molecular analyses (compared with $C.\ purinus$ and $C.\ torquatus$). Bueno and Defler (2007), agreeing that its karyotype argues for its elevation to a full species, concluded the possibility that $C.\ lugens$ (sensu stricto) may be limited to the east of the Rio Negro, while $C.\ torquatus$ (with three subspecies) may be restricted to the west. Their data indicated the need for further karyological studies and a re-assessment of the taxonomy of the group. Molecular genetic studies of $C.\ lugens$ on the upper Rio Negro in Brazil by Casado, Bonvicino and Seuánez (2007) indicated an even more complex situation. The karyotypes are the same (2n=16) either side of the Rio Negro, but they have distinct haplotypes, suggesting different "evolutionary lineages".

2.3.9 The Saki Monkeys, Pithecia

The taxonomy of the sakis, *Pithecia*, follows Hershkovitz (1987a), except in the recognition of *P. monachus napensis* from La Coca, Río Napo, Ecuador. It is evident, however, that further field, genetic, and museum studies will considerably increase the diversity in this genus (most particularly in Hershkovitz's [1987a] *Pithecia monachus* group). (L. Marsh pers. comm. 2006). Groves (2001) follows Hershkovitz's (1987a) taxonomy. Marsh (2004, 2006) reported that the saki at the Tiputini Biodiversity Station, on the Río Tiputini, Yasuní National Park, Ecuador, is not referable to *Pithecia aequatorialis* as was supposed by Hershkovitz (1987a), and may be a new form.

2.3.10 The Bearded Saki Monkeys, Chiropotes

The taxonomy of the bearded sakis, *Chiropotes*, is based on the revision of the genus by Hershkovitz (1985). The three subspecies of *C. satanas* (*satanas*, *chiropotes* and *utahicki*) are here listed as full species following the recommendation of Silva Jr. and Figueiredo (2002) and Figueiredo et al. (2006).

Bonvicino et al. (2003a) resurrected the name *israelita* for the bearded sakis discovered by J. P. Boubli to the west of the Rio Branco, tributary of the Rio Negro,

Amazonas, Brazil (Boubli 2002). Genetic and pelage differences distinguish it from the bearded sakis of the Guianas to the east of the Rio Branco. There is however, a possible confusion concerning the correct names. Silva Jr. and Figueiredo (2002) argue that the form west of the Rio Branco is, correctly *C. chiropotes*, according to its type locality, and the form to the east of the Rio Branco, extending through the states of Pará and Amapá, and into the Guianas (Guyana, Suriname, French Guiana) is *C. sagulatus* (Traill, 1821) from Demerara.

2.3.11 The Uacaris, Cacajao

The taxonomy of the uacaris (*Cacajao*) is based on the revision by Hershkovitz (1987b). Silva Jr. and Martins (1999) extended the range of C. c. novaesi to the upper Juruá, along the Rio Eiru, and reported on the occurrence of a white uacari along the Rio Jurupari, affluent of the Rio Envira, in Acre, that is distinct from novaesi. Recent observations in the middle Rio Juruá in the municipality of Carauari, have also revealed the presence of a white uacari, sympatric (but occupying different habitats) with what is presumed to be C. c. novaesi (A. Ravetta in litt. 31 August 2005). What relation this population might have to the Rio Jurupari population is not known. Genetic studies by W. Figueiredo (Museu Paraense Emílio Goeldi, Belém) are indicating that C. c. calvus (interfluvium of the rios Japurá and Solimões) and the white uacari of the Rio Juruá are genetically quite distinct and that the taxonomy of C. calvus, sensu Hershkovitz (1987b), requires revision (J. M. Cardoso da Silva pers. comm. 2005). Figueiredo et al. (2006) reported that their genetic analysis of the two black-headed uacaris—C. m. melanocephalus and C. m. ouakary—provided evidence that they should be considered different species.

2.3.12 The Howler Monkeys, Alouatta

Hill (1962) and Stanyon et al. (1995) listed nine subspecies of the red howling monkey, A. seniculus: A. s. seniculus, A. s. arctoidea, A. s. stramineus, A. s. macconelli, A. s. insulanus, A. s. amazonica, A. s. juara, A. s. puruensis, and A. s. sara. Alouatta seniculus from Cartagena, Bolívar, Colombia, is the red howling monkey from the northwestern Amazon. Alouatta s. arctoidea is recognized as a full species because Stanyon et al. (1995) concluded that the number of chromosomal differences between A. s. sara and A. s. arctoidea were on a similar scale to that found previously between A. s. sara and A. s. seniculus by Minezawa et al. (1986), which had resulted in A. s. sara being considered a full species. Groves (2001) neverthelesss maintained it as a subspecies of A. seniculus. Alouatta s. straminea is not a valid name for the red howling monkey because its type specimen is a female Alouatta caraya, as demonstrated by Rylands and Brandon-Jones (1998). Bonvicino, Fernandes and Seuánez (1995) believe that the red howler monkeys either side of the Rio Trombetas are karyotypically distinct and should be considered different species, and continue to use the name stramineus for the red howlers of the

Rio Negro basin west of the Rio Trombetas, while adopting the name macconnelli (type locality Demerara) for those east of the Rio Trombetas. In contrast to Bonvicino, Fernandes and Seuánez (1995), Sampaio, Schneider and Schneider (1996) concluded that the karyotypic differences between the howlers either side of the Rio Trombetas were inconsequential. In their molecular phylogenetic study, Bonvicino, Lemos and Seuánez (2001) found low levels of divergence between A. macconnelli, A. stramineus (howlers from the west of the Rio Trombetas) and A. nigerrima lower than recorded within A. caraya and A. belzebul. A molecular genetic study by Figueiredo et al. (1998) failed to show a difference between the red howlers either side of the Rio Trombetas. Gregorin (2006) concluded that variation in pelage coloration provided no evidence for more than one species in the northeastern Amazon, in the Guianas, east of the Rio Negro and on both sides of the Rio Trombetas. Alouatta macconnelli may, therefore, be the right name for the red howler monkey of the entire northeastern Amazon and Guianas, although there are two other candidates for the name: Mycetes auratus Gray, 1845 and M. laniger Gray, 1845 (Rylands and Brandon-Jones 1998).

Alouatta s. insulanus of the Island of Trinidad, is considered to be a synonym of A. macconnelli (see Groves 2001). Groves (2001) considered A. s. amazonica Lönnberg, 1941 from Codajáz, north of the Rio Solimões, west of the Rio Negro, and A. s. puruensis from the Rio Purus to be junior synonyms of A. s. juara. Gregorin (2006) tentatively considered amazonica to be a junior synonym of A. juara, extending the range of this species to the north of the Rio Solimões, but Gregorin himself stated that this was mere speculation, and the identity of the howler monkeys west of the Negro in the north-central Amazon (the eastern range limits of A. seniculus from Colombia) remains unclear. Alouatta s. juara from the Rio Juruá, is listed here as a full species following Gregorin (2006). Groves (2001) recognized juara as a subspecies of A. seniculus, with A. s. amazonica and A. s. puruensis (here considered distinct) as synonyms. Alouatta s. puruensis from Jaburú, Rio Purus, is recognized by Gregorin (2006). Alouatta s. sara is recognized as a full species following Minezawa et al. (1986; see also Stanyon et al. 1995; Groves 2001).

Cruz Lima (1945), Langguth et al. (1987), and Bonvicino, Langguth and Mittermeier (1989) studied the howling monkeys that Hill (1962) had listed as subspecies of *A. belzebul*. Following Cruz Lima (1945), Groves (2001), and Gregorin (2006), the form *nigerrima* is here considered a full species. Cytogenetic studies have also indicated that *nigerrima* is sufficiently distinct as to warrant species status (Armada et al. 1987; Lima and Seuánez 1989), and, besides, that it is more closely related to *seniculus* than to *belzebul* (see Oliveira 1996). Groves (2001) did not recognize any subspecies for *A. belzebul*: the forms *discolor*, *mexianae*, and *ululata* were given as junior synonyms. Here we follow Gregorin (2006) who recognized the forms *belzebul*, *discolor*, and *ululata* as full species, and placed *mexianae* as a junior synonym of *A. discolor*. Nascimento et al. (2005) were unable to differentiate the disjunct populations of *A. belzebul* from the Atlantic forest (Paraíba) and the Amazon (southern Pará).

Rylands and Brandon-Jones (1998) and Gregorin (2006) discussed the validity or otherwise of the use of the alternative names of *fusca* and *guariba* for the

brown howling monkey of the Atlantic forest of Brazil and Argentina. Rylands and Brandon-Jones (1998) indicated that guariba Humboldt, 1812 is the available name, Gregorin (2006) that *fusca* E. Geoffroy, 1812 is correct. Gregorin (2006), studying the morphology of the cranium and hyoid apparatus, considered that the two brown howlers listed by Rylands et al. (2000) and Groves (2001) as subspecies should be full species. We reserve judgment on this until genetic studies can be brought to bear. Harris et al. (2005) found differences between populations of A. guariba clamitans in southern Brazil—from Rio de Janeiro on the one hand and Santa Catarina on the other. They showed that these correspond to differences in karyotype recorded by Koiffman (1977) and Oliveira, Lima and Sbalqueiro (1995, Oliveira et al. 1998, 2002). Maximum genetic distances found by Harris et al. (2005) were considerably greater than those recorded for A. caraya and A. belzebul by Nascimento et al. (2005), and they argued that further research may result in the recognition of three species. We continue with the names and subspecific classification as used by Rylands et al. (2000) and Groves (2001, 2005) until the taxonomy becomes better defined.

Nascimento et al. (2005) showed that populations of *Alouatta caraya* from Santa Cruz, Bolivia (Chaco) are differentiated from those in various localities in the state of Mato Grosso and (one specimen) Goiás, further north, indicating the possibility of two rather than one taxa of the South American black howler. The taxonomy of the howlers of Mesoamerica and the Caribbean and Pacific coasts of Colombia and Ecuador is based on Lawrence (1933), Hill (1962), Hall (1981), Froehlich and Froehlich (1987), and Cortés-Ortiz et al. (2003). Groves (2001, 2005) recognized only *A. palliata* (no subspecies), *A. pigra*, and *A. coibensis* (no subspecies). Rylands et al. (2006) reviewed the taxonomy and distributions of *A. palliata*, *A. coibensis* and *A. pigra*.

Cortés-Ortiz et al. (2003) found that *A. palliata* and *A. coibensis* comprise a very closely related and monophyletic group of mtDNA lineages. Divergence between *A. palliata* and *A. coibensis* is similar to mtDNA distances observed between geographically-separated populations *within* each of these two species. Rylands et al. (2006) maintained the taxonomy suggested by Froehlich and Froehlich (1987) for the forms from the Azuero Peninsula (*A. coibensis coibensis*) and the Island of Coiba (Panama) (*A. c. trabeata*), but it is evident that the findings of the molecular genetic analyses of Cortés-Ortiz et al. (2003) would relegate them to synonyms of *A. palliata*. Groves (2001) listed *A. coibensis*, with *trabeata*, as a synonym. There is still some discussion concerning the correct name for the Central American black howler, *A. pigra*. Napier (1976) referred to it as *A. villosa* and, revisiting the issue, Brandon-Jones (2006) argued that *A. pigra* is a junior synonym.

2.3.13 The Spider Monkeys, Ateles

The taxonomy of the spider monkeys is based on Kellogg and Goldman (1944) and Hill (1962). The forms *hybridus*, *chamek* and *marginatus* are listed as distinct

species, and *A. fusciceps robustus* Allen, 1914 is considered a junior synonym of *A. f. rufiventris*, following Heltne and Kunkel (1975) (see Rylands et al. 2000, 2006). Silva-López, Motta-Gill and Sánchez-Hernández (1996) argued that *Ateles geoffroyi* pan Schlegel, 1876 was not a valid taxon. Hernández-Camacho and Defler (1991) and Defler (2004) argued for the validity of the form *brunneus*, listed here as a subspecies of *A. hybridus*. The taxonomy and distributions of *A. geoffroyi* and *A. fusciceps* were reviewed by Rylands et al. (2006).

Van Roosmalen (2003) reported on the rediscovery of *A. longimembris* Allen, 1914, from Barão de Melgaço, headwaters of the Rio Gy-paraná, Mato Grosso, Brazil. Cruz Lima (1945) recognized this spider monkey as a subspecies of *A. paniscus*. The description of the range given by Cruz Lima (1945; p. 127) extends west into what is currently recognized to be that of *A. chamek*. Groves (2001) considered it to be a synonym of *A. chamek*. Van Roosmalen described it as differing from *A. chamek* by "cranial characters (i.e., proportionally heavy jaws and canines not enabling adults to fully close their mouth), triangular pink muzzle including chin, black face, and black triangular blaze of backwardly directed black hairs on the forehead."

Collins (1999) and Collins and Dubach (2000) argued strongly for the species status of the form *hybridus*. Their position was reinforced by Nieves et al. (2005). Hernández-Camacho and Defler (1991) and Defler (2004) argued for the validity of the form *brunneus* from the Departments of Bolivar, Antioquia and Caldas, between the lower Ríos Cauca and Magdalena in Colombia. It is listed here as a subspecies of *A. hybridus*, as recommended by Defler (2004).

2.3.14 The Woolly Monkeys, Lagothrix and Oreonax

The taxonomy of *Lagothrix* is based on Fooden (1963), but follows Groves (2001) in recognizing *cana*, *lugens*, and *poeppigii* as full species rather than subspecies of *Lagotricha*. Groves (2001) also recognized *tschudii* Pucheran, 1857 from Peru (see Cruz Lima 1945). An isolated population of *Lagothrix* was discovered by Wallace and Painter (1999) in Madidi National Park, Bolivia, at 1500 m. This may be a new taxon or *L. cana tschudii*, and is the only modern record of *Lagothrix* occurring in Bolivia. The provenance of a juvenile woolly monkey with orange-colored pelage illustrated by Cruz Lima (1945) was unknown until recently. A population was found by Carlos A. Peres on the upper Rio Jutaí, upper Amazon (within the supposed range of *L. poeppigii*) and reported by Van Roosmalen (2003).

As a result of his comparative studies of cranial morphology in the atelines, Groves (2001, 2005) concluded that the yellow-tailed woolly monkey should properly be considered a monotypic genus, *Oreonax* Thomas, 1927.

2.3.15 The Muriquis, Brachyteles

Vieira (1944) recognized two subspecies of *Brachyteles*. Evidence provided by Lemos de Sá et al. (1990), Fonseca et al. (1991) and Lemos de Sá and Glander (1993)

indicated that Vieira's (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, Pissinatti and Rylands 1993). Groves (2001, 2005) listed the two muriquis as separate species.

2.4 Discussion

A full understanding of the diversity of primates in the Neotropical region is now an urgent task. The relentless ruination—fragmentation, degradation, and destruction—of the forests of South and Middle America is making it increasingly difficult to map the distributions of the primate species and subspecies currently recognized. In Mesoamerica and the eastern Brazilian Atlantic forest it is now impossible to detect clines and to fully document the natural variation that is so necessary to make judgements concerning the thresholds for determining that two populations are consistently different, and as such species—the unit we use to prioritize conservation investments. As we lose the population diversity of the neotropical primates we lose our capacity to detect phylogenetic processes and the true nature of the Neotropical primate radiation. It is quite possible that, what we would today judge to be species or subspecies have already been lost in the Atlantic forest and Mesoamerica, and Andean Colombia, Peru and Venezuela, where forest loss, fragmentation and hunting are most accentuated. Complex patterns of genetic and morphological variation are, in addition, confused irreparably by the constant transport of pets, and their release, often in large numbers, far from where they occur naturally. Marmosets and capuchin monkeys in the Atlantic forest are today quite severely mixed up due to interbreeding between geographically distant forms. The possibility that species have been, or will be, lost without us even detecting their existence is underlined by the fact that we are still finding species never before described—14 since 1990 (Table 2.3)—and even new genera (Callibella M. G. M van Roosmalen and T. van Roosmalen, 2003). Stranger still is the rediscovery of forms described many years ago but forgotten, such as the distinct bearded sakis west of the Rio Branco in the Brazilian Amazon (Boubli 2002; Bonvicino et al. 2003a), and Marcgrave's capuchin Cebus flavius (Schreber, 1774) on the coast of Pernambuco (see Oliveira and Langguth, 2006).

A neatly explained taxonomy with a well-drawn map unfortunately tends to inspire complacency. Both species' definitions and geographic distributions are hypotheses, which require continuous testing; evaluating the quality and quantity of information upon which they are based. Hershkovitz (1977), for example, indicated that *Saguinus mystax pluto* occurred between the Rios Purus and Madeira, from the Rio Solimões south into northern Bolivia. His hypothesis was based on a poorly defined type locality and just two other, dubious, locality records (Rylands, Coimbra-Filho and Mittermeier 1993). Although still poorly documented, it would seem that its true range is considerably smaller, and only to the west, not the east, of the (lower) Purus.

Table 2.3 Species and subspecies of Neotropical primates described since 1990

Callithrix nigriceps Ferrari and Lopes, 1992	Black-headed marmoset
Callithrix mauesi Mittermeier, Ayres &	Maués marmoset
Schwarz, 1992	wades marmoset
Callithrix argentata marcai Alperin, 1993	Marca's marmoset
Callithrix saterei Sousee Silva Jr & Noronha, 1998	Sateré marmoset
Callithrix humilis Van Roosmalen, Van Roosmalen,	Black-crowned dwarf marmoset
Mittermeier & Fonseca, 1998	
Callithrix manicorensis Van Roosmalen, Van	Manicoré marmoset
Roosmalen, Mittermeier & Fonseca, 2000	
Callithrix acariensis Van Roosmalen, Van	Rio Acarí marmoset
Roosmalen, Mittermeier & Fonseca, 2000	
Leontopithecus caissara Lorini and Persson, 1990	Black-faced lion tamarin
Callicebus bernhardi Van Roosmalen, Van	Prince Bernhard's titi monkey
Roosmalen and Mittermeier, 2002	•
Callicebus stephennashi Van Roosmalen, Van	Stephen Nash's titi monkey
Roosmalen and Mittermeier, 2002	•
Callicebus personatus barbarabrownae	Blond titi
Hershkovitz, 1990	
Callicebus coimbrai Kobayashi & Langguth, 1999	Coimbra-Filho's titi monkey
Callicebus aureipalatii Wallace, Gómez, A. Felton	Madidi titi monkey
& A. M. Felton, 2006	·
Cebus kaapori Queiroz, 1992	Ka'apor capuchin

Further research is urgently needed to verify and detail the taxonomies and distributions of all of the Neotropical primates. Modern taxonomic and biogeographic revisions are especially needed for the woolly monkeys (*Lagothrix*) (the most recent was Fooden [1963]), the sakis (*Pithecia*), the collared titis of the *Callicebus torquatus* group, and the untufted capuchins, currently ascribed to just two species, *Cebus olivaceus* and *C. albifrons* (see Hershkovitz 1949, Bodini and Pérez-Hernández 1987, Defler 2004). It is becoming evident that the taxonomy of *Pithecia* published by Hershkovitz in 1987, although a major contribution, is still very far from reflecting the true diversity of the genus (L. Marsh, pers. comm.). Other genera which have received much attention over recent years but are still subject to severely divergent opinions and confusion are the night monkeys (*Aotus*), the tufted capuchin monkeys (*Cebus*), and the squirrel monkeys (*Saimiri*).

2.5 Summary

The modern taxonomy of the Infraorder Platyrrhini has been deeply influenced by the numerous publications of the late Philip Hershkovitz. This has meant that in many aspects platyrrhine taxonomy has been extraordinarily stable over the last three decades, while his work has at the same time provided the wherewithal for considerable refinement and adjustments. It may well be that the legacy of Hershkovitz is the cause of there being more species and subspecies of primates in the New World than in Africa and Asia, providing as he did the capacity to compare findings

with what is known, both in terms of the physiognomy of the primates under scrutiny and their supposed distributions. The latest taxonomies of the non-human primates indicate approximately 630 species and subspecies in 71 genera and 17 families. Of these, five families, 19 genera and 199 species and subspecies are Neotropical— 31% of the primates. Africa has 169 species and subspecies and Asia 186. Notably, of the 53 "new" primates described since 1990, 15 were from the Neotropics of which nearly half (seven) are marmosets and five are titi monkeys (two are capuchin monkeys, and the black-faced lion tamarin, Leontopithecus caissara completes the set). Both the titi monkeys, Callicebus, and the marmosets were extensively revised by Hershkovitz prior to 1990. The groups that he did not revise prior to his death were the atelines and capuchin monkeys, both of which are still confused in their taxonomy, although the variability in the latter group particularly makes a better understanding of their systematics the biggest challenge among all the platyrrhine genera. Two further tendencies deserve mention. The first is associated with the desire to conserve the full diversity of primates, an aspect which drags taxonomy from the realm of cataloguing and academic pursuit into the applied sciences. Precaution allows people to unashamedly "split." The second is related to our increased knowledge of the geography of the phenotypes we observe in situ, which has made it increasingly difficult to accept single definitions or dichotomies of species and subspecies. This and the new insights resulting from molecular genetics and chromosome studies, have promoted the adoption of the Phylogenetic Species Concept and the gradual rejection of interpretations of variation using the category of subspecies. In this chapter, I discuss these aspects as related to the taxonomy of the New World monkeys, indicating particularly where change has been prevalent, and the challenges we still face in achieving an understanding of their full diversity, not least of which are the widespread loss of their forests and the introduction and spread of species outside of their natural ranges.

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