Part I: Introduction to Primatology and Virology

1
Classification of Nonhuman Primates

1.1. INTRODUCTION

The order Primata includes humans and animals that are our closest living "relatives" in the animal kingdom. There are many definitions of a primate. None of them are completely satisfactory. As a result, there are disagreements regarding inclusion of some animal taxa in the order Primata. At the same time, it is indisputable that the animals colloquially known as monkeys and apes are primates. From the zoological standpoint, humans are also apes, although the use of this term is usually restricted to chimpanzees, gorillas, orangutans, and gibbons.

1.2. CLASSIFICATION AND NOMENCLATURE OF PRIMATES

The classification of primates, as with any zoological classification, is a hierarchical system of taxa (singular form—taxon). The primate taxa are ranked in the following descending order:

Order
Suborder
Infraorder
Parvorder
Superfamily
Family
Subfamily
Tribe
Genus
Species
Subspecies

Species is the "elementary unit" of biodiversity. Strictly speaking, the only natural grouping of animals is a population. The species is defined as a group of populations whose individual members interbreed and produce fertile offspring in their natural habitat. In practice, the use of this definition may be problematic, for example, for clearly distinct and fertile hybrids existing in the wild. As a result, there are multiple disagreements regarding species rank for the morphologically and/or behaviorally distinguishable nonhuman primate (NHP) populations.[3,4,10,12]

The nomenclature of NHP species is binomial, that is, the scientific names of the species consist of two Latin words. The first capitalized word identifies the genus (plural—genera). The second, lowercase word identifies the species within the genus. The scientific names of species are *italicized*. For example, *Macaca mulatta* is the species *mulatta* within the genus *Macaca*.

The nomenclature of NHP subspecies is trinomial. The full scientific name of a subspecies name consists of three words: the binomial species name and the third word identifying the subspecies. For example, the common chimpanzee species (*Pan troglodytes*) is usually divided into four subspecies: *Pan troglodytes troglodytes*, *Pan troglodytes schweinfurthii*, *Pan troglodytes verus*, and *Pan troglodytes vellerosus*. The names of the subspecies are usually written in abbreviated form, for example, *P. t. troglodytes* and *P. t. schweinfurthii*. The notion of subspecies is very useful for understanding the natural history of simian viruses.

In addition to the scientific names, virtually all primate species and many subspecies have common or vernacular names. The common names are obviously different in various languages; however, the English names are used predominantly in the scientific literature.[11] For example, the common name for *Macaca mulatta* is rhesus monkey; its capitalized version, Rhesus Monkey, is also used. Some simian species have more than one common name; for example, *Papio hamadryas* is called the Sacred Baboon or Hamadryas Baboon. Despite the intrinsic ambiguity of common names, they are useful, for example, for describing NHPs whose taxonomic status is undetermined or controversial. Common names are also easier to pronounce and memorize than the Latin binomial designations.

Ideally, the hierarchy of primate taxa should reflect the evolutionary history. In such cases, classification would be invariant. However, the incompleteness of current knowledge allows multiple hierarchies of primate taxa—hence the existence of different classifications of primates. Most of the inconsistencies between various classifications are located at levels higher or lower than species. Taxa whose rank is higher than species are "artificial" in the sense that their definitions are based on subjectively chosen criteria.

In this book, we mainly follow Groves' classification of primates which is the most widely used.[10] This classification includes 375 simian species (Tables 1.1–1.4). Information on NHP subspecies is included only if it is relevant in a context of simian virology. At the subspecies level, we follow the classification described in literature.[4,12]

1.2.1. Higher Primate Taxa (Suborder, Infraorder, Parvorder, Superfamily)

The primates are divided into two suborders: Strepsirrhini and Haplorrhini (Figure 1.1). Strepsirrhini are divided into three infraorders: Lemuriformes (lemurs), Chiromyiformes (aye-ayes), and Lorisiformes (loris). Haplorrhini are divided into two infraorders: Tarsiiformes (tarsiers) and Simiiformes (simians, i.e., monkeys and apes). The problematic group is tarsiers, also called tree shrews. There is no agreement as to whether or not they belong to the primate order. Placing tarsiers together with simians is also disputed. Traditionally, lemurs, aye-ayes, lories, and tarsiers (if the latter are included in the primates) are considered as prosimians.

The simian part of primate classification starts at the parvorder level. The simians are divided into Platyrrhini (literally "broad or flat-nosed") and Catarrhini (literally "downward-nosed"). All Platyrrhini species live in South America—hence their common name the New World monkeys (NWMs). There are no Catarrhine species in the New World, except African green monkeys (AGMs), which were introduced to several Caribbean islands (St. Kitts, Nevis, and Barbados) in historically recent times (seventeenth century). All African and Asian simian species, except apes, are Old World monkeys (OWMs).

The division into monkeys and apes is formalized at the superfamily level: the members of Cercopithecoidea superfamily are monkeys while the members of Hominoidea superfamily are apes (Figure 1.2).

All 152 currently recognized OWM species are included in one family—Cercopithecidae. This family is divided into two subfamilies: Cercopithecinae and Colobinae (Figure 1.2). There are 11 Cercopithecinae genera and 10 Colobinae genera. Cercopithecinae genera with 42 chromosomes diploid karyotype (*Papio*, *Theropithecus*, *Mandrillus*, *Cercocebus*, *Lophocebus*, and *Macaca*) are combined in the tribe Papionini[14,35] (Figure 1.3). The tribe level is not universally used in the classifications of primates. For instance, it is not included in Groves' classification. However, the term Papionini is commonly used in the descriptions of simian immunodeficiency virus (SIV) and other simian retrovirus hosts.

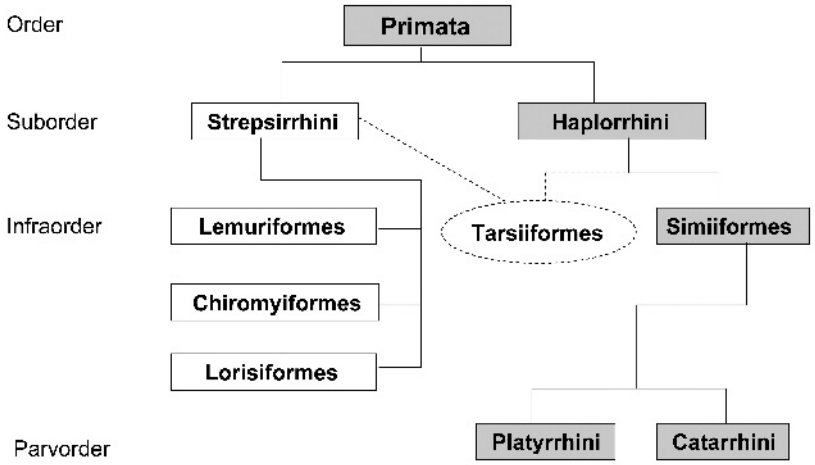

Figure 1.1. Higher primate taxa (order, suborder, infraorder, and parvorder). Shaded boxes—taxa which include monkeys and apes.

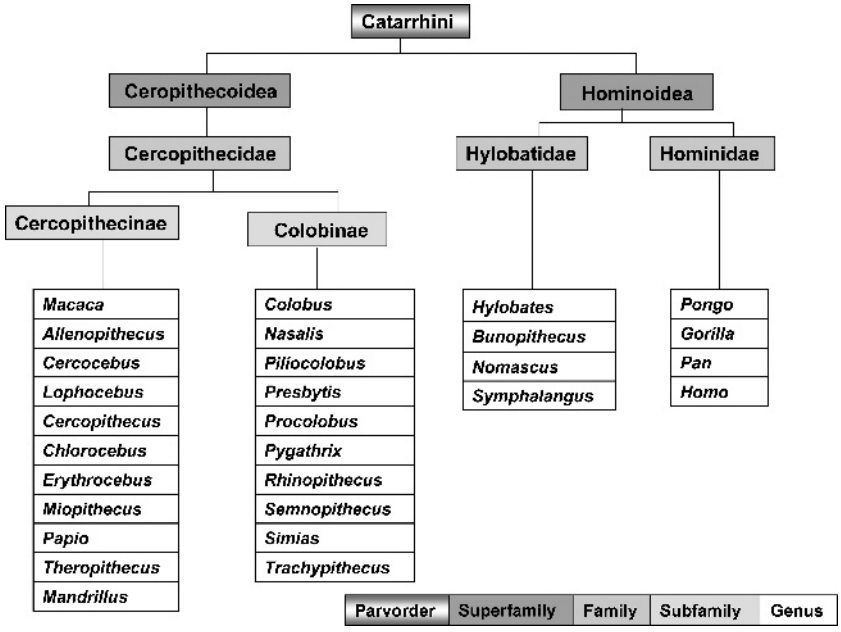

Figure 1.2. Catarrhini taxa (down to genus level).

Table 1.1. Old World Monkeys: Subfamily Cercopithecinae

Genus/Species	Common Name	Geographical Distribution
Chlorocebus	**African green monkey**	
C. aethiops	Grivet monkey or grivet	Sudan, Eritrea, Ethiopia
C. cynosuros	Malbrouck monkey	S DRC,* Angola, N Namibia, Zambia
C. djamdjamensis	Bale Mountains vervet	Ethiopia
C. pygerythrus	Vervet monkey or vervet	Ethiopia, Somalia, Kenya, Tanzania, Zambia, Zimbabwe, RSA†
C. sabaeus	Green monkey	Senegal, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Cote d'Ivoire, Ghana
C. tantalus	Tantalus monkey	Ghana, Togo, Benin, Nigeria, Cameroon, CAR,‡ Kenya
Cercopithecus		
C. albogularis	Sykes' monkey	Ethiopia to RSA, S&E DRC, NW Angola
C. ascanius	Red-tailed monkey	Uganda, DRC, Zambia, Angola, CAR, W Kenya
C. campbelli	Campbell's monkey	Senegal, Liberia, Cote d'Ivoire
C. cephus	Mustached guenon	Gabon, R of Congo,§ S Cameroon, Equatorial Guinea, SW CAR, NW Angola
C. denti	Dent's monkey	DRC, Rwanda, W Uganda, CAR
C. diana	Diana monkey	Sierra Leone, Liberia, Cote d'Ivoire
C. doggetti	Silver monkey	DRC, S Burundi, NW Tanzania, Rwanda, S Uganda
C. dryas	Dryas monkey	DRC
C. erythrogaster	White-throated guenon	S Nigeria, Benin
C. erythrotis	Red-eared guenon	S&E Nigeria, Cameroon, Bioko Isl (Equatorial Guinea)
C. hamlyni	Hamlyn's monkey	E DRC, Rwanda
C. kandti	Golden monkey	DRC, Uganda, Rwanda
C. l'hoesti	L'Hoest's monkey	E DRC, W Uganda, Rwanda, Burundi
C. lowei	Lowe's monkey	Cote d'Ivoire, Ghana
C. mitis	Blue monkey	DRC, Kenya, Rwanda, N Angola, NW Zambia
C. mona	Mona monkey	Ghana, Togo, Benin, Nigeria, Cameroon
C. neglectus	De Brazza's monkey	SE Cameroon, R of Congo, DRC, Equatorial Guinea, Gabon, Uganda, N Angola, W Kenya, SW Ethiopia, S Sudan
C. nictitans	Greater spot-nosed monkey	Liberia, Cote d'Ivoire, Nigeria, DRC, CAR, Equatorial Guinea, Cameroon
C. petaurista	Lesser spot-nosed monkey	Gambia, Guinea, Guinea-Bissau, Sierra Leone, Liberia, Cote d'Ivoire, Ghana, Togo
C. pogonias	Crowned monkey	SE Nigeria, Cameroon, Equatorial Guinea, N&W Gabon, W DRC
C. preussi	Preuss's monkey	Cameroon, Equatorial Guinea
C. roloway	Roloway monkey	Cote d'Ivoire, Ghana
C. sclateri	Sclater's guenon	SE Nigeria
C. solatus	Sun-tailed monkey	Gabon
C. wolfi	Wolf's monkey	DRC, NE Angola

Table 1.1. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
Erythrocebus	**Patas**	
E. patas	Patas monkey	Savannahs, from W Africa to Ethiopia, Kenya, and Tanzania
Miopithecus	**Talapoin**	
M. ogouensis	Gabon talapoin	S Cameroon, Rio Muni (Equatorial Guinea), Gabon, Angola
M. talapoin	Angolan talapoin	Angola, SW DRC
Allenopithecus		
A. nigroviridis	Allen's swamp monkey	NW DRC, NE Angola
Papio	**Baboon**	
P. hamadryas	Hamadryas or sacred baboon	Red Sea coast of Ethiopia, Sudan, Eritrea, N Somalia, Yemen, Saudi Arabia
P. anubis	Olive or anubis baboon	Mali to Ethiopia, Kenya, NW Tanzania
P. cynocephalus	Yellow baboon	Somalia coast, Kenya, Tanzania to Zambezi River
P. papio	Guinea or red baboon	Senegal, Guinea and Guinea-Bissau to Mauritania, Mali
P. ursinus	Chacma baboon	S of Zambezi River to S Angola, SW Zambia
Theropithecus	**Gelada**	
T. gelada	Gelada	Highlands of N Ethiopia
Mandrillus	**Mandrill and drill**	
M. sphinx	Mandrill	Cameroon, S of Sanaga River, Rio Muni (Equatorial Guinea), Gabon, R of Congo
M. leucophaeus	Drill	SE Nigeria, Cameroon, N of Sanaga River, Bioko Isl (Equatorial Guinea)
Cercocebus	**Mangabey**	
C. agilis	Agile mangabey	Rio Muni (Equatorial Guinea), Cameroon, NE Gabon, CAR, N R of Congo, DRC, N of Congo River
C. atys	Sooty mangabey	Senegal to Ghana
C. chrysogaster	Golden-bellied mangabey	DRC, S of Congo River
C. galeritus	Tana River mangabey	Lower Tana River (Kenya)
C. sanjei	Sanje mangabey	Tanzania
C. torquatus	Red-capped or collared mangabey	W Nigeria, Cameroon, Equatorial Guinea, Gabon
Lophocebus	**Mangabey**	
L. albigena	Gray-cheeked mangabey	Cross River (SE Nigeria), Cameroon, R of Congo, Gabon, Equatorial Guinea, NE Angola, CAR, DRC, N and E of Congo–Lualaba Rivers, W Uganda, Burundi
L. aterrimus	Black crested mangabey	DRC, S of Congo River
L. opdenboschi	Opdenbosch's mangabey	DRC, Angola

(*Continued*)

Table 1.1. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
Macaca	**Macaque**	
M. arctoides	Stump-tailed macaque	Assam (India) to S China, N Malay Peninsula
M. assamensis	Assam macaque	Nepal to N Vietnam, S China
M. cyclopis	Formosan rock or Taiwan macaque	Taiwan
M. fascicularis	Crab-eating or cynomolgus macaque	S Indochina, Burma to Borneo and Timor, the Philippines
M. fuscata	Japanese macaque	Honshu, Shikoku, Kyushu and adjacent small islands, Yaku, Ryukyu (Japan)
M. hecki	Heck's macaque	N Sulawesi (Indonesia)
M. leonina	Northern pig-tailed macaque	Coast and Mergui Archipelago (Burma), N Thailand
M. maura	Moor macaque	S Sulawesi (Indonesia)
M. mulatta	Rhesus monkey	Afghanistan and India to N Thailand, China
M. nemestrina	Southern pig-tailed macaque or pig-tailed macaque	Malay Peninsula, Borneo, Sumatra and Bangka Isl (Indonesia), Thailand
M. nigra	Celebes crested macaque or Celebes black macaque or Celebes black ape¶	Sulawesi, east of Onggak Dumoga River, Lembeh Isl, Bacan Isl (Indonesia)
M. nigrescens	Gorontalo macaque	Sulawesi, E of Gorontalo to Onggak Dumoga River (Indonesia)
M. ochreata	Booted macaque	SE Sulawesi, Kabaena, Muna, Butung (Indonesia)
M. pagensis	Pagai Island macaque	Sipura, N&S Pagai Isl (Indonesia)
M. radiata	Bonnet macaque	S India
M. siberu	Siberut macaque	Siberut (Indonesia)
M. silenus	Lion-tailed macaque	SW India, W Ghats (India)
M. sinica	Toque macaque	Sri Lanka
M. sylvanus	Barbary macaque or Barbary ape¶	Morocco, Algeria, Gibraltar
M. thibetana	Milne-Edwards's macaque	E Tibet, Szechwan to Kwangtung (China)
M. tonkeana	Tonkean macaque	Sulawesi, Togian Isl (Indonesia)

Adapted from Groves.[10]
*Democratic Republic of Congo (DRC).
†Republic of South Africa (RSA).
‡Central African Republic (CAR).
§Republic of Congo (R of Congo).
¶Although the name ape has been used for these tailless monkeys, they are typical macaques, not apes.

Table 1.2. Old World Monkeys: Subfamily Colobinae

Genus/Species	Common Name	Geographical Distribution
Colobus	**Colobus**	
C. angolensis	Angola colobus	NE Angola, S&E DRC,* Burundi, NE Zambia, SE Kenya, E Tanzania
C. guereza	Mantled guereza	Nigeria to Ethiopia, Kenya, Uganda, Tanzania
C. polykomos	King colobus	Gambia to the Nzo-Sassandra system (Cote d'lvoire)
C. satanas	Black colobus	SW Gabon, Rio Muni and Bioko (Equatorial Guinea), SW Cameroon, R of Congo†
C. vellerosus	Ursine colobus	Nzi-Bandama system (Cote d'Ivoire) to W Nigeria
Nasalis		
N. larvatus	Proboscis monkey	Borneo
Piliocolobus	**Red colobus**	
P. badius	Western red colobus	Senegal to Ghana
P. foai	Central African red colobus	Sangha, Oubangui (R of Congo), DRC (N of Congo River, E of Lualaba), Ngotto (CAR),‡ S Sudan
P. gordonorum	Uzungwa red colobus	Uzungwa mountains and forests between Little Ruaha and Ulanga Rivers (Tanzania)
P. kirkii	Zanzibar red colobus	Zanzibar
P. pennantii	Pennant's red colobus	Bioko (Equatorial Guinea), Niger Delta (Nigeria), Sangha-Likouala (R of Congo)
P. preussi	Preuss's red colobus	Yabassi (Cameroon)
P. rufomitratus	Tana River red colobus	Lower Tana River (Kenya)
P. tephrosceles	Ugandan red colobus	Uganda, Rwanda, Burundi, W Tanzania to Lake Rukwa
P. tholloni	Thollon's red colobus	South of Congo River, W of Lomami River (DRC)
Presbytis	**Surili/langur**	
P. chrysomelas	Sarawak surili	Kalimantan, N of Kapuas River (Indonesia), Sarawak, Sabah (Malaysia)
P. comata	Javan surili	W and Central Java (Indonesia)
P. femoralis	Banded surili	S and NW of Malay Peninsula, peninsular part of Thailand and Burma, Singapore, NE Sumatra
P. frontata	White-fronted langur	Central and E Borneo, from Central Sarawak to S coast
P. hosei	Hose's langur	N and E Borneo, Brunei, E Sarawak, Sabah (Malaysia), S to Karangan River in Kalimantan (Indonesia)
P. melalophos	Sumatran surili	Sumatra (Indonesia)
P. natunae	Natuna Island surili	Bunguran Isl (Indonesia)
P. potenziani	Mentawai langur	Mentawai Isl (Indonesia)
P. rubicunda	Maroon leaf-monkey	Borneo, Karimat Isl (Indonesia)
P. siamensis	White-thighed surili	Malay Peninsula, except far S and NW, E Sumatra between Siak and Inderagiri Rivers, between Rokan and Barimun Rivers, Lake Toba region, Kundur, Bintang, Batam, and Galang Isl, Riau Archipelago (Indonesia)
P. thomasi	Thomas's langur	Sumatra/Aceh (Indonesia)
Procolobus		
P. verus	Olive colobus	Sierra Leone to Togo, Idah (E Nigeria)

(*Continued*)

Table 1.2. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
Pygathrix	**Shanked douc**	
P. cinerea	Gray-shanked douc	Central Vietnam
P. nemaeus	Red-shanked douc	Central Vietnam, E Laos
P. nigripes	Black-shanked douc	S Vietnam, Cambodia, E of Mekong River
Rhinopithecus	**Snub-nosed monkey**	
R. avunculus	Tonkin snub-nosed monkey	NW Vietnam
R. bieti	Black snub-nosed monkey	Ridge of Mekong-Salween divide, Yunnan (China)
R. brelichi	Gray snub-nosed monkey	Guizhou (China)
R. roxellana	Golden snub-nosed monkey	Sichuan Mountains, S Ganssu, Hubei, Shaanxi (China)
Semnopithecus	**Gray langur**	
S. ajax	Kashmir gray langur	Dehradun (India) and W into Pakistani Kashmir
S. dussumieri	Southern Plains gray langur	SW and W and Central India
S. entellus	Northern Plains gray langur	Pakistan and India, lowlands N of Godavari and Krishna Rivers, S of Ganges
S. hector	Tarai gray langur	Kumaun (India) to Hazaria (Nepal)
S. hypoleucos	Black-footed gray langur	Kerala, South Coorg region (India)
S. priam	Tufted gray langur	SE India, Sri Lanka
S. schistaceus	Nepal gray langur	E of Gorkha to Sikkim (Nepal), and parts of southernmost Tibet (China)
Simias		
S. concolor	Simakobu or pig-tailed langurs	Mentawai Isl (Indonesia)
Trachypithecus	**Lutung/langur**	
T. auratus	Javan lutung	Java, Bali, Lombok (Indonesia)
T. barbei	Tenasserim lutung	N Burma, Thailand
T. cristatus	Silvery lutung	Borneo, Natuna Isl, Bangka, Belitung, Sumatra, Riau Archipelago (Indonesia), W coast of Malay Peninsula
T. delacouri	Delacour's langur	Vietnam, S of Red River
T. ebenus	Indochinese black langur	Lai Chau or Fan Si Pan chain, Hin Namno (Laos)
T. francoisi	Francois's langur	N Vietnam, C Laos, Kwangsi (China)
T. geei	Gee's Golden langur	Between Sankosh and Manas Rivers, Indo-Bhutan border (India, Bhutan)
T. germaini	Indochinese lutung	Thailand and Burma, Cambodia, Vietnam
T. hatinhensis	Hatinh langur	Quang Binh and neighboring regions (Vietnam)
T. johnii	Nilgiri langur	S India
T. laotum	Laotian langur	Central Laos
T.obscurus	Dusky leaf-monkey	S Thailand, Malay Peninsula, and small adjacent islands
T. phayrei	Phayre's leaf-monkey	Laos, Burma, Central Vietnam, Central and N Thailand, Yunnan (China)
T. pileatus	Capped langur	Assam (India)
T. poliocephalus	White-headed langur	Cat Ba Isl (Vietnam), Guangxi (China)
T. shortridgei	Shortridge's langur	Burma, E of Chindwin River, Gongshan, Yunnan (China)
T. vetulus	Purple-faced langur	Sri Lanka

Adapted from Groves.[10]
*Democratic Republic of Congo (DRC).
†Republic of Congo (R of Congo).
‡Central African Republic (CAR).

Table 1.3. Apes: Family Hominidae

Genus/Species	Common Name	Geographical Distribution
Hylobates	**Gibbon**	
H. agilis	Agile gibbon	Sumatra (Indonesia)
H. albibarbis	Bornean white-beared gibbon	Borneo (Indonesia)
H. klossii	Kloss's gibbon	Mentawai (Indonesia)
H. lar	Lar gibbon	Yunnan (China), Thailand, S Malaysia, Sumatra (Indonesia), SE Burma
H. moloch	Javan silvery gibbon	Java (Indonesia)
H. muelleri	Müller's Bornean gibbon	Borneo (Indonesia)
H. pileatus	Pileated gibbon	SE Thailand, Cambodia
Bunopithecus	**Gibbon**	
B. hoolock	Hoolock gibbon	Assam (India)
Nomascus	**Gibbon**	
N. concolor	Black crested gibbon	S Laos, S Vietnam
N. gabriellae	Red-cheeked gibbon	S Laos, S Vietnam, E Cambodia
N. hainanus	Hainan gibbon	Hainan (China), Vietnam
N. leucogenys	Northern white-cheeked gibbon	Yunnan (China), N Vietnam, N Laos
N. siki	Southern white-cheeked gibbon	Vietnam, Laos
Symphalangus	**Siamang**	
S. syndactylus	Siamang	Sumatra (Indonesia), Malaysia
Pongo	**Orangutan**	
P. abelii	Sumatran orangutan	Sumatra (Indonesia)
P. pygmaeus	Bornean orangutan	Borneo (Indonesia)
Gorilla	**Gorilla**	
G. gorilla	Western gorilla	SE Nigeria, Cameroon, Equatorial Guinea, R of Congo,* SW CAR,† Gabon
G. beringei	Eastern gorilla	N&E DRC,‡ SW Uganda, N Rwanda
Pan	**Chimpanzee**	
P. troglodytes	Common chimpanzee	S Cameroon, Gabon, S R of Congo, Uganda, W Tanzania, N DRC, W CAR, Guinea, Guinea-Bissau, Liberia
P. paniscus	Bonobo or pygmy chimpanzee	DRC, S of Congo River

Adapted from Groves.[10]
*Republic of Congo (R of Congo).
†Central African Republic (CAR).
‡Democratic Republic of Congo (DRC).

Table 1.4. New World Monkeys: Order Ptatyrrhini

Genus/Species	Common Name	Geographical Distribution
Catlithrix	**Marmoset**	
C. acariensis	Rio Acari marmoset	Rios Acari and Sucunduri (Brazil)
C. argentata	Silvery marmoset	N and Central Brazil, E Bolivia
C. aiirita	Buffy-tufted marmoset	SE Brazilian coast
C. chrysoleuca	Gold-and-white marmoset	Between the Aripuana-Madeira and Canuma-Uraria, N to the Amazon (Brazil)
C. emiliae	Emilia's marmoset	Tapajos and Iriri, N to Maica, on the lower Tapajos (Brazil)
C. flaviceps	Buffy-headed marmoset	S Espirito Santo (Brazil)
C. geoffroyi	White-headed marmoset	Coastal Bahia (Brazil)
C. humeralifera	Santarem marmoset	S of the Amazon between the Maues-Acu and Tapajos Rivers (Brazil)
C. humilis	Roosmalens' dwarf marmoset	Between the Rios Aripuana and Madeira (Brazil)
C. intermedia	Hershkovitz's marmoset	Rios Aripuana and Roosevelt (Brazil)
C. jacchus	Common marmoset	Coast of Piaui, Ceara, and Pernambuco (Brazil)
C. kuhlii	Wied's marmoset	Between Rio de Contas and Rio Jequitinhonha, SW Brazil
C. leucippe	White marmoset	Rios Tapajos and Cupari (Brazil)
C. manicorensis	Manicore marmoset	Rios Aripuana and Manicore, from the Rio Madeira S to the Rio Roosevelt (Brazil)
C. marcai	Marca's marmoset	Amazonas, Fozdo Rio Castanho (Brazil)
C. mauesi	Maues marmoset	Rios Uraria-Abacaxis and Maues-Ac'u (Brazil)
C. melanura	Black-tailed marmoset	S Brazil, between the Rios Aripuana and Juruena, SW to the Rio Beni in Bolivia
C. nigriceps	Black-headed marmoset	Rios Marmelos and Madeira, N of the Ji-Parana River (Brazil)
C. penicillata	Black-tufted marmoset	Brazilian coast, Bahia to Sao Paulo, inland to Goias
C. pygmaea	Pygmy marmoset	N and W Brazil, N Peru, Ecuador
C. saterei	Satere marmoset	Rios Abacaxis and Canuma-Sucunduri (Brazil)
Callimico	**Marmoset**	
C. goeldii	Goeldi's marmoset	W Brazil, N Bolivia, E Peru, Colombia, Upper Amazon rainforests
Saguinus	**Tamarin**	
S. bicolar	Pied tamarin	N Brazil, possibly NE Peru
S. fuscicollis	Brown-mantled tamarin	N and W Brazil, N Bolivia, E Peru, E Ecuador, SW Colombia
S. geoffroyi	Geoffroy's tamarin	SE Costa Rica to NW Colombia
S. graellsi	Graells's tamarin	Peru, Ecuador, Colombia, W of Rio Napo, from Rio Putumayo S to Rio Maranon, W to Rio Santiago
S. imperator	Emperor tamarin	W Brazil, E Peru, Bolivia
S. inustus	Mottle-faced tamarin	NW Brazil, SW Colombia
S. labiatus	White-lipped tamarin	W Brazil, E Peru, Bolivia

Table 1.4. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
S. leucopus	White-footed tamarin	N Colombia
S. martinsi	Martins's tamarin	Very small area N of the Amazon, on both sides of the Rio Nhamunda (Brazil)
S. melanoleucus	White-mantled tamarin	Between Rios Jurua and Tarauca (Brazil)
S. midas	Red-handed tamarin	Brazil, Guyana, Cayenne, Surinam, N of the Amazon, E of the Rio Negro
S. mystax	Moustached tamarin	W Brazil, Peru, S of Amazon–Solimoes–Maranon, between lower Rio Huallaga and Rio Madeira
S. niger	Black tamarin	Brazil, S of the Amazon, E of the Rio Xingu, including Marajo Isl
S. nigricollis	Black-mantled tamarin	W Brazil, E Peru, E Ecuador
S. oedipus	Cottontop tamarin	N Colombia, Panama
S. pileatus	Red-capped tamarin	W Brazil, E of Rio Tefe, W of Rio Purus
S. tripartitus	Golden-mantled tamarin	E of Rio Curaray, Brazil–Colombia border
Leontopithecus	**Lion tamarin**	
L. caissara	Superagui lion tamarin	Superagui Isl and a small region on the opposite mainland (Brazil)
L. chrysomelas	Golden-headed lion tamarin	Coastal Bahia (Brazil)
L. chrysopygus	Black lion tamarin	Sao Paulo region (Brazil)
L. rosalia	Golden lion tamarin	SE Brazil, Rio Doce (Espirito Santo), S of Rio de Janeiro and Guanabara
Cebus	**Capuchin**	
C. albifrons	White-fronted capuchin	Venezuela, Colombia, Ecuador, N Peru, NW Brazil, Trinidad, Bolivia
C. apella	Tufted capuchin	N and W South America, from Guyana, Venezuela (S from the Rio Orinoco delta) and Colombia south across the Amazon in Brazil
C. capucinus	White-headed capuchin	W Ecuador to Honduras
C. kaapori	Kaapori capuchin	Between Rios Gurupi and Pindare (Brazil)
C. libidinosus	Black-striped capuchin	Highland region of S Brazil to Bolivia and Paraguay
C. nigritus	Black capuchin	Brazilian coast 16–30°S
C. olivaceus	Weeper capuchin	Guyana, French Guiana, Surinam, N Brazil, Venezuela, possibly N Colombia
C. xanthosternos	Golden-bellied capuchin	Brazil, formerly between Rio Sao Francisco and Rio Jequitinhonha, now much reduced
Saimiri	**Squirrel monkey**	
S. boliviensis	Black-capped squirrel monkey	Upper Amazon in Peru, SW Brazil, Bolivia
S. oerstedii	Central American squirrel monkey	Panama, Costa Rica
S. sciureus	Common squirrel monkey	N Brazil, N of the Amazon-Jurua system, S of the Amazon E, east Rio Xingu or the Rio Iriri, Marajo Isl (Brazil), Guyana, French Guiana, Surinam, Venezuela, Colombia, E Ecuador, NE Peru

(*Continued*)

Table 1.4. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
S. ustus	Bare-eared squirrel monkey	S Brazil, S of Rio Amazon, probably from Rio Xingu to Lage Tefe
S. vanzolinii	Black squirrel monkey	Between Rios Japura, Solimoes and (probably) Paranadojaraua (Brazil), Tarara and Capucho Ils (Brazil)
Aotus	**Night or owl monkey**	
A. azarae	Azara's night monkey	Bolivia S of Amazon, between Rios Tocantins and Tapajos-Juruena, S to Paraguay and N Argentina
A. hershkovitzi	Hershkovitz's night monkey	Colombia
A. lemurinus	Gray-bellied night monkey	Panama, Equador, and Colombia W of Cordillera Oriental
A. miconax	Peruvian night monkey	Between Rio Ucayali and the Andes, S of Rio Maranon (Peru)
A. nancymaae	Nancy Ma's night monkey	Loreto (Peru) to Rio Jandiatuba, S of Rio Solimoes (Brazil), enclave between Rios Tigre and Pastaza (Peru)
A. nigriceps	Black-headed night monkey	Brazil, S of Rio Solimoes, W of Rio Tapajos Juruena, W into Peru, Bolivia
A. trivirgatus	Three-striped night monkey	Venezuela, S of Rio Orinoco, S to Brazil N of Rios Negro and Amazon
A. vociferans	Spix's night monkey	Colombia, E of Cordillera Oriental, W of Rio Negro, S to Brazil (N of Amazon–Solimoes Rivers)
Alouatta	**Howler**	
A. belzebul	Red-handed howler	N Brazil (mainly S of Lower Amazon, E of Rio Madeira), Mexiana Isl, Para Province (Brazil), N of Amazon
A. caraya	Black howler	N Argentina to Mato Grosso (Brazil), Bolivia
A. coibensis	Coiba Island howler	Coiba Isl and Azuero Penninsula (Panama)
A. guariba	Brown howler	N Bolivia, SE and EC Brazil, N to the Rio Sao Francisco
A. macconnelli	Guyanan red howler	Guyana, coast region
A. nigerrima	Amazon black howler	N Brazil, E of the Rio Trombetas to the Rio Tapajos, possibly to the Rio Tocantins
A. palliata	Mantled howler	W Ecuador to Veracruz and Oaxaca (Mexico)
A. pigra	Guatemalan black howler	Yucatan and Chiapas (Mexico) to Belize and Guatemala
A. sara	Bolivian red howler	Bolivia (Sara Province), Peru, and Brazil to the Rio Negro and Rondonia
A. seniculus	Venezuelan red howler	Colombia to Venezuela and NW Brazil
Ateles	**Spider monkey**	
A. belzebuth	White-fronted spider monkey	Cordillera Oriental, Colombia to Venezuela and N Peru
A. chamek	Peruvian spider monkey	NE Peru, E Bolivia to Brazil west of Rio Jurua and S of Rio Solimoes
A. fusciceps	Black-headed spider monkey	SE Panama to Ecuador, Colombia to W Cordillera (Paraguay)

Table 1.4. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
A. geoffroyi	Geoffrey's spider monkey	S Mexico to Panama
A. hybridus	Brown spider monkey	N Colombia and NW Venezuela
A. marginatus	White-cheeked spider monkey	S of Lower Amazon, Rio Tapajos to Rio Tocantins (Brazil)
A. paniscus	Red-faced spider monkey	Guianas and Brazil, N of the Amazon, E of Rio Negro
Lagothrix	**Woolly monkey**	
L. cana	Gray woolly monkey	Brazil, S of Amazon, S highlands of Peru, an isolated population in northern Bolivia
L. lagotricha	Brown woolly monkey	Brazil N of Rio Napo-Amazon system, SE Colombia, extreme N Peru and NE Ecuador
L. lugens	Colombian woolly monkey	Colombia, headwaters of Orinoco tributaries, Venezuela, Sarare River drainage
L. poeppigii	Silvery woolly monkey	Highlands of E Ecuador and N Peru, to about 70°W, 5°S in Brazil
Oreonax	**Woolly monkey**	
O. flavicauda	Yellow-tailed woolly monkey	E Andes in San Martin (Peru) and Amazonas (Brazil)
Brachyteles	**Muriqui**	
B. arachnoides	Southern muriqui	SE Brazil, states of Rio de Janeiro and Sao Paulo
B. hypoxanthus	Northern muriqui	E Brazil, Bahia, Minas Gerais, Espiritu Santo
Callicebus	**Titi**	
C. baptistsa	Baptista Lake titi	Central Brazil, N of the Parana do Uraria and Parana do Ramos and S of the Amazon and lowermost Rio Madeira, a small wedge between the Rio Uira-Curupa and Rio Andira
C. barbarabrownae	Barbara Brown's titi	E Brazil, between Rio Paraguacu and Rio Itapicuru, except where *C. coimbrai* is found
C. bernhardi	Prince Bernhard's titi	Brazil, Amazonas, and Rodonia states, between Rios Madeira-Ji-Parana and Rios Aripuana-Roosevelt
C. brunneus	Brown titi	Middle to upper Madeira basin in Peru and Brazil, to upper Rio Purus (Brazil) and Ucayali (Peru), Bolivia
C. caligatus	Chestnut-bellied titi	S of the Rio Solimoes from Rio Purus to Rio Madeira (Brazil)
C. cinerascens	Ashy black titi	Rio Madeira basin (Brazil)
C. coimbrai	Coimbra Filho's titi	NE Brazil, between Rio Sao Francisco and Rio Real
C. cupreus	Coppery titi	S of the Amazon from Rio Purus to Rio Ucayali, Brazil, and Peru, probably Bolivia

(*Continued*)

Table 1.4. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
C. discolor	White-tailed titi	Upper Amazonian region in Peru, Ecuador, and Colombia, and possibly into Brazil, between the Rios Ucayali and Huallaga and N of Rio Maranon across the Rio Napo to the Rio Putumayo and Rio Guames
C. donacophilus	White-eared titi	WC Bolivia, El Beni, and Santa Cruz, Upper Rios Marmore-Grande and San Miguel basins
C. dubius	Hershkovitz's titi	Brazil, Ituxi River or the Mucuim River, E to the Madeira River S of Humaita, and W to the Purus River
C. hoffmannsi	Hoffmanns's titi	Central Brazil, S of Amazon, between Rios Canuma and Tapajos-Jurena, S to the Rio Sucunduri
C. lucifer	Lucifer titi	Peru, Ecuador, and Brazil, between Rios Caqueta-Japua and Rios Napo-Solimoes
C. lugens	Black titi	Brazil, Colombia, and Venezuela, W of Rio Branco and N of Rios Negro/Uaupes/Vaupes, then W of Rio Apaporis and N of Rio Caqueta, E of Andes N to Rio Tomo, possibly to Rio Orinoco (only between Rio Caura and Rio Caroni)
C. medemi	Colombian black-handed titi	Amazonian region of Colombia
C. melanochir	Coastal black-handed titi	Between Rio Mucuri and Rio Itapicuru (Brazil)
C. modestus	Rio Beni titi	Upper Rio Beni basin (Bolivia)
C. moloch	Red-bellied titi	Central Brazil, S of Amazon, between Rios Tapajos and Tocantins-Araguaia
C. nigrifrons	Black-fronted titi	SE Brazil, states of Rio de Janeiro, Sao Paulo (north of Rio Tiete), and S Minas Gerais
C. oenanthe	Rio Mayo titi	Rio Mayo valley (N Peru)
C. olallae	Ollala Brothers' titi	Bolivia, El Beni Province, La Laguna
C. ornatus	Ornate titi	Colombia, headwaters of Rio Meta and Rio Guiviare
C. pallescens	White-coated titi	Paraguay, W of Rio Paraguay in Gran Chaco, Mato Grosso do Sul, in the Pantanal (Brazil), probably Bolivia
C. personatus	Atlantic titi	SE Brazil, Espirito Santo, possibly into NW Minas Gerais
C. purinus	Rio Purus titi	Brazil S of the Rio Solimoes between the Rio Tapaua and Rio Jurua
C. regulus	Red-headed titi	Brazil, between Rios Javari/Solimoes and Rio Jurua
C. stephennashi	Stephen Nash's titi	Brazil, probably along the right bank of the Rio Purus, in between the distributions of *C. caligatus* and *C. dubius*
C. torquatus	Collared titi	Brazil, between Rios Negro/Uaupes and Rios Solimoes/Japura/Apaporis

Table 1.4. (*Continued*)

Genus/Species	Common Name	Geographical Distribution
Pithecia	**Saki**	
P. aequatorialis	Equatorial saki	Napo (Ecuador) to Loreto (Peru)
P. albicans	White-footed saki	S bank of Amazon, between lower Jurua and lower Purus Rivers
P. irrorata	Rio Tapajos saki	S of the Amazon in SW Brazil, SW Peru, E Bolivia
P. monachus	Monk saki	W of Rio Jurua and Rio Japura-Caqueta (Brazil), Colombia, Ecuador and Peru
P. pithecia	White-faced saki	Guyana, French Guiana, Surinam, N Amazon, E of Rio Negro and Rio Orinoco (Brazil), S Venezuela
Chiropotes	**Saki**	
C. albinasus	White-nosed saki	N and Central Brazil
C. chiropotes	Red-backed bearded saki	Guyana, French Guiana, Surinam, Brazil E of the Rio Branco
C. israelita	Brown-backed bearded saki	Brazil N of the Amazon and E of the Rio Branco, S Venezuela E of the Rio Orinoco
C. satanas	Black bearded saki	Brazil S of Amazon estuary, between Rios Tocantins and Gurupi
C. utahickae	Uta Hick's bearded saki	N Brazil, S of Amazon, between Rios Xingu and Tocantins, S to Serra dos Carajas and Rio Itacaiuna
Cacajao	**Uacari**	
C. calvus	Bald uakari	NW Brazil, E Peru
C. melanocephalus	Black-headed uakari	SW Venezuela, NW Brazil

Adapted from Groves.[10]

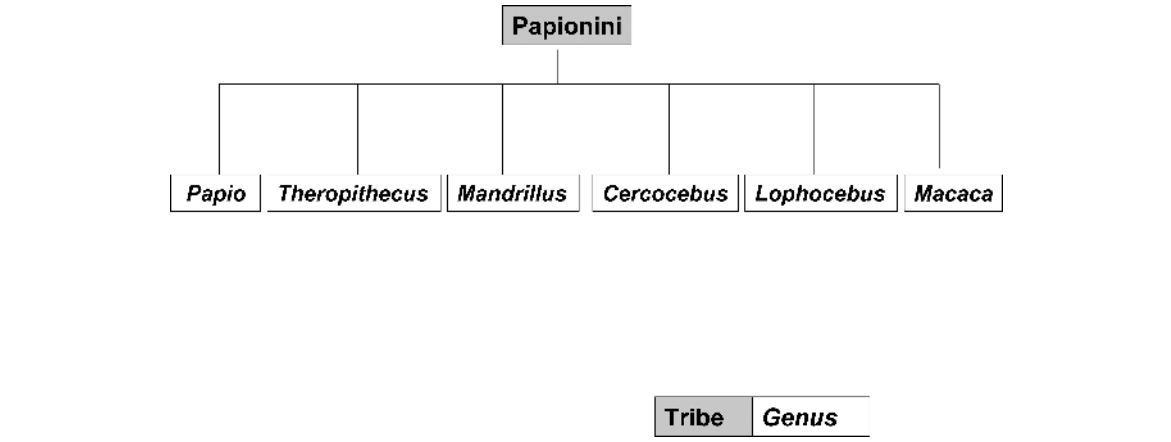

Figure 1.3. Genera included in Papionini tribe.

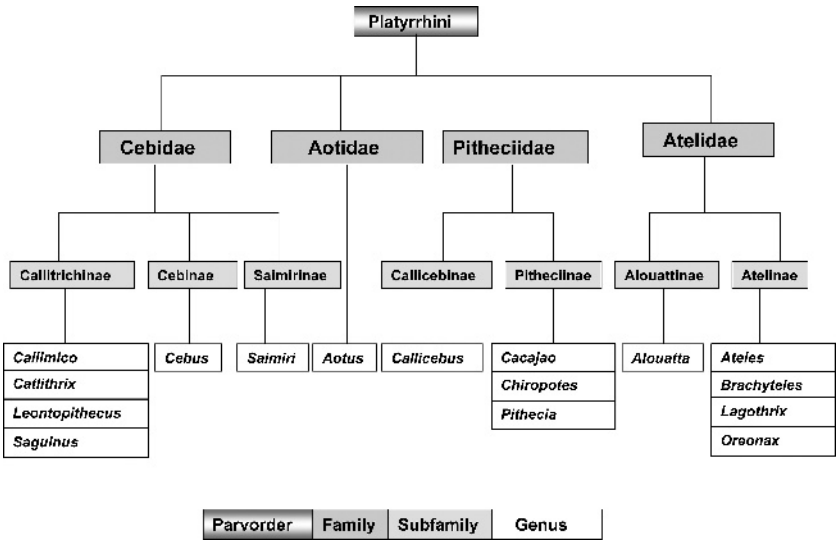

Figure 1.4. Platyrrhini taxa (down to genus level).

Ape is a generic common name for species included in the superfamily Hominoidea. There are two types of simian apes: the lesser apes (species belonging to the family Hylobatidae) and the great apes (species belonging to the family Hominidae). The subfamily level in the classification of hominoids is omitted. The list of simian ape genera and species is presented in Table 1.3.

The NWMs (Platyrrhini) are divided into four families: Cebidae, Pitheciidae, Atelidae, and Aotidae (Figure 1.4). The first three of those families are divided into subfamilies. The subfamilies within Cebidae are Cebinae, Callitrichinae, and Saimiriinae; within Pitheciidae—Pitheciinae and Callicebinae; and within Atelidae—Atelinae and Alouattinae. There are no subfamilies in the Aotidae family. The list of NWM genera and species is presented in Table 1.4.

1.2.2. Molecular Taxonomy and Molecular Identification of NHPs

Traditionally, taxonomic identification of NHPs was based on the description and analysis of external morphological and anatomical traits. Many early descriptions of simian species were made entirely from museum specimens. Gradually, purely morphological identifications were supplemented with more detailed and reliable information on the geographical distribution and behavioral characteristics of simian species, subspecies, and local populations obtained in field studies.

Although morphology, behavioral characteristics, and habitat data continue to be important, they are supplemented with molecular taxonomic data. As a concept, molecular taxonomy, an approach that is based on protein and DNA sequence data analyses, is not new. It has been explored since the early 1960s. However, with the advent of polymerase chain reaction (PCR) and automatic DNA sequencing, the use of molecular taxonomy has grown explosively. The wide availability of sophisticated phylogenetic analysis programs and powerful computers has also contributed to the "popularity" of this approach. Molecular taxonomy has proven to be a powerful tool for resolving uncertainties and controversies in the classification of NHPs that were based on classical approaches.[14,17,22,30,35,37,39,43–45] Importantly, molecular taxonomic studies provide estimates of timing for divergence of various primate taxa; although these estimates should be treated with caution because they are based on many assumptions that may or may not be correct.

The practical application of molecular taxonomy allows accurate species identification of specimens containing extractable DNA.[15,20] Such genotyping is extremely important for samples collected in the field. Moreover, genotyping allows unequivocal individual

identification of "anonymous" samples, such as fecal specimens[5] or hairs from wild monkeys and apes. A few hairs pulled from a specimen or live animal usually contain sufficient DNA for these analyses. Another important practical application of genotyping is tracing the origin of imported wild-caught or captive-born monkeys or apes when relevant information is insufficient or unreliable.[7,18,28]

In this chapter, where possible, we provide brief descriptions of the latest molecular taxonomy data relevant to specific NHP taxa.

1.3. OLD WORLD MONKEYS

1.3.1. Guenons and Allies

The common name "guenons" was used originally for "tree-dwelling" monkeys grouped into *Cercopithecus* genus. Its current meaning is broader. The guenons are monkeys grouped into the tribe Cercopithecini that includes *Cercopithecus*, *Chlorocebus*, *Erythrocebus*, *Miopithecus*, and *Allenopithecus* genera. Some of these guenons are "arboreal" (tree-dwelling), others are "terrestrial" (ground-dwelling). Molecular taxonomic evidence indicates that both arboreal and terrestrial groups are monophyletic; that is, they evolved from a single common ancestor. The terrestrial lineage is more ancient. Evolutionarily, the oldest guenon species is *Allenopithecus nigroviridis*, a terrestrial monkey.[44] Among arboreal guenons, the oldest evolutionarily species are the talapoin monkeys (*Miopithecus* spp.).

The division into arboreal and terrestrial species does not coincide completely with taxonomic boundaries. Most arboreal guenons belong to one genus *Cercopithecus*; only one *Cercopithecus* species *C. l'hoesti* is terrestrial. The terrestrial group also includes the *Chlorocebus* and *Patas* species.

1.3.1.1. African Green Monkeys

AGM is the common name for a group of species in which the prototype is the grivet monkey (*Cercopithecus aethiops* or *Chlorocebus aethiops*). The *Chlorocebus* genus was introduced recently and some authors still continue to place AGM into the *Cercopithecus* genus.[12] Both scientific names, that is *Chlorocebus* spp. and *Cercopithecus* spp., are used for AGMs, but the former is gradually replacing the latter.

There are four clearly distinguishable major forms of AGMs: grivet (*Chlorocebus aethiops*), vervet (*C. pygerythrus*) (Figure 1.5), green or sabaeus monkey (*C. sabaeus*), tantalus monkey (*C. tantalus*) (Figure 1.6); and two minor forms: Bale Mountains grivet (*C. djamdjamensis*) and Malbrouck monkey (*C. cynosuros*). These forms are ranked as separate species.[10,12] Within three of these species (*aethiops*, *pygerythrus*, and *tantalus*), there are distinguishable forms, particularly numerous in *C. pygerythrus*. Taxonomic ranking of these forms is disputable; however, usually they are classified as subspecies (Table 1.5).[12]

There are large feral populations of sabaeus AGMs on the Caribbean islands of Barbados, St. Kitts, Nevis, and St. Marten. The founders of these populations were brought by slave traders in the seventeenth and eighteenth centuries. Genetically, Caribbean AGMs are much more homogenous than their counterparts in Africa. Caribbean AGMs are also free of several viruses found in AGMs on the African continent; most notably, they are SIV-free (see Chapter 3).

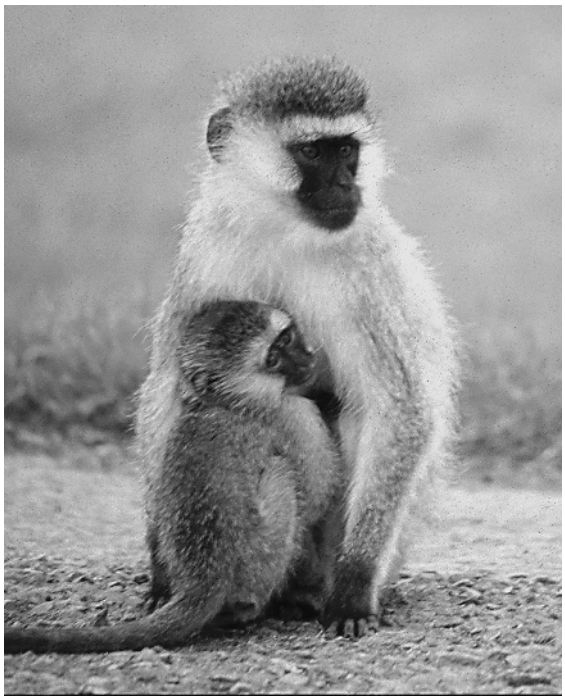

Figure 1.5. Vervet monkeys (*Chlorocebus pygerythrus*, possibly *C. p. callidus*), the Lake Nakuro region, Kenya. (Image is kindly provided by Dr. Jean P. Boubli.) See color version page 1.

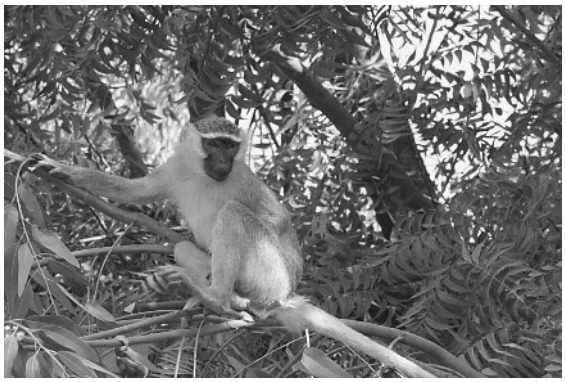

Figure 1.6. Tantalus monkey (*Chlorocebus tantalus*), Nigeria. (Image is kindly provided by Dr. Janette Wallis.) See color version page 1.

The oldest AGM lineage leading to modern green monkeys is estimated to have diverged 2.78 ± 0.29 Mya. The common ancestor of other AGMs is dated at 1.53 ± 0.15 Mya. Apparently, the closest relatives among the AGMs are the grivets and tantalus monkeys. The timing of the divergence of vervet and grivet/tantalus lineages is not well resolved in currently available estimates.[39]

Table 1.5. African Green Monkeys Subspecies Groups*

Aethiops	Pygerythrus	Tantalus
C. a. aethiops	*C. p. pygerythrus*	*C. t. tantalus*
C. a. hilgerii	*C. p. cloetei*	*C. t. budgetti*
C. a. ellenbecki	*C. p. helvescens*	*C. t. marrensis*
	C. p. ngamiensis	
	C. p. marjoriae	
	C. p. whytei	
	C. p. ruboviridis	
	C. p. johnstoni	
	C. p. rubellus	
	C. p. centralis	
	C. p. callidus	
	C. p. nesiotes	
	C. p. excubitor	
	C. p. aranarius	
	C. p. zavattarii	

Adapted from Grubb *et al.*[12]
*There is no subspecies of sabaeus monkey (*C. sabaeus*).

The AGMs, particularly grivets, vervets, and Caribbean sabaeus, are widely used in biomedical experiments.

1.3.1.2. Other Guenons

This remarkably diverse group of guenons includes multiple *Cercopithecus* species, patas monkeys (*Erythrocebus patas*) (Figure 1.7), two species of talapoin monkeys (*Miopithecus talapoin* and *M. ogouensis*), and Allen's swamp monkey (*Allenopithecus nigroviridis*).[19]

Two schemes are used by different authors for classifying cercopithecini guenons: "species–subspecies" and "superspecies–species–subspecies." There are many classifications of non-AGM guenons, and it is unlikely that a consensus will be reached in the foreseeable future. At the same time, it is generally accepted that the arboreal *Cercopithecus* can be divided into seven species/subspecies groups: Cephus, Mitis, Mona, Neglectus, Diana, Dryas, and Hamlini (Table 1.6, Figures 1.8 and 1.9). Phylogenetic analysis strongly supports the monophyletic origin for the Cephus–Mitis and Mona–Neglectus–Diana aggregated groups, Arboreal Clades I and II, respectively.[34] Two arboreal species, C. *hamlyni* and *C. dryas*, stand apart from all other arboreal guenons.

The terrestrial *Cercopithecus* guenons are represented by l'Hoesti species group, also named Preussi group (Table 1.6). One species in this group, the Preuss's monkey is divided into two subspecies: *C. preussi preussi* and *C. p. insularis.*[12] The l'Hoesti guenons are related

Figure 1.7. Male patas monkey (*Erythrocebus patas*), Nigeria. (Image is kindly provided by Dr. Janette Wallis.) See color version page 1.

Table 1.6. *Cercopithecus* Species Groups

Group	Species	Phylogenetic Clade[34]
Cephus	*C. cephus*	Arboreal Clade I (Cephus-Mitis)
	C. ascanius	
	C. petaurista	
	C. erythrotis	
	c. erythrogaster	
	C. sclateri	
Mitis	*C. mitis*	Arboreal Clade I (Cephus-Mitis)
	C. albogularis	
	C. nictitans	
	C. kandti	
	C. doggetti	
Mona	*C. mona*	Arboreal Clade II (Mona-Neglectus-Diana)
	C. campbelli	
	C. pogonias	
	C. wolfi	
	C. denti	
	C. lowei	
Neglectus	*C. neglectus*	Arboreal Clade II (Mona-Neglectus-Diana)
Diana	*C. diana*	Arboreal Clade II (Mona-Neglectus-Diana)
	C. roloway	
Hamlini	*C. hamlyni*	Uncertain
Dryas	*C. dryas*	Uncertain
l'Hoesti	*C. l'hoesti*	Terrestrial Clade I
	C. preussi	(l'Hoesti-Aethiops-Patas)
	C. solatus	

to AGMs, patas, and talapoin monkeys. However, phylogenetic analysis does not resolve relationships between these groups. According to phylogeny based on Y and X chromosome sequences, *C. l'hoesti* has a common origin with *E. patas* and *C. aethiops*, whereas mtDNA phylogeny suggests a monophyletic origin for *C. l'hoesti* and *M. talapoin*.[34,36]

Although there is a clear variation in the phenotype of patas monkeys from different locales, only one species (*Erythrocebus patas*) is currently recognized. However, the division of this species into subspecies—*E. p. patas*, *E. p. pyrrhonotus*, *E. p. baumstarki*, and *E. p. villiersi*—has been suggested.[12]

There are two forms of talapoin monkeys ranked either as species or subspecies: *M. talapoin*/*M. t. talapoin* (northern talapoin monkey) and *M. ogouensis*/*M. t. ogouensis* (southern talapoin monkey). They are separated by the Ogoôoué River.

Allen's swamp monkey (*Allenopithecus nigroviridis*) is the only species in the genus *Allenopithecus*.

1.3.2. Baboons and Allies

This group includes large, "strongly-built" monkeys commonly called baboons, geladas, mandrills, drills, and the much smaller, but related, mangabeys. All these monkeys live in Africa.

1.3.2.1. Baboons and Geladas

The baboon is a common name for the species included in genus *Papio* (Figure 1.10). They are distributed throughout most of sub-Saharan Africa. There are five major morphologically distinguishable forms of baboons: Hamadryas, Olive, Yellow, Guinea, and Chacma. In Groves' classification,[10] they are classified as species (Table 1.1). In some other classifications,

Figure 1.8. Juvenile red-eared guenon (*Cercopithecus erythrotis*), Limbe Zoo, Limbe, Cameroon. (Photo by Preston Marx.) See color version page 1.

Figure 1.10. Olive baboons (*Papio anubis*), Yankari Game Reserve, Nigeria. (Image is kindly provided by Dr. Janette Wallis.) See color version page 2.

these forms are ranked as subspecies. In this case, a single baboon species based on the priority rule is designated *P. hamadryas* (this name was introduced first). As a result, both binomial and trinomial nomenclatures are used. For example, *P. cynocephalus* and *P. hamadryas cynocephalus* (*P. h. cynocephalus*) are scientific names for Yellow baboon; *P. anubis* and *P. hamadryas anubis* for Olive baboon and so on. In this book, binomial nomenclature is used.

The variability of baboons is not limited to the major five species. Indeed, there are distinctive morphological variants of *P. cynocephalus* (Typical, Ibean, and Kinda Yellow baboons) and *P. ursinus* (Typical, Grey-footed, Transvaal, and Kalahari Chacma baboons). In addition, morphologically distinguishable natural hybrids of different baboon species and intraspecific forms are observed at boundary zones.

Most of the territory populated by baboons comprises a continuum in which neighboring baboon populations are not strictly isolated from each other. The transition from one species to another can be described as the geographical series.[16] The north to south series is: Anubis → Ibean Yellow → Typical Yellow → Gray-footed Chacma → Transvaal Chacma → Typical Chacma. The Anubis segment of the series overlaps with Typical Guinea, Kinda, and Kalahari Chacma in the west and Hamadryas in the east. In addition, there are three baboon enclaves. Two of these, Anubis Aïr and Anubis Tibesti, are located in the Sahara desert, the third enclave, Arabian Hamadryas, is located in the southwest corner of the Arabian Peninsula.[42]

The oldest extant *Papio* lineage is Chacma (estimated divergence time: 1.69–2.09 Mya). The Guinea lineage diverged next (1.23–1.51 Mya) followed by the

Figure 1.9. Juvenile greater spot-nosed monkey (*Cercopithecus nictitans*), Medical Research Station, Kumba, Cameroon. (Photo by Preston Marx.) See color version page 2.

Hamadryas lineage (577–660 Tya). The youngest extant baboon lineages are the Olive and Yellow (150–172 Tya).[21]

Geladas (*Theropithecus gelada*) are the closest relatives of the baboons. They are quite large monkeys, approximately the same size as baboons. The eye-catching morphological feature of geladas is an hourglass-shaped area of naked pink skin on the neck and chest. In the females, it is framed by "fringed" vesicles, which swell during estrus. The natural habitat of geladas is restricted to the highlands of Ethiopia (2,000–4,000 m altitude). There are two morphologically distinguishable forms, recognized as subspecies: western gelada (*T. gelada gelada*) and eastern gelada (*T. g. obscurus*).[12] However, there is no clear-cut boundary between these subspecies. In addition, there is a distinct form, so-called Wabe Shabelle gelada found in a "gelada enclave" located in Wabe Shebelle gorge. Wabe Shabelle geladas are not formally recognized as a subspecies.

It is estimated that the gelada lineage diverged from a common *Papio–Theropithecus* ancestor 3.5–4.0 Mya.[20]

The geladas do not breed well in captivity. In the 1960s–1980s, wild-caught geladas were widely used in biomedical experiments but this was discontinued. In contrast, baboons breed very well in captivity and are among the monkeys most commonly used in biomedical research.[38]

1.3.2.2. Mandrills and Drills

Mandrills (*Mandrillus sphinx*) and drills (*M. leucophaeus*) are the closest relatives of baboons. Male mandrills are the biggest, heaviest, and the most spectacular in appearance among all OWMs. Their face is fascinatingly colored in red, white, and blue; the bare skin in the perianal area and the penis are also brightly colored (Figure 1.11).

Mandrills are hunted for bush-meat, which is considered a delicacy, which poses a major danger to these animals.

The mandrill habitat is located in the West African coastal rainforest between the Sanaga and Zaire Rivers and expands up to 300 km inland. Mandrill populations separated by the Ogooué River are genetically distinct.[33]

The natural habitat of drills is located north of the mandrill range. It is noncontinuous, consisting of two parts: the continental (between the Cross and Sanaga Rivers) and Bioko Island (Equatorial Guinea). They are populated by different subspecies, the mainland drills (*M. leucophaeus leucophaeus*) (Figure 1.12) and Bioko drills (*M. l. poensis*).

Figure 1.11. Adult male mandrill (*Mandrillus sphinx*) (center), International Center for Medical Research, Franceville, Gabon. (Photo by Preston Marx.) See color version page 2.

Mandrills and drills are rarely used in biomedical research; although viruses harbored by wild mandrills, particularly retroviruses and herpesviruses are quite extensively studied.

Figure 1.12. Adult male drill (*Mandrillus leucophaeus*), Limbe Zoo, Limbe, Cameroon. (Photo by Preston Marx.) See color version page 2.

1.3.2.3. Mangabeys

There are two types of mangabeys, drill-mangabeys (*Cercocebus* spp.) and baboon-mangabeys (*Lophocebus* spp.). Drill-mangabeys and baboon-mangabeys are less related to each other than to mandrills/drills and baboons, respectively. However, the general "look" of all mangabeys is similar. They are much smaller than their "grand" relatives and do not have the eye-catching sexual dimorphic characteristics of baboons and mandrills. Mangabeys live in the rainforest in and around equatorial West and Central Africa.

A distinctive trait of drill-mangabeys is white upper eyelids—hence their nickname "eyelid monkeys" (Figures 1.13 and 1.14).

Groves' classification includes six *Cercocebus* species (Table 1.1). However, more than six morphologically distinguishable forms of drill-mangabeys are known and there is no consensus regarding ranking some of them as species or subspecies.[12] The most controversial is taxonomic identification of the white-naped mangabey. This mangabey is classified as a subspecies of sooty mangabey (*C. atys lunulatus*); at the same time, there are data supporting its closer relatedness to red-capped mangabey (*C. torquatus*).[12]

Taxonomy of baboon-mangabeys is less complicated than that of drill-mangabeys; however, a consensus in this field has also not been reached. Three species of baboon-mangabeys are distinguished in Groves' classification: gray-cheeked (*L. albigena*), black-crested (*L. aterrimus*), and Opdenbosch's (*L. opdenboschi*) mangabeys. The latter is considered as a subspecies of *L. aterrimus* by others.[12]

A new baboon-mangabey species, the highland mangabey (*L. kipunji* or *Rungwecebus kipunji*), has recently been described.[6] This is the first description of a new OWM species in 85 years. Very little is known about these extremely rare mangabeys which have been identified in two mountain sites in Tanzania. However, available data indicate that the difference between classical baboon-mangabeys and this species may be sufficient for placing highland mangabeys in a new genus. The name *Rungwecebus* has been suggested for this genus.[6]

Figure 1.13. Adult sooty mangabey (*Cercocebus atys*), Tulane National Primate Research Center, USA. (Image is kindly provided by Mrs. Robin Rodrigues.) See color version page 3.

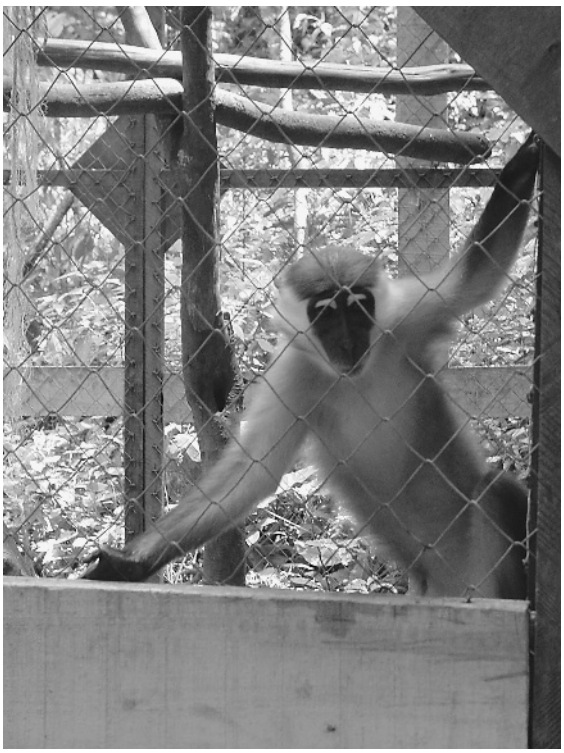

Figure 1.14. Adult red-capped mangabey (*Cercocebus torquatus*), Yaoundé, Cameroon. (Photo by Preston Marx.) See color version page 3.

1.3.3. Macaques

Macaques (*Macaca* spp.) live almost exclusively in Asia. The only exception among 21 macaque species is a barbary macaque (*M. sylvanus*) whose natural habitat is located in the western corner of North Africa. However, the macaque lineage originated in Africa—hence the inclusion of the macaques in the Papionini tribe. A common ancestor of macaques, baboons, and geladas lived in Africa approximately 8.6–10.9 Mya.[24] The migration of common ancestors of extant Asian macaque species to Eurasia is dated at 6–5.5 Mya. All ancient European macaque species became extinct. The same also happened to all African ancient macaques, except the lineage leading to *M. sylvanus*.

Asian macaque species can be divided into four groups: Mulatta, Nemestrina, Fascicularis, and Sinica (Table 1.7, Figures 1.15–1.17). The prototype species for three of these groups, *M. mulatta*, *M. fascicularis*, *and M. nemestrina*, are the monkeys most commonly used in biomedical research. Importantly, susceptibility of different macaque species to different medically important viruses varies significantly.

Rhesus monkey (*M. mulatta*), undoubtedly, is the best-studied primate species, next to *Homo sapiens* (Figure 1.15). Suffice it to mention that *M. mulatta* is the only monkey species for which virtually the complete genome sequence is known.[25] Rhesus monkeys originating from different regions of Asia are quite distinct. Seven *M. mulatta* subspecies have been formally recognized (Table 1.8).[4] Most of the rhesus monkeys used in biomedical experiments before the 1980s were either imported from India or originated from breeding colonies, whose founders were Indian-origin rhesus macaques. The situation changed when India introduced a ban on the export of monkeys. Currently, most imported rhesus macaques available for biomedical experiments are of Chinese origin. The Chinese or Indian origin of rhesus monkeys can be validated by genetic analysis.[18,28,31]

Figure 1.15. Adult female and infant rhesus monkeys (*Macaca mulatta*), Swoyambhu Temple, Kathmandu, Nepal. (Image is kindly provided by Prof. Randall C. Kyes.) See color version page 3.

Table 1.7. Macaque Species Groups

Mulatta	Fascicularis	Sinica	Nemestrina	Sylvanus
M. mulatta	*M. fascicularis*	*M. sinica*	*M. nemestrina*	*M. sylvanus*
M. cyclopis	*M. arctoides*	*M. radiata*	*M. silenus*	
M. fuscata		*M. assamensis*	*M. nigra*	
		M. thibetana	*M. nigrescens*	
			M. hecki	
			M. tonkeana	
			M. maura	
			M. ochreata	
			M. leonina	
			M. pagensis	
			M. siberu	

Adapted from Groves.[10]

Figure 1.16. Adult male cynomolgus macaque (*Macaca fascicularis*), Tinjil Island, Indonesia. (Image is kindly provided by Prof. Randall C. Kyes.) See color version page 3.

Cynomolgus macaques (*M. fascicularis*), also named crab-eating or long-tailed macaques, are second to rhesus monkeys in their significance to biomedical research (Figure 1.16).

Figure 1.17. Juvenile male Celebes black macaque (*Macacanigra*), Tangkoko Nature Reserve, North Sulawesi, Indonesia. (Image is kindly provided by Prof. Randall C. Kyes.) See color version page 4.

The largest captive monkey colony in the world (Nafovanny, Vietnam) houses about 30,000 cynomolgus macaques. Cynomolgus macaques are smaller than rhesus monkeys and they breed in captivity year around (rhesus monkeys are seasonal breeders). Genetically, rhesus and cynomolgus macaques are closely related; for instance, they share many single nucleotide polymorphisms (SNPs).[31] At the same time, cynomolgus macaques originating from different geographical regions are sufficiently distinct to be classified as subspecies (Table 1.8).[4,29]

1.3.4. Colobines

Colobines (*Colobinae* spp.) live both in Africa and Asia. These monkeys are strict "vegetarians"—hence their colloquial name "leaf-eaters." In addition, different colobines are known under different common names: colobuse, langur, surili, lutung. There are 10 genera of colobines: *Colobus* (5 species), *Presbitis* (11 species), *Trachypithecus* (17 species), *Semnopithecus* (7 species), *Nasalis* (1 species), *Pygathrix* (3 species), *Pilicolobus* (9 species), *Procolobus* (1 species), *Simias* (1 species), and *Rhinipothecus* (4 species).

Colobus are medium-sized monkeys with small heads, disproportionably large bodies, and long limbs. They live in forested areas of Africa, from the west to east coast. Their body composition and long "acrobatic balancer" tails are well suited for the arboreal "lifestyle." Colobus monkeys are also well adapted for processing "hard-to-digest" plant food. They have powerful jaw muscles, large salivary glands, and very large multi-chambered stomachs, containing microorganisms that ferment cellulose. A distinctive feature of colobus monkeys is the lack of a thumb—hence their name—a derivative of the Greek *colobe* for cripple. Colobus species are grouped into three genera: *Colobus*, *Pilicolobus*, and *Procolobus.* It is estimated that colobuses diverged from other African monkeys 14.7 ± 1.5 Mya.[30]

It is very difficult to breed colobus monkeys in captivity and they are not used as experimental animals.

Asian colobines are a more diverse group than the colobus.[2] It is estimated that they diverged from their African "relatives" 10.8 ± 1 Mya.[30]

Gray langurs (*Semnopithecus* spp.) are the largest among Asian colobines. They inhabit many regions of the Indian subcontinent including urban areas (Figure 1.18).

Table 1.8. Subspecies of *M. mulatta* and *M. fascicularis*

Species/Subspecies	Common Name	Geographical Distribution
Macaca mulatta	**Rhesus monkey**	
M. mulatta mulatta	Indian rhesus monkey	E Afghanistan, Bangladesh, Bhutan, N peninsular India, Nepal, N Pakistan
M. mulatta lasiota	West Chinese rhesus monkey	China (SE Qinghai, W Sichuan, NE Yunnan)
M. mulatta littoralis	South Chinese rhesus monkey	China (Fujian, Guangdong, Far E Guangxi)
M. mulatta sanctijohannis	Insular Chinese rhesus monkey	China (Hainan, Islands around Hong Kong, Wanshan Isl)
M. mulatta siamica	Indochinese rhesus monkey	Burma, China (Anhui, NW Guangxi, Guizhou, Hubei, Hunan, C&E Sichuan, W&S and Central Yunnan), Laos, N Thailand, N Vietnam
M. mulatta tcheliensis	North Chinese rhesus monkey	China (Hebei, N Henan, and S Shanxi)
M. mulatta vestita	Tibetan rhesus monkey	China (SE Tibet and NW Yunnan)
Macaca fascicularis	**Cynomolgus macaque***	
M. fascicularis atriceps	Dark-crowned long-tailed macaque	SE Thailand (Khram Yai Island)
M. fascicularis aurea	Burmese long-tailed macaque	S Bangladesh, S Burma, W and Central Thailand
M. fascicularis condorensis	Con Son long-tailed macaque	Vietnam (Con Son)
M. fascicularis fusca	Simeulue long-tailed macaque	Indonesia (Simeulue Isl)
M. fascicularis karimondjawae	Karimunjawa long-tailed macaque	Indonesia (Karimunjawa Isl)
M. fascicularis lasiae	Lasia long-tailed macaque	Indonesia (Lasia Isl)
M. fascicularis philippinensis	Philippine long-tailed macaque	Philippines (Balabac, Culion, Leyte, Luzon, NE Mindanao, Mindoro, Palawan, Samar)
M. fascicularis tua	Maratua long-tailed macaque	Indonesia (Maratua Isl)
M. fascicularis umbrosa	Nicobar long-tailed macaque	India (Katchall Isl, Little Nicobar Isl)

Adapted from Brandon-Jones *et al*.[4]
*Synonymous names: long-tailed or crab-eating macaque.

In contrast to most colobines, gray langurs are mainly terrestrial animals. The gray langur is a diverse group. However, there is no consensus regarding formal classification of various forms. Groves' classification distinguishes 76 species of gray langurs (Table 1.2). Others recognize 14 *Semnopithecus* subspecies combined in 3 species (*S. entellus*, *S. jornii*, and *S. vetulus*); particularly, numerous are the *S. entellus* subspecies.[4] The classification of the purple-faced langur (*S. vetulus*) and Nilgiri langur (*S. jornii*) as *Semnopithecus* species is disputable. In Groves' classification, they are included in the *Trachypithecus* genus. However, this placement is not supported by molecular taxonomic data.[17]

Surilis (*Presbytis* spp.) are arboreal colobine monkeys living in the southern part of the Malay Peninsula, on Sumatra, Java, Borneo, and adjacent small islands. Some *Presbytis* species are called surilis, others are called langurs (Table 1.2). Surilis and surili-langurs

Figure 1.18. Adult female Northern Plains gray langur (*Semnopithecus entellus*), Jodhpur, India. (Image is kindly provided by Prof. Randall C. Kyes.) See color version page 4.

have a characteristic hair tuft on their heads—hence their nickname "capped langur." Groves' classification includes 11 *Presbytis* species. However, the number of distinguishable forms in this genus is much greater; 29 surili taxa ranked as species or subspecies have been suggested.[4]

Lutungs are colobine monkeys belonging to the *Trachypithecus* genus. This genus also includes some langurs and so-called leaf monkeys (Table 1.2). Seventeen *Trachypithecus* species are included in Groves's classification. The natural habitat of these species is "disjunctive"; that is there are two widely separated areas populated by the trachypithecines: southwest of India and Sri Lanka and northeast of India and Southeast Asia. The inclusion of some species into the *Trachypithecus* genus has been challenged by molecular taxonomic data, which indicate that southwest Indian and Sri Lankan langurs (Nilgiri and purple faced) are more related to the gray langurs (*Semnopithecus*) than to other *Trachypithecus* species.[17]

The "odd-nosed" group of species includes *Nasalis*, *Simias*, *Pygathrix*, and *Rhinipithecus* species. The group is diverse, but as its name implies, all these monkeys have characteristic morphological traits in the facial area. The most distinctive in this respect is the long-nosed or proboscis monkey (*Nasalis larvatus*). Males of this species have a very large protruding nose. Long-nosed monkeys live mostly in trees in swamps of the costal areas of Borneo. They swim well and can walk upright. The latter characteristic is exceptional for OWMs.

The closest relatives of the long-nosed monkeys are pig-tailed langurs or simakobu monkeys (*Simias concolor*),[30,41] a species endemic on the Mentawai Islands, Indonesia. These monkeys, with a characteristic upwards pointed nose, are the most endangered species among Asian NHPs.

1.4. APES

1.4.1. Lesser Apes (Gibbons and Siamangs)

Lesser apes inhabit rainforests throughout Southeast Asia, from eastern India to Vietnam, southern China, and Indonesia. They are divided into four groups ranked as genera in most classifications: *Hylobates*, *Bunopithecus*, *Nomascus*, and *Symphalangus*. A diploid number of chromosomes is characteristic of each genus: 44, 38, 52, and 50 for *Hylobates, Bunopithecus*, *Nomascus*, and *Symphalangus*, respectively. Molecular phylogeny based on the analysis of mtDNA sequences also supports this classification.[32]

Most of the gibbon species belong to the *Hylobates* genus (Table 1.3). There are many gibbon subspecies (Table 1.9). Hylobates gibbons are commonly named the Lar group, after the type species *Hylobates lar*.

The Lar gibbons inhabit central and southern parts of Indochina, including the Malay Peninsula, Sumatra, Borneo, and western Java. Within this habitat, *H. lar* and *H. moloch* (Figure 1.19) are the northernmost and southernmost species. Accurate species identification of Lar gibbons is possible based on the D-loop mitochondrial DNA sequence.[40]

Crested gibbons (*Nomascus* spp.) inhabit eastern Indochina and southern China. Crested gibbons are also named the Concolor group, after a type species *Nomascus concolor*. The natural boundary separating the Lar and Concolor gibbons is the Mekong River. There are many subspecies of crested gibbons.

The *Bunopithecus* genus includes only one species, hoolock (*B. hoolock*). Hoolock gibbons inhabit an area northeast of the continental gibbon habitat, the territory between the Brahmaputra and Salween rivers. There are two subspecies of the hoolocks, western (*B. hoolock hoolock*) and eastern (*B. hoolock leucopenedys*).

The *Symphalangus* genus also includes only one species, siamang (*Symphalangus syndactilist*). Siamangs inhabit the southern part of the Malay Peninsula and the mountains of the Indian Ocean coast of Sumatra.

Table 1.9. Ape Subspecies

Species/Subspecies	Common Name
Hylobates agilis	**Agile gibbon**
Hylobates agilis agilis	Mountain agile gibbon
Hylobates agilis albibarbis	Bornean agile gibbon
Hylobates agilis unko	Lowland agile gibbon
Hylobates lar	**Lar gibbon or white-handed gibbon**
H. lar lar	Malayan white-handed gibbon
H. lar carpenteri	Carpenter's white-handed gibbon
H. lar entelloides	Central white-handed gibbon
H. lar vestitus	Sumatran white-handed gibbon
H. lar yunnanensis	Yunnan white-handed gibbon
Hylobates moloch	**Javan silvery gibbon**
H. moloch moloch	West Javan silvery gibbon
H. moloch pongoalsoni	Central Javan silvery gibbon
Hylobates muelleri	**Müller's Bornean gibbon**
H. muelleri muelleri	Müller's gray gibbon
H. muelleri abbotti	Abbott's gray gibbon
H. muelleri funerus	Nothern gray gibbon
Nomascus concolor	**Black crested gibbon**
N. concolor concolor	Tonkin black crested gibbon
N. concolor furvogaster	West Yunnan black crested gibbon
N. concolor jingdongensis	Central Yunnan black crested gibbon
N. concolor lu	Laotian black crested gibbon
Nomascus leucogenys	**Northern white-cheeked gibbon**
N. leucogenys leucogenys	Northern white-cheeked gibbon*
N. leucogenys siki	Southern white-cheeked gibbon*
Bunopithecus hoolock	**Hoolock gibbon**
B. hoolock hoolock	Western hoolock gibbon
B. hoolock leuconedys	Eastern hoolock gibbon
Symphalangus syndactylus	**Siamangs**
S. syndactylus syndactylus	Sumatran siamang
S. syndactylus continentis	Malayan siamang
Pongo pygmaeus	**Bornean orangutan**
P. pygmaeus pygmaeus	Western Bornean orangutan
P. pygmaeus wurmbii	Southern Bornean orangutan
Gorilla gorilla	**Western gorilla**
G. gorilla gorilla	Western lowland gorilla
G. gorilla diehli	Cross River gorilla
Gorilla beringei	**Eastern gorilla**
G. beringei beringei	Mountain gorilla
G. beringei graueri	Grauer's gorilla
P. troglodytes	**Common chimpanzee**
P. troglodytes troglodytes	Common or robust chimpanzee
P. troglodytes vellerosus	Nigeria chimpanzee
P. troglodytes schweinfurthii	Eastern chimpanzee
P. troglodytes verus	Western chimpanzee

Adapted from Brandon-Jones *et al.*[4] and Grubb *et al.*[12]
*Classified as species by Groves.[10]

Figure 1.19. Adult female and infant Javan silvery gibbon (*Hylobates moloch*), Primate Research Center at Bogor Agricultural University, Bogor, Indonesia. (Image is kindly provided by Prof. Randall C. Kyes.) See color version page 4.

Figure 1.20. Adult common chimpanzee (*Pan troglodytes*), Bakumba, Gabon. (Photo by Preston Marx.) See color version page 4.

It is estimated that the common ancestor of all four extant gibbon lineages diverged from the common ancestor of the other apes 16–23 Mya. Apparently, the *Hylobates* lineage is the youngest, whereas the *Bunopithecus* lineage is the oldest.[32]

Gibbons are susceptible to human viruses and may carry oncogenic retroviruses.

1.4.2. Great Apes (Chimpanzees, Gorillas, and Orangutans)

Chimpanzees (genus *Pan*) undoubtedly are our closest relatives. The natural habitat of these remarkably intelligent animals extends from West to Equatorial Africa. Most chimpanzees, both wild and captive, belong to the common chimpanzee species (*P. troglodytes*) (Figure 1.20). Common chimpanzees are also called robust chimpanzees, but this name is rarely used.

The second chimpanzee species, the pygmy chimpanzee, also named gracile chimpanzee (*P. paniscus*), has a much more restricted range.

Within the *P. troglodytes* species, there are several morphologically and geographically distinguishable forms classified as subspecies: central chimpanzee (*P. t. troglodytes*), Nigeria chimpanzee (*P. t. vellerosus*), eastern chimpanzee (*P. t. schweinfurthii*), and western chimpanzee (*P. t. verus*; Table 1.9).[12,23] It is worth mentioning that the classification of common chimpanzees into subspecies has been challenged by the proponents of molecular taxonomy. The extent of genetic diversity in chimpanzees belonging to different subspecies is comparable to that in various human populations.[8] Phylogenetic analysis of mitochondrial DNA sequences supports the division of common chimpanzees into two groups: western (*P. t. verus*) and central-eastern (*P. t. troglodytes*/*P. t. schweinfurthii*).[13] Analysis of another set of chimpanzee mitochondrial DNA sequences indicates that the major phylogenetic break between common chimpanzee lineages separates chimps along the Sanaga River in Cameroon.[9]

The captive chimpanzee population in the United States includes approximately 1,000 animals, most of which were born in captivity. These chimpanzees originated predominantly from *P. t. verus*, with 95% of the population founders belonging to this subspecies.[7] Many thousands of common chimpanzees were used in biomedical experiments in the United States from the 1950s to the 1990s. In 2007, the NIH announced a permanent ban on the breeding of chimpanzees in US government-funded facilities. Although the scale of biomedical experiments using common chimpanzees is steadily decreasing, it is unlikely that use of chimpanzee models of human diseases will be completely terminated. Unfortunately, there is no alternative to the chimpanzee model for preclinical testing of the efficacy of candidate vaccines extremely important for public health, for instance, the development of a vaccine against hepatitis C.

Figure 1.21. Adult male lowland gorilla, International Center for Medical Research, Franceville, Gabon. (Photo by Preston Marx.) See color version page 5.

Figure 1.22. Adult male Bornean orangutan (*Pongo pygmaeus*), Woodland Park Zoo, Seattle, Washington, USA. (Image is kindly provided by Prof. Randall C. Kyes.) See color version page 5.

Gorillas (genus *Gorilla*) are the largest and the heaviest NHPs (height up to 180 cm, weight 90–180 kg) (Figure 1.21).

Genetically, gorillas are the closest relatives to humans, after chimpanzees. Unfortunately, gorillas are endangered species. The size of the natural gorilla population has decreased dramatically over the last 20 years, partly due to human activities and partly as a result of devastating outbreaks of Ebola hemorrhagic fever in wild gorilla populations.[1]

Taxonomically, gorillas are divided into two species: western gorilla (*G. gorilla*) and eastern gorilla (*G. beringei*). Within each of these species, there are distinguishable forms classified as subspecies in the latest classification (Table 1.9).[12] The western gorilla species is divided into western lowland gorilla (*G. g. gorilla*) and Cross River gorilla (*G. g. diehli*). Two subspecies are also distinguished within eastern gorilla species: mountain gorilla (*G. b. beringei*) also known as *G. b. bwindi* and Grauer's gorilla (*G. b. graueri*).

Asian great apes, orangutans (*Pongo* spp.), are large (115–160 cm, 40–100 kg), mostly arboreal, animals living in the tropical rainforests on two islands, Borneo (Kalimantan) and Sumatra (Figure 1.22). Orangutan males are much larger than females. Their lifestyle is solitary. Orangutans reproduce slowly and their life span is quite long (the longest recorded in captive orangutans is 57 years). Orangutans' diet is mainly vegetarian; however, occasionally they eat bird eggs and may prey on small vertebrate animals. Bornean and Sumatran orangutans are recognized as separate species, *P. pygmaeus* and *P. abelii*, respectively (Table 1.3). Bornean orangutans are significantly larger than Sumatran orangutans. There are at least two distinguishable forms of Bornean orangutans. In some classifications, they are ranked as subspecies: *P. p. pygmaeus* (western Bornean orangutan) and *P. p. wurmblii* (eastern Bornean orangutan; Table 1.9).[4] Orangutans are also endangered species and they are not bred in captivity for research purposes. However, they adapt well to zoo conditions and a number of orangutans have been born in captivity. Orangutans in zoos invariably attract attention for their eye-catching reddish color, size (captive orangutans are overweight, sometimes exceeding 200 kg in weight), and "intellectual" facial expressions.

1.5. NEW WORLD MONKEYS

According to Groves' classification, there are 121 extant species of the NWMs divided into four families and seven subfamilies[10] (Figure 1.3, Table 1.4). These monkeys live in continental Central and South America as well as Trinidad and Tobago. The characteristic morphological feature of NWMs is a flat nose with circular side-facing nostrils spaced far apart—hence their names "flat-nosed" or "broad-nosed." The other characteristic

traits are a distinctive dental formula, absence of buttock pads, and cheek pouches. All NWMs have long tails; in some species the tail serves as an additional "arm," called prehensile tails. In general, NWMs are smaller than OWMs; although howlers and muriquis are quite large. Virtually all NWMs are arboreal species.

The common ancestor of NWMs, presumably, lived in Africa. The divergence of the NWM lineage from the other primates occurred approximately 35 Mya.[22] How common ancestors of NWMs ("flat-nosed Eve and Adam") arrived in South America is a matter of speculation. The "floating vegetation raft" hypothesis appears to be a likely scenario. According to molecular phylogenetic reconstructions, the divergence of NWM species started approximately 25 Mya. The most ancient is the lineage leading to the Pitheciidae family. A common ancestor of three other NWM families (Cebidae, Atelidae, and Aotidae) is estimated to have lived 23 Mya. The diversification of NWM taxa was particularly extensive during the Miocene 15–10 Mya.[22,27] The "youngest" NWM genera are *Cacajao* and *Chiropotes*; their common ancestor is dated at approximately 7 Mya. Molecular phylogenetic analysis separates extant NWMs into four groups that are not equidistant and not fully concordant with the families and subfamilies in the zoological classification.[22]

1.5.1. Marmosets and Tamarins

Marmosets and tamarins are generally smaller than other NWMs (body length without tail 17–40 cm). Their distinguishing morphological traits are the presence of claws instead of nails on all digits except the big toe, nonopposable thumbs, and characteristic dental makeup. Both marmosets and tamarins are arboreal, omnivorous monkeys.

All but one marmoset species belong to the *Callithrix* genus. The exception is Goeldi's marmoset (*Callimico goeldii*) which is the only marmoset species in the *Callimico* genus. The marmosets are usually born as twins. Interestingly, all tissues, including ovaries and testicles, in the marmoset twins (*Callithrix kuhlii*) are chimeric. As a consequence, marmosets can transmit sibling gametes to the offspring, a unique situation among primates in which the biological parent cannot be identified by genetic analysis.[26]

Common marmosets (*Callithrix jacchus*) adapt and breed well in captivity, assuming proper husbandry (Figure 1.23). That is why these monkeys are widely used in biomedical research. A number of marmoset viruses are known, most notably various herpesviruses.

Figure 1.23. Common marmosets (*Callithrix jacchus*). (Image is kindly provided by Prof. Júlio César Bicca-Marques.) See color version page 5.

Most tamarins belong to the *Saquinus* genus (17 species). Less numerous are lion tamarins species belong to the *Leontopithecus* genus (4 species). Characteristic morphological traits of tamarins are mustache-like facial hairs and long lower canine teeth. On average, tamarins are larger than marmosets. Although tamarins can be adapted to captivity, their maintenance is more demanding than that of marmosets. For this reason, tamarins are much less used in biomedical research; although sometimes virological experiments are performed in captive tamarins (Figure 1.24).

1.5.2. Capuchins, Owl, and Squirrel Monkeys

Capuchins (*Cebus* spp.) are so named because their coloration resembles cowls of Franciscan Capuchins, an order of monks. Capuchins are relatively small (30–55 cm without tail, weight 1–4 kg), but very intelligent monkeys. They are frequently kept as pets and perform as "organ grinder" monkeys. More importantly, they can be trained to assist quadriplegics. Capuchins are rarely used in virological research (Figure 1.25).

Squirrel monkeys (*Saimiri* spp.), as their name suggests, are small, squirrel-size animals (25–35 cm, 0.75–1 kg) (Figure 1.26).

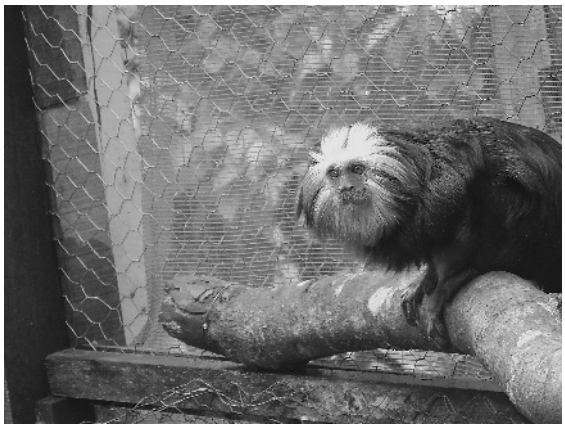

Figure 1.24. Golden-headed lion tamarin (*Leontopithecus chrysomelas*). (Image is kindly provided by Prof. Júlio César Bicca-Marques.) See color version page 5.

Figure 1.26. Common squirrel monkey (*Saimiri sciureus*). (Image is kindly provided by Prof. Júlio César Bicca-Marques.) See color version page 6.

Interestingly, squirrel monkey brain mass relative to body weight is the largest among all primates. However, this is not translated into remarkable intelligence. Common squirrel monkeys (*S. sciureus*) are widely used in virological research.

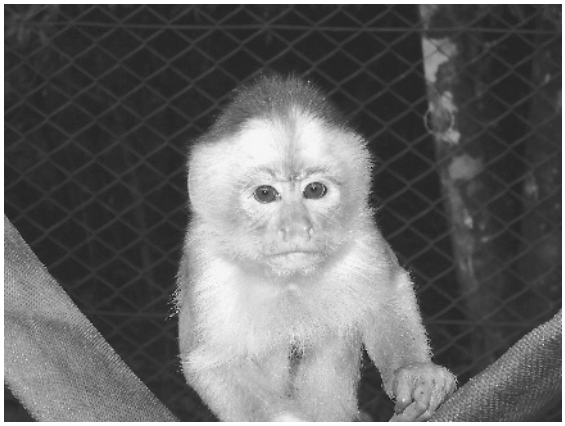

Figure 1.25. White-fronted capuchin (*Cebus albifrons*). (Image is kindly provided by Prof. Júlio César Bicca-Marques.) See color version page 6.

Owl monkeys, also named night monkeys, have small external ears—hence the name of the genus *Aotus*—which literally means "earless" (Figure 1.27).

As their common name suggests, these animals are nocturnal; that is, they are active at night. An interesting behavioral characteristic of owl monkeys is their remarkably wide repertoire of vocal sounds. Their vision is well adapted to low light conditions so they can move and feed efficiently at night. Quite unusually for NHPs, owl monkeys in natural conditions are monogamous. The three-striped night monkey (*Aotus trivirgatus*) has been used in biomedical research, usually under the name "owl monkey."

1.5.3. Howlers, Muriquis, Spider, and Woolly Monkeys

All these monkeys belong to the family Pitheciidae. They are relatively large as compared to other NWMs. The largest in terms of body size are howlers (55–90 cm without tail) (Figures 1.28 and 1.29). Howlers can produce a very loud barking sound figuratively named "the howl"—hence their name. Unlike most of the NWM species, howlers are "phlegmatic," they rest most of the time in trees. Although fights between howlers may happen, in general, they are very tranquil animals. Exceptionally for NWMs howlers have trichromatic color vision.

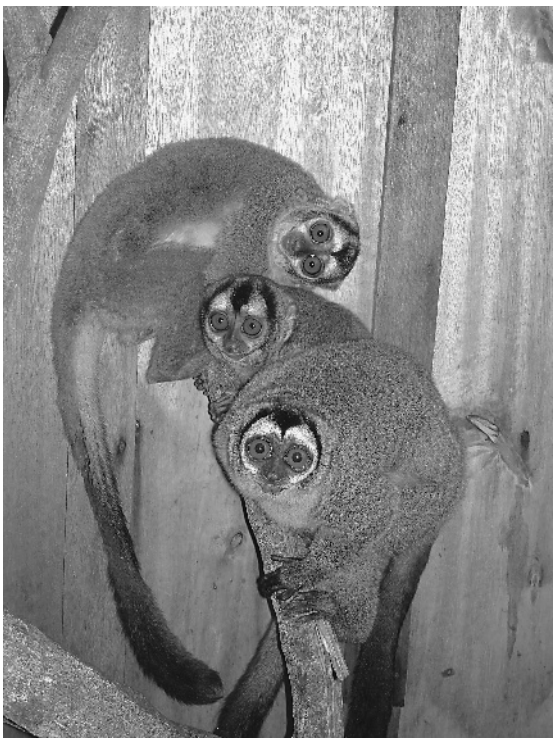

Figure 1.27. Black-headed owl monkey, also called night monkey (*Aotus nigriceps*). (Image is kindly provided by Prof. Júlio César Bicca-Marques.) See color version page 6.

Figure 1.28. Brown howler monkey (*Alouatta guariba*). (Image is kindly provided by Prof. Júlio César Bicca-Marques.) See color version page 6.

Figure 1.29. Black howler (*Alouatta pigra*), Balancan, Tabasco, Mexico. (Image is kindly provided by Dr. Juan Carlos Serio Silva.) See color version page 7.

Spider monkeys (*Ateles* spp.) are so named for their disproportionately long limbs (Figure 1.30). Spider monkeys are quite large (38–64 cm without tail, weight 6–10 kg) with a long (up to 90 cm) prehensile tail. Their face, with nostrils spaced very far apart, is quite distinctive. Another distinctive and unusual morphological trait of the female spider monkeys is an elongated clitoris

Figure 1.30. Spider monkeys (*Ateles geoffroyi vellerosus*), Balancan, Tabasco, Mexico. (Image is kindly provided by Dr. Juan Carlos Serio Silva.) See color version page 7.

Figure 1.31. Gray woolly monkey (*Lagothrix cana*). (Image is kindly provided by Prof. Júlio César Bicca-Marques.) See color version page 7.

Figure 1.32. Adult male Northern muriqui (*Brachyteles hypoxanthus*), Caratinga Biological Station, Minas Gerais, Brazil. (Image is kindly provided by Dr. Jean P. Boubli.) See color version page 7.

resembling a penis. Spider monkeys are very intelligent animals, perhaps the most intelligent among NWMs.

Spider monkeys are rarely used in biomedical research. However, several herpesviruses harbored by these monkeys have been isolated and studied.

Woolly monkeys are, on average, larger than spider monkeys and more uniform in size (51–69 cm without tail) (Figure 1.31). Woolly monkeys are divided into two genera, the "classical" genus *Lagothrix* with four species and the recently introduced genus *Oreonax*. The latter includes only one species, the yellow-tailed woolly monkey (*O. flavicauda*). Woolly monkeys are rarely used in biomedical research. However, it happens that this name is better known to virologists than the names of most NWMs. This is because the only known primate acutely transforming retrovirus, the simian sarcoma virus 1 (SSV-1), has been isolated from woolly monkeys.

Two rare species of NWM, the muriquis (*Brachyteles* spp.), share characteristics of both spider and woolly monkeys—hence their second name woolly spider monkeys. The word "muriqui" in Tupi, an Amerindian language, means "very large monkey." Indeed, these monkeys, although shorter than the howlers (46–63 cm) are much heavier (12–15 kg versus 4–10 kg). Muriquis are an endangered species and are not used in biomedical research (see Figure 1.32).

1.5.4. Titis, Sakis, and Uakaris

Titis (*Callicebus* spp.) are NWM-related species (28 species) with long soft fur and long furry tails that are not prehensile (Figure 1.33). The size and coloring of titis significantly varies (24–61 cm, weight 0.5–2 kg). Titis are very good jumpers, being referred to as "jumping

Figure 1.33. Collared titi (*Callicebus torquatus*), Sustainable Development Reserve Amanã, Lake Amanã, Amazonas, Brazil. (Image is kindly provided by Marcela Alvares Oliviera.) See color version page 8.

Figure 1.34. Rio Tapajos saki (*Pithecia irrorata*), Belo Horizonte Zoo, Minas Gerai, Brazil. (Image is kindly provided by Eduardo Franco.) See color version page 8.

monkeys" in German. Titis are known for their life-long monogamous mating. Titis are not used in biomedical research.

Sakis (*Pithecia* spp.) (Figure 1.34) and bearded sakis (*Chiropotes* spp.) are related species which have characteristic head hairs resembling a hood or a cap. These monkeys are extremely well adapted to life on trees. Similar to titis, sakis are monogamous. Sakis are not used in biomedical research.

Uakaris (*Cacajao* spp.) are medium-sized monkeys (30–50 cm, weight 2.5–3.5 kg) living in the Amazon Basin. Their common name, as well as the name of the genus, is believed to originate from indigenous Amerindian languages, although the exact meaning of these words is not known. The distinctive morphological features of these NWMs are a hairless, "skull-like" face, very little subcutaneous fat and an unusually short tail (Figure 1.35). Uakaris adapt poorly to captivity and are not used in biomedical research.

1.6. CONCLUDING REMARKS

It should be emphasized that taxonomic and biogeographical information presented in this chapter are adapted for the novice in Primatology. Those interested in deeper knowledge will find relevant information in the experts' reviews.[4,10,12] A large collection of NHP images is available at Primate Info Net (http://pin.primate.wisc.edu/av/images/index.html).

Figure 1.35. Neblina black-headed uakari (*Cacajao melanocephalus*), the Pico da Neblina National Park, Brazil; classified also as a separate species (*C. hosomi*). (Image is kindly provided by Dr. Jean P. Boubli.). See color version page 8.

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