

Introduction

Over the course of the past two centuries, there have been a number of publications dedicated to reviews of the Order Primates. The most noteworthy of these were Forbes's two-volume series of 1896–1897, the monumental work of D. G. Elliot in three volumes in 1913, and the greatest of them all, the eight volume series of monographs by W. C. O. Hill, published from 1953 to 1974, but sadly never completed. More recently, there have been individual volumes that have provided overviews of the primates, of which J. R. Napier and P. H. Napier's *A Handbook of Living Primates* of 1967 was the most noteworthy, and inspired many of us in the early days of our careers.

Beginning in 1980, Anthony Rylands and I, both of us working on the monkeys of the Atlantic forest region of Brazil at the time, decided we needed a modern volume covering all primates, lavishly illustrated with photos and drawings and covering all aspects of the taxonomy, distribution, behavior, ecology, and conservation of these animals. A year later, in 1981, Rylands was contacted by Stephen Nash, a student of Natural History Illustration at the Royal College of Art, London, who had a passion for primates. Nash had just completed a painting “Darwin and Friends”—Charles Darwin surrounded by representative prosimians, monkeys, and apes—that was commissioned by Professor Robert D. Martin, then at the Anthropology Department of University College London. With a callitrichid field guide in mind, Nash had produced a series of remarkable sketches of marmosets and tamarins. Martin introduced him to Rylands, who in turn contacted me, and I found him a job with the World Wildlife Fund – US, where I was Director of the Primate Program, and we were off and running.

Although we have produced a great variety of primate publications and educational material over the years, we never did get around to doing a comprehensive volume on the primates—in large part because we were engaged in so many different primate conservation and research activities under the auspices of the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC)'s Primate Specialist Group (PSG), which I have chaired since 1977 and for which Anthony Rylands has been Deputy Chair since 1996. In the interim, in 1996 Noel Rowe produced an excellent book on the Order Primates, entitled *The Pictorial Guide to the Living Primates*, and later, in 2010, converted it into a website called “All the World's Primates.”

In 2004, Matthew Richardson, a Canadian writer fascinated with primates, contacted us with the idea of doing an encyclopedia of primates. We encouraged him and provided modest support to enable him to move this project forward. But our good intentions to produce such an ambitious volume continued to be sidetracked by our many other responsibilities. As it turned out Matt Richardson helped to lay the groundwork for this volume, and he is one of the principal contributing editors.

When Josep del Hoyo contacted me in 2005 to discuss a mammal series to parallel his epic, 16-volume *Handbook of the Birds of the World*, I was intrigued with the possibility, and helped to find the core funding that would enable Lynx to jumpstart the new series. But always in the back of my mind was that this series would provide an impetus to us and a deadline to finally produce the comprehensive primate volume, and, as a bonus, to situate it within the broader context of the mammals as a whole.

With Don Wilson and myself as Chief Editors, Lynx produced the first two volumes on the carnivores and the ungulates, and here we are, at long last, with “Volume 3: Primates.” The non-human primates are our closest living relatives, with some, the great apes, sharing more than 98% of our DNA. What is more, primates are a prominent and essential component of the fauna of a very large part of the world's tropical forests. Field studies that provide us with an understanding of their diversity, their habits and habitats, and their role in the maintenance and ecological dynamics of tropical forest ecosystems began in earnest in the 1970s. However, it is only today that we are beginning to understand the importance of primates as seed dispersers and pollinators, as leaf eaters, predators, and prey in the extraordinarily rich and complex environments in which

they live. Early studies provided us with a rudimentary understanding of the diverse niches they occupy and insights into the adaptive patterns replicated by different species in Asia, Africa, and the Neotropics. In recent years, and especially in the last 15–20 years, we have made enormous progress in our understanding of the diversity of this mammalian Order. Back in the 1980s, there was a general consensus that there were in total about 160 species of primates worldwide. The most recent compilation by the IUCN/SSC Primate Specialist Group, which is reflected in this book, recognizes 16 families, 77 genera, 479 species, and 681 taxa of primates, a dramatic increase that reflects both our rapidly growing understanding as well as our surprising ignorance of this important group of animals.

Primates can be divided into the prosimians, monkeys, and apes. The prosimians include the African galagos and bushbabies of the family Galagidae (five genera, 18 species, and 34 taxa), the African and Asian lorises and pottos in the family Lorisidae (four genera, twelve species, and 18 taxa), the lemurs of Madagascar (five families, 15 genera, 98 species, and 102 taxa), and the tarsiers of the family Tarsiidae (three genera, eleven species, and 16 taxa). Monkeys are divided into those from Neotropics, also called the New World monkeys (five families, 20 genera, 156 species, and 204 taxa), and those from Africa and Asia, the Old World monkeys (one family, 23 genera, 159 species, and 270 taxa). The apes, all from the Old World, include the gibbons or lesser apes of the family Hylobatidae (four genera, 19 species, and 24 taxa) and the great apes, the orangutans, Chimpanzee, Bonobo and gorillas of the family Hominidae (three genera, six species, and 13 taxa in all), and of course our own worldwide species, *Homo sapiens*. The majority of primates are monkeys (70% of the taxa), with the next most diverse group being the prosimians (25% of the taxa) with 15% contributed by the lemurs of Madagascar. Great apes account for only about 2% of all taxa, even though they are the primates that the public knows best.

	Family	Genus	Species	% of species	Taxa	% of taxa
Africa	4	25	110	23%	197	29%
Madagascar	5	15	98	20%	102	15%
Asia	5	18	116	24%	179	26%
Neotropics	5	20	156	33%	204	30%
African prosimians	2	7	23	5%	41	6%
Asian prosimians	2	5	18	4%	27	4%
Malagasy prosimians	5	15	98	20%	102	15%
All prosimians	8	27	139	29%	170	25%
Neotropical monkeys	5	20	156	33%	204	30%
African monkeys	1	16	83	17%	147	22%
Asian monkeys	1	8	77	16%	123	18%
All monkeys	6	22	315	66%	473	70%
Gibbons	1	4	19	4%	24	3.5%
African apes	1	2	4	1%	9	1%
Asian apes	2	5	21	4%	28	4%
Great Apes	1	3	6	1%	13	2%
All apes	2	7	25	5%	37	5%
All primates	16	77*	479**		681**	

Prosimians, monkeys and apes in Africa, Madagascar, Asia and the Neotropics.

*The column for the regions, Africa, Asia, Madagascar, and Neotropics, adds up to one more than the total given because Asia and Africa share one genus: *Macaca*.

**The column for the regions, Africa, Asia, Madagascar, and Neotropics, adds up to one more than the total given because Asia and Africa share one species: *Papio hamadryas*.

The number of recognized primate species has increased dramatically since the 1970s for several reasons. One has been the increasing application of molecular genetic techniques that have modified our perceptions of “differentness”—allowing us not only to detect strong genetic differences poorly manifested in outward appearances and morphology but also when two forms diverged from a common ancestor—thus providing us with a map and chronology of the evolution of the different groups. Forms considered just varieties (races) or even synonyms have now been found to be clearly distinct populations that we can call species.

Another reason has been an increasing effort to study primates (and mammals as a whole) because of the devastation of tropical forests that began largely in the 1970s—global demands for timber, crops (e.g. soy and oil palm), and development (e.g. ranching, mining, dams, and settlements) targeting the great tropical forest wilderness areas of South-east Asia (Indochina, Peninsular Malaysia, East Malaysia and Brunei, Indonesia, and the Philippines), Central and West Africa, and Amazonia. In 1970, about 1% of the Amazon forest had been destroyed. Estimates now indicate 20%. Such destruction inspired a search for new primates to better understand the extent of their geographic distributions and to document and save species which might otherwise never even be known to humans. Paradoxically, the destruction of the forests and the construction of highways into remote regions have facilitated this search, providing access to parts of Amazonia and the Congo forests, for example, that were previously inaccessible.

As a result of this increased field research and the ever more sophisticated genetic techniques available, 96 primate species and subspecies have been discovered and described since 1990: 47 from Madagascar, eleven from Africa, 16 from Asia, and 22 from the Neotropics. Fifty-five of the primates described since 1990 are prosimians, 40 are monkeys, and one of them is a gibbon. Sixty-six primates have been described since 2000, and many more possibly new species are under study. Even more remarkable, it is not just new species and subspecies that are being discovered, but even new genera, the Dwarf Marmoset *Callibella* from the Central Amazon in 2003 and the Kipunji *Rungwecebus* (an arboreal primate with affinities to the terrestrial baboons) from Tanzania in 2006. What is more, increasingly sophisticated genetic data combined with morphological studies has also enabled us to demonstrate relationships among primate genera, and not just species. This has resulted in a number of taxonomic adjustments. Recent examples include: the recognition of the African monkey genera *Allochrocebus* and *Chlorocebus*, separating them out from the guenons of the

genus *Cercopithecus*; the division of tarsiers into three genera, *Tarsius*, *Carlito*, and *Cephalopachus* in South-east Asia; and the New World capuchins into two genera, *Sapajus* and *Cebus*.

The primates are mostly tropical in distribution, with more than 90% occurring north of the Tropic of Capricorn and south of the Tropic of Cancer. Native wild populations occur in 91 countries in four major regions: tropical and subtropical South and Central America and Mexico; mainland Africa; tropical, subtropical, and some parts of south temperate Asia; and the island of Madagascar, which stands as a primate region in its own right. A few countries can be highlighted for their extraordinarily rich diversity of primate species. They are Brazil, Madagascar, Indonesia, and the DR Congo. Brazil is the richest country in primates with 116 species and 139 taxa. Sixty percent of them are endemic, but Brazil has only four endemic genera out of the 19 that occur there. Madagascar's rich primate fauna is second on the list and is composed of five families, 15 genera, 98 species, and 102 taxa, all of which are endemic. They are all packed into a land area that is only about 7% the size of Brazil and that has already lost more than 90% of its original natural vegetation.

*Top Countries for Non-human
Primate Species Diversity*

Country	Families	Genera	Species	Taxa
Brazil	5	19	116	139
Madagascar	5	15	98	102
Indonesia	5	10	56	70
DR Congo	4	18	49	66
Colombia	5	13	45	52
Peru	5	14	44	50

*Primate Endemism in the Most Diverse
Countries – SPECIES*

Country	Families	Genera	Species	Endemism
Madagascar	5/5	15/15	98/98	100%
Indonesia	0/5	2/10	38/56	68%
Brazil	0/5	4/19	61/116	53%
Colombia	0/5	0/13	12/45	27%
DR Congo	0/4	0/18	10/49	20%
Peru	0/5	1/14	6/44	14%

*Primate Endemism in the Most Diverse
Countries – TAXA*

Country	Families	Genera	Taxa	Endemism
Madagascar	5/5	15/15	102/102	100%
Indonesia	0/5	2/10	55/71	77%
Brazil	0/5	4/19	83/139	60%
Colombia	0/5	0/13	17/52	32%
DR Congo	0/4	1/18	15/66	23%
Peru	0/6	1/14	7/50	14%

Our improved understanding of the evolution and diversity of our own mammalian order and its fundamental role in the ecological dynamics of tropical forests (and in the case of baboons, green monkeys, and Patas Monkeys in that of tropical savannas) underlines the importance of protecting primate species not just as components of our evolutionary history but as fundamental components of the health of these ecosystems and consequently the health and wellbeing of human communities in the regions in which they occur. The most recent assessment of the conservation status of the world's 5487 mammals in 2008 produced alarming results even for those of us who know the situation well and have been working on extinction avoidance for decades.

The assessment of the conservation status of primates, carried out by the Species Survival Commission of IUCN and its Primate Specialist Group, in close collaboration with Conservation International (CI), involved a prolonged and exhaustive compilation of relevant information on each species, finalized and discussed in four regional expert workshops held between 2005 and 2008 (Africa, Madagascar, Asia, and Africa, involving more than 150 specialist participants). *The IUCN Red List* assessment covered 634 primate species and subspecies, and found that 303 were threatened—fully 48%, nearly half of all living primates! Almost 11% were in the category of Critically Endangered (imminent extinction if conservation measures are not taken immediately), including several species that are down to only a few dozen or a few hundred individuals, but which can be saved; 21% were Endangered, and 15% Vulnerable. Sixteen percent were classed as Data Deficient. Many of the species for which information was lacking were those described only recently.

Taking into account the dramatic deterioration in the conservation measures for and the protection of wildlife in Madagascar since the change in government in early 2009, and the fact that numerous species were classified as Data Deficient, the PSG held a Lemur Red-Listing and Conservation Planning Workshop in Antananarivo, 9–15 July 2012. Ninety-six lemur taxa were reassessed and a further seven taxa were assessed for the first time against *The IUCN Red List* criteria. The preliminary results of the *Red List* assessments were as follows: 23 taxa Critically Endangered, 52 taxa Endangered, 19 taxa Vulnerable, 2 taxa Near Threatened, 3 taxa Least Concern, and 4 taxa Data Deficient. With 91% of all lemurs listed in one of the three categories of threat, this makes lemurs the most endangered larger mammal group worldwide. Overall it resulted in increasing the number of taxa assessed as threatened to 358, an alarming 52% of all primates worldwide.

Habitat destruction (including degradation, fragmentation, and outright loss) and hunting are the two major threats to primates. A third factor, of immense significance especially for the African great apes, is disease—the Ebola virus, for example, has devastated populations of gorillas and chimpanzees in Central Africa. These threats vary from region to region. In the Neotropics, deforestation—habitat loss—is the principal threat, but hunting for some of the larger species (for example, spider monkeys, genus *Ateles*, and woolly monkeys, genus *Lagothrix*) can eliminate populations even in areas of intact forest such as those that can still be found in western Amazonia. When forests are

reduced to fragments surrounded by farms, roads, and towns, hunting and the challenges faced by very small population sizes (e.g. inbreeding, disease, and chance disasters) become the major threats. Thirty-nine percent of all Neotropical primates are now threatened. In East and West Africa, forests are now heavily fragmented, and hunting is a major factor in the once primate-rich forests of West Africa's Upper Guinean region. Indeed, the first primate extinctions in modern times could occur in Ghana and Ivory Coast, where several regional endemics are down to tiny remaining populations. In both heavily fragmented West Africa and still largely intact Central Africa, there is a widespread and insidious commerce in bushmeat, which has increased enormously over the last two decades, facilitated and encouraged by the gradual penetration of logging companies into formerly remote and inaccessible forests. The phenomenon of the "empty forest" is increasingly common and widespread in West and Central Africa. Thirty-seven percent of Africa's primates are now threatened with extinction, most of them in the remnant forests of East and West Africa.

In Asia, the situation is very severely aggravated by the massive trade in animals, not just for their meat but also their tissues and body parts as essential components of a widespread and deeply rooted culture of traditional medicine and talismans. In the past, this was largely artisanal or at least relatively small-scale; today it has become a major commerce of export and import, with much of it going to an increasingly affluent China. Asia brings together all the major threats: widespread forest loss, degradation, and fragmentation (e.g. timber, rice, oil palm, forest fires), and hunting, both subsistence and commercial—all in the context of a region with the highest human population densities on Earth. Seventy-one percent of the Asian primates are now ranked as threatened with extinction, and quite a few, especially in countries such as Vietnam, Indonesia, and China, hang on only in tiny populations.

The forests of Madagascar have suffered a 2000-year history of devastation since the arrival of humans. For the most part, they are now reduced to minuscule patches, and the lemurs that occur there all have small to very small geographic ranges, especially when viewed in global terms. The loss of even a tiny patch of forest there can result in the loss of the remaining habitat of an entire species. Surviving forests are being constantly whittled away and degraded by local populations, which are highly dependent on natural resources for their subsistence—a situation exacerbated still more by the political instability following a coup in early 2009. As already mentioned, the reassessment of the conservation status of the lemurs in 2012 resulted in the finding that 91% are threatened, which is indicative of the severity of the crisis there. Madagascar is also a clear example of the fact that large-scale primate extinctions are not a figment of our imagination, and that they have taken place as a result of human activity in just the past few hundred years. Indeed, since human arrival on Madagascar just 2000 years ago, a minimum of eight genera and at least 17 species of "giant" lemurs (all of them larger than the extant species) have disappeared, some of them perhaps as recently as the late 1800s.

IUCN's Species Survival Commission (SSC) is a knowledge network of some 7000 volunteer members working in almost every country of the world, with more than 120 Specialist Groups and Task Forces. Members of the SSC and the Primate Specialist Group include government officials, protected area managers, wildlife biologists, anthropologists, zoo specialists, and veterinarians. The Primate Specialist Group has been in existence since the early 1960s, and in its current form since 1977. Its principal activities include: 1) the development of action plans and synthetic analyses to review the conservation needs of a species or species group and to recommend conservation action sufficient to ensure long-term survival; 2) the promotion of measures to facilitate the implementation of action plan recommendations; 3) the establishment and maintenance of primate conservation networks, especially through the publication of regional newsletters (*Neotropical Primates*, *Asian Primates Journal*, *African Primates*, and *Lemur News*) and a journal (*Primate Conservation*) to divulge information (research, field surveys, taxonomy, biogeography, and analyses of conservation status and threats) vital for conservation measures; 4) the publication of field guides and pocket guides to promote primate ecotourism and an understanding of primate diversity and biogeography; 5) the publication of a series "*Best Practice Guidelines*" for primate conservation in general, and particularly for great ape conservation (so far aspects have included logging, reintroduction, population survey methods, great ape/human conflict, and great ape tourism); 6) the organization of workshops and meetings to discuss program activities and aspects such as taxonomy and the regional coordination of conservation measures; 7) the compilation and organization of pertinent data and the assessment of the conservation status of all primate species and subspecies through *The IUCN Red List* process (see www.iucnredlist.org); 8) the biennial production of a list of the world's 25 Most Endangered Primates, in collaboration with Conservation International and the International Primatological Society (IPS), accompanied by a report explaining the plight of each, and general media outreach to ensure that primate conservation remains in the news; 9) the maintenance of a website that serves as a resource for PSG members, researchers, and the general public, providing information on primate diversity, threat status and current conservation efforts (see www.primatesg.org); 10) the management of a Primate Action Fund fed by an annual grant of US\$ 135,000 from the Margot Marsh Biodiversity Foundation, and providing awards of up to US\$ 5000 to support and promote primate conservation activities worldwide, through direct conservation action, field research, and publications, as well as supporting workshops and other relevant events; and 11) the continual search for additional resources to fund primate conservation in the field.

The PSG is chaired by Russell A. Mittermeier and the Deputy Chair is Anthony B. Rylands, both at Conservation International, and there are two Red List Focal Points, Christoph Schwitzer from the Bristol Zoo Gardens, UK, and Sanjay Molur from Zoo Outreach Organization (ZOO) in Coimbatore, India. There is a section of 115 members which deals specifically with great apes (coordinated by Liz Williamson, Stirling University, UK) and a recently created section on gibbons (coordinated by Benjamin Rawson, Fauna and Flora International, Cambridge, UK), and an additional nine sections for regions in which primates occur (i.e. Brazil and the Guianas, the Andean region of South America, Mesoamerica, Madagascar, West and Central Africa, East and Southern Africa, South Asia, Southeast Asia, and China), each of them with at least one regional vice-chair. The total number of members exceeds 400.

Much of the work of the Primate Specialist Group over the past 24 years has been made possible by Conservation International, which has housed the Chair and the Deputy Chair over that period and has provided for and facilitated many activities on behalf of primates. These include those mentioned above, and also large-scale protection of many areas of primate rainforest habitat through the Global Conservation Fund (GCF), the Critical Ecosystem Partnership Fund (CEPF), and the Centers for Biodiversity Conservation (CBCs) in South America and Madagascar. It is no exaggeration to say that this support has been instrumental in maintaining the diversity of the Order Primates worldwide, with not a single species or subspecies having gone extinct over that period and indeed over the past century.

Now, however, the time has come to begin ramping up our efforts. The more we learn, the more we see how important primates are—as flagship species for education and awareness efforts for rainforests, as pollinators, and as seed dispersers that may even be instrumental in maintaining high carbon sequestration capacity in the forests of Amazonia, Central Africa, and South-east Asia. What is more, as the need grows to evaluate, verify, and monitor the long-term health of tropical forests as part of a new wave of REDD+ projects, a number of primate species will serve as some of the best indicators of forest health (for example, woolly monkeys and spider monkeys in Amazonia; gorillas, chimps, guenons, and colobus monkeys in Africa; and orangutans and langurs in Asia).

We know how to keep primates from going extinct. We have developed the methods and have both the experience and the trained personnel to put the right projects in place. What we have lacked thus far is sufficient funding to deploy these experts into the highest priority places with the greatest extinction risk. This differs from many other less studied groups of organisms where either the manpower or the expertise, or both, are still in short supply. For the primates, we have the people and we have the knowledge; what we need over the next five years is at least an order of magnitude additional funding to make it all happen.

We are hopeful that this book, published as part of such a prestigious series, will make great strides in helping to stimulate interest in primates, and, in so doing, make a major contribution to the conservation of this important group of animals.

With regard to presentation, we organize this volume by family, beginning with the prosimians, which comprise 25% of the living primates. Most of them are lemurs, an extraordinary and diverse radiation of five families—Cheirogaleidae, Lepilemuridae, Lemuridae, Indriidae, and Daubentonidae—from the infraorders Lemuriformes and Chiromyiformes with 98 living species and 102 taxa inhabiting the island of Madagascar. What is remarkable about the lemurs is that we continue to find new species in spite of the fact that at least 90% of Madagascar's forests have already been lost, and what remains of their natural habitat covers no more than 50,000–60,000 km². Indeed, the known lemur fauna has doubled over the past 20 years and the largest number of primates that have been discovered since 1990 have been from Madagascar; 47 of the 96 thus far, and we are aware of at least half a dozen new species that await description. The Cheirogaleidae includes five genera of very small to small nocturnal forest-dwelling species, all of them arboreal. The mouse lemurs (*Microcebus*) include the smallest of all primates; Madame Berthe's Mouse Lemur, (*Microcebus berthae*), which weighs only about 30 g. Most have been discovered only recently. In 1998, only four species were recognized; a further 15 species have been discovered and described since then, and this is one of the genera in which quite a few new species are expected to be described in the next few years. Mouse lemurs range in weight from 30 g to 65 g. In contrast, there is just one species of Hairy-eared Dwarf Lemur (*Allocebus*). A little larger than the mouse lemurs (c.85 g), it is rare and remains very poorly known. The Giant Mouse Lemurs (*Mirza*) also show little variation, being represented thus far by just two species, one of which was discovered and described just eight years ago. They are also nocturnal and arboreal, and occur patchily only in the western dry forest region of Madagascar. These lemurs are more than four times the weight of the mouse lemurs, ranging from 290 g to 320 g. The dwarf lemurs of the genus *Cheirogaleus*, are still very poorly understood. Although we recognize five species in this volume, there are several clades within three of them, and it is highly likely that more species will be recognized in the years to come. They are larger than *Microcebus* and *Allocebus*, ranging in weight from 135 g to 458 g. They are also unusual among the primates in that they fatten up and go into torpor during the cold season; at least two species store a large quantity of fat in the tail, increasing their body weight by up to 30%. The last of the cheirogaleid genera is *Phaner*, the fork-marked lemurs, represented by at least four species, with one more in the process of being described. These are highly active gum specialists, and range in size from 300 g to 460 g.

The second family, the Lepilemuridae, is represented by only one genus, *Lepilemur*. With 26 species it is the most diverse lemur genus, and the second most diverse of all primates, beaten only by the titi monkeys (*Callicebus*) with 31. Twenty years ago, only five to seven species were recognized but, like the mouse lemurs, many have been described only recently, and several more probably remain to be discovered. They are the smallest of the folivorous primates, weighing from c.600 g to 1.2 kg, and are found throughout the remaining forested areas of Madagascar, where, if not hunted, they can reach very high densities.

The Lemuridae has five genera that range from small to medium-large. The family includes the famous Ring-tailed Lemur (*Lemur catta*), the best known lemur and the primate species most widely kept in captivity, the “typical” lemurs of the genus *Eulemur*, the ruffed lemurs (*Varecia*) and the bamboo lemurs (*Haplemur* and *Prolemur*). *Lemur catta* is the only member of its genus, weighs c.2.2 kg, has a wide range in southern Madagascar, and is the most terrestrial of the lemurs, although it is also very much at home in the trees. The genus *Eulemur* is widespread in remaining forests in Madagascar. The twelve species are quadrupedal, arboreal, and frugivorous; some of them are diurnal, some cathemeral (regularly active for parts of the day and night). The two species of ruffed lemurs are the largest members of the family, weighing from 3 kg to 3.7 kg, and they are restricted to the eastern rainforests. The most frugivorous of the lemurs, they are among the most heavily hunted, and are Critically Endangered. The two genera of bamboo lemurs, *Haplemur* and *Prolemur*, are very interesting in that bamboo specialists like them are rare among the mammals. The smaller *Haplemur* includes five species and are found in the east, the north and parts of the

northwest; they range in size from 800 g to 1.5 kg. One species, *H. alaotrensis*, is the only primate restricted to the reed beds of a single lake. The monotypic *Prolemur*, the most specialized, is larger than the *Hapalemur*, weighing in at 2.2–2.5 kg. It is one of the two most endangered primate genera in the world (the other being *Rungwecebus* from Tanzania), and down to around 200 individuals in patches of the eastern rainforest.

The family Indriidae is composed of three genera, and includes the largest of the living lemurs that are among the most spectacular of all mammals. The monotypic genus *Indri* is the largest, with individuals weighing up to 9 kg, and is the only lemur with a very short tail. It is diurnal and arboreal, only occasionally descending to the ground, and largely folivorous. The Indri's flagship value for Madagascar is comparable to that of the Giant Panda in China. The genus *Propithecus*, the sifakas, is composed of nine diurnal, arboreal species that range in weight from 2.6 kg to 7 kg. In contrast to the Indri, all the sifakas have long tails. The third genus is *Avahi*, the woolly lemurs, of which there are nine species. They are also fully arboreal but, unlike the Indri and the sifakas, are entirely nocturnal and, at 830 g to 1.2 kg, are much smaller. All of the indriids are “vertical clingers and leapers,” jumping from tree to tree in a vertical posture. Their legs are much longer than their arms, and when on the ground they move by bipedal jumps.

The family Daubentoniidae is the most divergent of all primates. Although related to the lemurs and, like them, restricted to Madagascar, it is placed in a separate Infraorder Chiromyiformes. Genetic studies have shown that it was the first of the extant forms to split from the other lemurs, early in their evolutionary history, c.66 million years ago. There is only one living species, the Aye-aye (*Daubentonia madagascariensis*), that weighs c.2.5 kg, but a giant species, the 13- to 14-kg *D. robusta*, may have survived until AD 891–1027 AD. Aye-ayes have a number of very unusual features, including continuously growing incisor teeth (as is found in rodents), huge ears, a very reduced dentition, and a special, skeleton-like, long, middle finger on a ball-and-socket joint that is used to extract insect larvae from tree holes and under bark.

The Galagidae and Lorisidae make up the Infraorder Lorisiformes. They are very small to small, nocturnal, arboreal species found in mainland Africa and South and South-east Asia. The Galagidae is composed of five genera, 18 species, and 34 taxa of galagos and bushbabies found in sub-Saharan Africa, all of them arboreal and nocturnal. There are seven species and 13 taxa of dwarf galagos (*Galagoides*), some of which are among the smallest of the primates, with weights ranging from 35 g to 200 g. The widespread genus *Galago* (galagos and bushbabies) has four species and seven taxa that are somewhat larger, ranging from 110 g to 300 g. The two species and four taxa of the needle-clawed galagos (*Euoticus*) range in size from 200 g to 360 g, while the three species of squirrel galagos (*Sciurocheirus*) are somewhat larger, with weights from 200 g to 500 g. The largest members of the family are the two greater galagos of the genus *Otolemur*, which can weigh as much as 1.8 kg. Although most of the Galagidae inhabit tropical rainforest, members of the genus *Galago* are also found in woodland-savanna habitats, and *Otolemur* is found mainly in drier biomes. With the exception of a handful of species, the Galagidae remain relatively poorly studied, especially in the rainforest regions of Central Africa. A number of species still await description, and we expect that quite a few more will come to light in the next decade.

The Lorisidae are found in both sub-Saharan Africa and tropical Asia, and are represented by four genera, twelve species, and 18 taxa. All are arboreal, nocturnal and insectivorous. The three species and six taxa of pottos (*Perodicticus*), ranging in weight from 850 g to 1.6 kg, are found in the rainforests of West, Central and East Africa. There are just two species of the smaller Angwantibo (*Arctocebus*); they weigh 230–465 g. They are restricted to the rainforests of West Africa. All of these animals remain relatively poorly known in the wild. In Asia, the family is represented by two genera: *Loris* (slender lorises) and *Nycticebus* (slow lorises). *Loris* is restricted to south India and Sri Lanka and has two species and six taxa, ranging in size from 85 g to 294 g. The more widespread slow lorises (*Nycticebus*) range from northeastern India through mainland tropical Asia to Java, Borneo, and Sumatra. There are five species in this genus, but several more have yet to be described.

The tarsiers, family Tarsiidae, are a highly distinctive group of very small primates (50–150 g) found only in insular South-east Asia, on the islands of Borneo, Sumatra, Sulawesi, and the Philippines. Although for long classified as prosimians, allied with the non-anthropoid lemurs, galagos, and lorises, they have a number of features which place them with the monkeys and apes, the most pertinent being the lack of a rhinarium, the moist tip to the nose. Lorises, pottos, angwantibos, galagos, and lemurs all have a wet nose, whereas monkeys, apes, and humans do not. Other features which ally tarsiers with the monkeys and apes include the loss of the ability to produce Vitamin C, aspects of the fetal membranes, a mobile upper lip free from the gum, a postorbital plate, and the absence of a tapetum lucidum behind the retina (the membrane that results in eyeshine), which has, rather, a macula lutea (an oval, yellow spot near the center of the retina) and fovea centralis (a small pit in the macula), which provide for sharp central vision. This confounded the classificatory notion of “pre-monkey” primates (the prosimians) and “monkey-like” primates (us, apes and monkeys), and led to a reclassification of the extant species into two suborders: the Strepsirrhini (wet-nosed primates—infraorders Lemuriformes, Chiromyiformes, and Lorisiformes) and the Haplorrhini (dry-nosed primates—the tarsiers, Tarsiiformes, and the monkeys, apes, and humans, the Simiiformes). It has now been shown that tarsiers diverged from other haplorrhines about 87 million years ago, soon after the haplorrhines split from the strepsirrhines. Until recently, they were all included under a single genus *Tarsius*. However, in 2010, C. P. Groves and M. Shekelle split them into three genera, *Tarsius* from Sulawesi, *Cephalopachus* from Borneo, Sumatra, Bangka Island, the Natuna Islands, and Belitung Island, and *Carlito* from the Philippines. In all there are eleven species and 16 taxa currently described, but this number will increase over the next few years; several other species of the Sulawesi (eastern) tarsiers have already been discovered and await description.

The monkeys and apes are divided into two groups: the New World monkeys and the Old World monkeys with the apes, referred to as platyrrhines and catarrhines, respectively. The platyrrhines are so called because of the broad, flat shape of the nose; the catarrhines have narrow nostrils, close together. The Platyrrhini have a number of other features which distinguish them, notably: three premolar teeth (the primitive condition), no bony ear tube, and the zygomatic and parietal

bones meet at a symphysis on the side of the brain case. Catarrhini have two premolar teeth, an ear tube, and the zygomatic and parietal bones do not fuse, being separated by a symphysis between the frontal and sphenoid bones.

Forty years ago, when many of us first became involved in primatology, the Platyrrhini were classified into just two families: the Callitrichidae for the small, clawed marmosets and tamarins, and the Cebidae for the remaining larger New World monkeys. Since the early 1980s, numerous studies in comparative morphology, molecular genetics, and cytogenetics have focused on discerning a more precise and phylogenetically coherent taxonomy at the family level. The number of families recognized has varied from three to five. The Callitrichidae, Pitheciidae (titis, sakis and uacaris), and Atelidae (howlers, spider and woolly monkeys) have been consistently recognized as natural groupings, as have the squirrel monkeys and capuchins in a redefined Cebidae. The callitrichids are closest to the Cebidae and some place them as a subfamily of the same, the Callitrichinae. The origins and evolutionary relations of the titi monkeys and night monkeys are rather more obscure. The titi monkeys have now been settled as being closest to the sakis and uacaris and are placed in the Pitheciidae. The night monkeys have been placed by some as members of the Cebidae, and by others as a tribe, the Homunculini, of the Pitheciidae. The arrangement that we have settled on here recognizes five families, the Callitrichidae (seven genera), the Cebidae (three genera), the Aotidae (one genus), the Pitheciidae (four genera), and the Atelidae (five genera).

The family Callitrichidae includes the smallest of the New World monkeys. All have claws rather than nails on all digits except the hallux (big toe), and, with the exception of the very unusual *Callicomaco*, all have two molars in each quadrant of the jaw (not the typical platyrrhine three), and twin births. There are seven genera, 47 species, and 62 taxa in total, with a very high likelihood that several remain to be discovered, especially in the vast Amazon region. They are all highly insectivorous and frugivorous, with some specializing on eating plant gums and even including fungi in their diets.

The Pygmy Marmoset (*Cebuella*) has just one species with two subspecies that are widely distributed in western Amazonia. It is the smallest of all monkeys, weighing only c.125 g, and with *Callithrix*, *Mico*, and *Callibella*, it has the “short-tusked condition,” and is perhaps the most specialized gummivore of all Neotropical primates. The monotypic *Callibella*, the dwarf marmoset, was only discovered in 1996. *Callibella humilis* is the second smallest of the simian primates, weighing in at 150–185 g, and is found only in a tiny area of the central Brazilian Amazon. Until recently, the Amazonian marmosets (*Mico*) were lumped with *Callithrix*. They are mostly Amazonian, with just one species, *M. melanurus*, extending south into the Brazilian Cerrado (woodland savannah) and Pantanal and into the neighboring countries of Bolivia and Paraguay. They range in weight from 250 g to about 400 g. They eat gums, although their degree of dependence on this food source is less than that of the Atlantic forest marmosets (*Callithrix*). Fourteen species are currently recognized, and this is one of the genera where new species discoveries are highly likely. The marmosets (*Callithrix*) are found in the Atlantic forest region of Brazil and the neighboring “Cerrado” and “Caatinga” (i.e. dry forest and scrub). Six species are recognized, ranging in size from 230–450 g. These four genera of marmosets are characterized by a high percentage of gums in their diet, with a specialized dentition (“the short-tusked condition,” with elongated lower incisors) that enables them to gouge holes in trees and lianes to cause the flow of gums.

With 20 species and 34 taxa in all, the tamarins (*Saguinus*) make up one of the larger genera among the primates. They are found over a wide area of Amazonia, with three species extending north-west into non-Amazonian Colombia and Panama. They have a more normal incisor to canine relationship, “the long-tusked condition,” with longer canines and shorter incisors. They also eat gums, but only opportunistically when they are readily available; exuded, for example, due to damage or attack by such as wood-boring beetles. Many of the tamarins are slightly larger than marmosets, they range in weight from 230 g to 630 g, and, as with all the callitrichids, they are diurnal and arboreal. The genus *Leontopithecus* includes the famous lion tamarins of Brazil. Endemic to Brazil’s Atlantic forest, they are among South America’s most important flagship species and an example of a great success story in primate conservation, having been brought back from the brink of extinction in the 1970s through a concerted international effort that continues to this day. There are four species, one of which, the Black-faced Lion Tamarin (*L. caissara*), eluded discovery until 1990. They are the largest of the callitrichids, ranging in weight from about 630 g to nearly 800 g.

The last member of the Callitrichidae is the enigmatic Goeldi’s Monkey, *Callimico goeldii*, a monotypic genus found only in small, widely scattered populations in the western Amazon. Since it shares certain features with the larger New World monkeys (it has three molar teeth and gives birth to singletons not twins), it once resided in its own family, the Callimiconidae, and was believed to be ancestral. The findings of a number of genetic studies, however, have placed it as a member of the Callitrichidae; and even show that it is more closely related to the marmosets than are the tamarins. Goeldi’s Monkey is comparable in size to other callitrichids, weighing c.360 g. It is a specialist in its habitat preferences, spending most of its time low in the forest and near the ground in dense foliage, particularly favoring dense patches of bamboo.

The family Cebidae includes the capuchins and squirrel monkeys, now in three genera: seven species and eleven taxa of squirrel monkeys (*Saimiri*); eight species and nine taxa of the robust or tufted capuchins (*Sapajus*); and 14 species and 16 taxa of the gracile or untufted capuchins (*Cebus*). All capuchins were considered to belong to the one genus *Cebus* until 2011, when genetic studies showed that the gracile and robust forms, the former with an ancestry from the Amazon, the latter from the Atlantic forest, had diverged some 6 million years ago. With their distinct morphological differences (the more robust skeleton of *Sapajus* associated with its destructive foraging and adaptations for durophagy), it became appropriate to classify them as distinct genera. *Sapajus* has the second-largest range of any New World genus, being found over much of Amazonia, north-western Colombia, the Atlantic forest region of Brazil, and drier forest formations such as the Caatinga, the Cerrado, and forested portions of the Pantanal, extending as far south as northern Argentina and Paraguay. *Cebus* is found mainly in Amazonia, but also crosses the Andes into Pacific coastal South America and extends into Central America as far as Honduras. The capuchins are

the most omnivorous of the platyrrhines, eating a wide variety of plant foods, invertebrates, and small vertebrates. All are diurnal and mainly arboreal, although they go to the ground more than any other New World genera. They are comparable in weight: about 2 kg to nearly 5 kg for the big males. They are also among the seven genera of New World monkeys with prehensile tails, but lack the large pad of volar skin on the tail that is found in the Atelidae. The highly insectivorous squirrel monkeys are the smallest of the non-callitrichid New World monkeys, ranging in weight from 550 g to 1.4 kg. They live in large to very large groups and are widespread in Amazonia extending to central Colombia, and with one species and two subspecies having a disjunct distribution in Costa Rica and Panama. The cebids have large brains in relation to their body sizes. The capuchins are considered the most intelligent of the New World monkeys and some members of the genus *Sapajus* have a complex tool-use technology, otherwise shown only by the great apes.

The night monkeys, family Aotidae, are all of one genus (*Aotus*), with eleven species, and 13 taxa. Their phylogenetic position amongst the platyrrhines is difficult to discern, and they have been placed in various families over the years. Today, some experts place them with the titi monkeys (*Callicebus*) in the Pitheciidae. We maintain them as a separate family. These are the only nocturnal New World monkeys, although in some parts of their ranges, for example, in Paraguay and northern Argentina, they are also partially diurnal. They range in size from c.600 g to c.1.45 kg, and are distributed widely over much of Amazonia (but not the Guianas), extending north into Panama and south as far as Paraguay and northern Argentina (but absent from the Atlantic forest).

The fourth family of the New World monkeys is the Pitheciidae. Previously including only the sakis (*Chiropotes* and *Pithecia*) and uacaris (*Cacajao*), there is morphological and genetic evidence that also places the titis (*Callicebus*) in this family. Discoveries of eight previously undescribed titis since 1990 have resulted in this now being the most diverse genus in the world in terms of species. At present, there are 31 of them, and more are likely to be described in the near future. (The African genus *Cercopithecus* is more diverse overall, having 23 species but 58 recognized taxa when subspecies are included.) Titis range in weight from about 800 g to 1.65 kg. They are diurnal and arboreal, and live in small family groups of a single adult pair. They are found over a wide area of the Amazon basin (but not north of the lower Amazon, or in the Guianas) and the Atlantic forest, and extend into non-Amazonian parts of Colombia, Bolivia, and Paraguay. The sakis (*Pithecia*) and the bearded sakis (*Chiropotes*) are strictly Amazonian in distribution. *Pithecia* is found over much of Amazonia, but *Chiropotes* occurs only in the eastern part of this vast forest, east of the Rio Negro and north of the middle and lower Amazon on the Guiana Shield. Five species and eight taxa of *Pithecia* are currently recognized, but a systematic revision currently underway will likely more than double this number. They range in size from 1.4 kg to 3 kg with the largest species, the Buffy Saki (*P. albicans*) probably reaching 3.5 kg. The sakis are elusive and little known primates. They are frugivores and seed predators, are particularly fond of liane fruits, and are generally found in small groups of 2–4, sometimes six or seven individuals. The bearded sakis (*Chiropotes*) have five species. Somewhat larger than *Pithecia* and *Callicebus*, they range in weight from 2 kg to 4 kg. They live in large groups of as many as 20–30, and are specialized seed predators, with wedge-shaped canines and powerful jaw muscles to break open fruits of the Brazil nut family (Lecythidaceae) and the tough fruits of many other tree and liane species. The uacaris, or uakaris (*Cacajao*) are the only New World monkeys with a short tail. They are exclusively Amazonian in distribution, being found mainly in western Amazonia in an area largely complementary to that of *Chiropotes*. The uacaris are similar to the bearded sakis in many ways, being comparable in size (2–4.5 kg), living in large groups, and specializing on the seeds of unripe fruits. Three species and seven taxa are currently recognized, but several more may be discovered in the near future.

The last of the New World families, Atelidae, includes the largest of the South and Central American monkeys and is currently divided into five genera: the howlers (*Alouatta*), with twelve species and 19 taxa; the spider monkeys (*Ateles*), with seven species and 15 taxa; the woolly monkeys (*Lagothrix*), with three species and five taxa; the Peruvian Yellow-tailed Woolly Monkey (*Oreonax*), with only one species; and the miquis (*Brachyteles*), with two species. All five genera have a prehensile tail with a pad of volar skin on the ventral surface of the tip, and all but the howlers are brachiators, moving through the trees both quadrupedally and by swinging by their arms below branches. The difference between the brachiation of these Neotropical genera and that of the gibbons is in their use of the prehensile tail. *Alouatta* also has a strongly prehensile tail, but locomotion is mainly quadrupedal and above branch, with the tail used mainly in postural behavior while feeding. By far the largest of the New World monkeys, these animals weigh from c.4 kg to c.10 kg, with the miquis, which reportedly can reach 14–15 kg, being the largest non-human primate in the Neotropics. All are diurnal and arboreal, with *Alouatta* descending to the ground to move between patches of forest more often than the other genera. *Alouatta* is also a good swimmer and regularly crosses rivers; the other four genera cannot swim, so rivers form barriers delimiting the ranges of the species.

The howlers (*Alouatta*) are quite different from the other Atelidae in their locomotion and morphological features. They have an enlarged hyoid bone that forms a voice box and enables them to produce loud roaring vocalizations. They are the most folivorous member of the family and also the most wide-ranging of any Neotropical monkey genus, being found from southern Mexico through Central America and the west (Pacific) coast of South America as far south as northern Peru, through the Venezuelan Llanos (Orinoco savannas), Amazonia, the Atlantic forest, all of the Cerrado and Pantanal of Brazil, to Bolivia, Paraguay, and northern Argentina. Howlers are highly adaptable and able to survive in a much wider range of habitats, and are more resistant to hunting and forest degradation and fragmentation than other atelids.

The more agile, long-limbed spider monkeys (*Ateles*) have not been subjected to an in-depth taxonomic revision since 1944, and there are almost certainly new species to be described. The genus has a wide range that includes most of Amazonia, the forests of the Pacific coast of Ecuador and Colombia, and all of Central America, extending north as far as the Mexican state of Tamaulipas, the northernmost distribution of any Neotropical monkey. Spider monkeys are the most frugivorous of the New World monkeys. In Amazonia, they are found almost exclusively in intact

tropical rainforest, but in Central America and Mexico they occupy a wider range of habitats, including tropical dry forests.

Like *Ateles*, the taxonomy of *Lagothrix* is in need of a modern revision, and new species of woolly monkeys will likely be described. Woolly monkeys are found in western Amazonia, with one species extending north along the foothills of the Eastern Cordillera of the Andes into central Colombia. Spider monkeys and woolly monkeys are heavily hunted for food and for pets in Amazonia, and have been wiped out in many forests that are otherwise still largely pristine. The distinctive Peruvian Yellow-tailed Woolly monkey (*Oreonax*), was included in the genus *Lagothrix* until 2001. It has a very limited range in the mountains of the northern Peruvian Andes, and is the largest mammal endemic to Peru and an extremely important flagship species for wildlife conservation in that country. The muriquis (*Brachyteles*) are restricted to the Atlantic forest region of Brazil between the states of Bahia and Paraná. At one point, the muriqui was considered monotypic, but it was divided into two species in 1993. Being the largest of the Neotropical primates and the largest mammals endemic to Brazil, they, like the Peruvian Yellow-tailed Woolly Monkey in Peru, are extremely important flagship species for the Atlantic forest and for the country as a whole.

The family Cercopithecidae, the Old World monkeys or Catarrhini, is the largest of all primate families, with 23 genera, 159 species, and 270 taxa. It is divided into two subfamilies, the Cercopithecinae and the Colobinae, which some authors prefer to recognize as separate families in their own right. The Cercopithecinae includes the macaques, the baboons, drills, and mangabeys, the green monkeys, and the very diverse guenons (13 genera in all), while the Colobinae has within it the Asian langurs and the African colobus monkeys (ten genera).

The macaques (*Macaca*) are divided into 22 species and 37 taxa, and have the widest range of any non-human primate genus; from Pakistan and Afghanistan through all of tropical and subtropical Asia, and a significant part of temperate Asia as well, extending well into China and as far north as Japan. They occur in the greatest variety of habitat types; from high mountains above 4000 m to dense tropical rainforests, to large cities. It is one of the two non-human primate genera that occur on two continents (actually three if you count Gibraltar, where it once occurred naturally), and the only primate genus that crosses Wallace's Line into eastern Indonesia, with a radiation of macaque species on the island of Sulawesi and the crab-eating macaque ranging as far east as Halamahera and the Nusa Penida-Timor Island chain, where they may have been introduced. Introduced populations of one species, the crab-eating macaque, are also now established on Mauritius, on Palau in the Pacific, and even around Jayapura on the island of New Guinea. The one African species, the Barbary macaque, occurs in Morocco and Algeria and on the Rock of Gibraltar, and in Africa is the only non-human primate found north of the Sahara. The macaques are sexually dimorphic and medium to large in size, with females ranging in weight from c.4 kg to 9 kg, but males in some species being as large as 18 kg. They are diurnal, strongly omnivorous, and all are at home in the trees; some spend most of their time on the ground, whereas others only go to the ground occasionally to forage. In Asia, they are the most ubiquitous and adaptable of primates, with some species such as the Rhesus and the Crab-eating macaques even living in urban environments.

The mangabeys are entirely sub-Saharan in distribution. Until 1978, they were considered to all belong to a single genus, but in 1978 they were split into two: *Cercocebus* (the capped mangabeys) and *Lophocebus* (the crested mangabeys). Moreover, genetic studies in the early 1990s showed that the two genera had different phylogenetic relationships with other members of the tribe Papionini: the Gelada, the baboons, the Mandrill, and the Drill. *Cercocebus* is most closely related to the Mandrill and the Drill whereas *Lophocebus* is most closely related to the Gelada and baboons. The Kipunji (*Rungwecebus*) was first described in 2005 as a large (15 kg) member of the genus *Lophocebus*, but subsequent genetic and morphological studies found that it was quite different and more closely aligned with baboons (*Papio*) and the Gelada (*Theropithecus*) than with either of the mangabeys. Mangabeys are medium-sized to large monkeys, ranging in weight from c.4 kg to 14 kg; males are larger than females. The mangabeys and the Kipunji are diurnal and arboreal, although most species regularly descend to the ground to forage. There are seven species of capped mangabeys (*Cercocebus*), found mainly in Central and West Africa, with two species extending into widely separated forest islands in Kenya and Tanzania. The six species of crested mangabeys (*Lophocebus*) occur over much the same area. The Kipunji occurs in Tanzania, and has the smallest range of any primate genus; just two tiny forest fragments.

The forest baboon genus *Mandrillus*, the Mandrill and the Drill, has only two species and three taxa and is found only in West Africa, in the countries of Cameroon, Gabon, and Equatorial Guinea. These are the among the weightiest of the living monkeys; large males reach 33 kg, the females are much smaller at 6–13 kg. Mandrills also form the largest social groups of any primate, with more than 1000 animals having been recorded in the forests of Gabon.

The baboons (*Papio*) are one of the most widespread and successful of all primates. They are found throughout sub-Saharan Africa, with one species, the Hamadryas Baboon, crossing over into Yemen and extreme southern Saudi Arabia. Six species and nine taxa are currently recognized. They are found in a wide variety of different woodland savanna and other open country habitats. Opportunistic omnivores, they are generally diurnal and largely terrestrial, but are also at home in the trees. Baboons are large to very large monkeys, and large males of the Chacma Baboon (*P. ursinus*) can weigh as much as 35 kg.

The very unusual genus *Theropithecus*, the Gelada, has only one species and two taxa, and is restricted to Ethiopia. A diurnal, terrestrial grazer that lives in high altitude grasslands, it too forms very large multimale groups that can reach 260 or more animals; sometimes groups merge to form temporary herds of up to 1000. Like the baboons and mandrills, it is quite large, with adult males weighing as much as 30 kg.

Next come the guenons and their relatives, which are now divided into six genera, one of them, *Cercopithecus*, very large, with 23 species and 58 taxa, and the other five with just one to four species. Until recently, *Cercopithecus* was even larger. In a review of the taxonomy of the African primates by P. Grubb and coworkers published in 2003, the six species of green monkeys (the so-called *Cercopithecus aethiops* group) and three terrestrial guenons (the *Cercopithecus preussi* group) were

maintained as members of the genus *Cercopithecus*. However, C. P. Groves in his earlier 2001 review entitled *Primate Taxonomy* recognized *Chlorocebus* as a distinct genus, and a molecular genetic study in 2007 showed that they, the Patas Monkey (*Erythrocebus*), and (separately) the terrestrial guenons of the *C. preussi* group (*Allochrocebus*) formed a clade that was basal to the remaining guenons (*Cercopithecus*) and the talapoins (*Miopithecus*). His separation of the genus *Cercopithecus* into three genera, *Cercopithecus*, *Chlorocebus*, and *Allochrocebus*, is followed here.

Allen's Swamp Monkey (*Allenopithecus*) is basal to all other guenons, terrestrial and arboreal, and is found mainly in riparian and swamp forest in the DR Congo, Republic of the Congo, and possibly Angola. The two species of *Miopithecus*, the talapoins, are the smallest of the Cercopithecidae; females weigh 750–1100 g and males weigh 1.2–1.4 kg. They occupy a similar ecological niche to the squirrel monkeys of South and Central America. The Patas Monkey (*Erythrocebus*) with one species and three taxa is a large (females reach 7 kg, males 13 kg), long-limbed, savanna dweller. It is largely terrestrial, and occurs in a wide band across sub-Saharan Africa, mainly in the Sahelian region.

Chlorocebus, the green monkeys, are widespread and highly adaptable woodland savanna dwellers that often occupy the same habitats as *Papio*. Like baboons, they are diurnal, spend a lot of time on the ground, and are opportunistic omnivores, but they are much smaller; females range in weight from about 1.5 to 5 kg, and males from 3 kg to 6.4 kg. Six species and twelve taxa are currently recognized and they have a wide distribution in the drier habitats of sub-Saharan Africa, but are absent from tropical rainforest, except for the very unusual *C. djambjambensis* from Ethiopia. One species, *C. sabaeus*, is also well-established on several Caribbean islands, including St. Kitts and Nevis and Barbados, having been introduced there early in the colonial period.

The terrestrial guenons of the genus *Allochrocebus* (just three species and four taxa) are found in two widely separated parts of tropical Africa. *A. preussi* has a restricted and patchy range in the western portion of Central Africa in Nigeria, Cameroon and Equatorial Guinea (including Bioko). *A. lhoesti* occurs on the eastern side of the rainforest in Uganda, Rwanda, Burundi, and the eastern part of the DR Congo, and the Sun-tailed Monkey (*A. solatus*) in a small area of central Gabon. These monkeys are medium in size: females range from about 3 kg to 4.5 kg, males 4.7–10 kg. They spend much more time on the ground than other guenons, although they are equally at home in the trees.

Cercopithecus, the typical guenons, are found mainly in the tropical rainforests of Central and West Africa, with several species extending into eastern and southern Africa, where they occupy both rainforest isolates and drier forest formations. One species, *C. mona*, is also established on the Caribbean island of Grenada, having been introduced there during the colonial period. They are generally medium to large monkeys, with females ranging in weight from about 2 kg to 4 kg, and males 3 kg to 7.5 kg. All are diurnal and largely arboreal, with some species spending more time on the ground than others. They are opportunistic omnivores, and often form multispecies associations with other members of the genus and with other primate genera as well. These guenons make up the most diverse genus of African monkeys and are also the most diverse primate genus overall, with 23 species and 58 taxa.

Next is the subfamily Colobinae, the folivorous monkeys of Africa and Asia. In all, there are three genera, 23 species, and 38 taxa in sub-Saharan Africa and seven genera, 55 species, and 87 taxa in Asia. Their taxonomy is complex and much discussed, with animals sometimes being placed in one genus and sometimes in another and with some experts splitting genera and others lumping them. The arrangement we present here is based on our interpretation of the best information available at this time, but there may well be changes in the future.

The African colobines can be divided into three groups, the black-and-white colobus monkeys, the red colobus monkeys, and the monotypic Olive Colobus. At various times in the past, these have all been lumped together in one genus, *Colobus*, listed as three subgenera of one genus, divided into two genera, *Colobus* and *Procolobus*, or split into three genera with the black-and-white colobus monkeys in the genus *Colobus*, the red colobus monkeys in the genus *Piliocolobus*, and only the Olive Colobus in the genus *Procolobus*. We believe that the last-mentioned arrangement, with three distinct genera, best reflects the diversity of these monkeys, and that is the arrangement we use here.

The black-and-white colobus monkeys, genus *Colobus*, are the most widespread and adaptable of the African colobines, and, like all colobines, are largely folivorous. They are diurnal and arboreal and occur across tropical and subtropical Africa, in a wide variety of habitats from tropical rainforest to drier forest types. Black-and-white colobus are large monkeys, females ranging in weight from 5.5 kg to 11 kg, and males 7.6 kg to 13.5 kg. Most are black and white; just one species (*C. satanas*) is entirely black. Five species and 20 taxa are currently recognized. The red colobus monkeys, genus *Piliocolobus*, are mainly found in the tropical rainforests of West and Central Africa, with several species occurring in isolated formations in Kenya and Tanzania, and one species on the island of Zanzibar. They are similar in size to the black-and-white colobus monkeys; females weigh 6–9 kg, males 8–12.5 kg. Following a revision by C. P. Groves in 2007, we recognize 17 species and no subspecies. These monkeys are particularly vulnerable to hunting and are even the favorite target monkey for chimpanzee hunting parties; they are in a dire situation in many parts of their range. Indeed, we may already have lost one species, Miss Waldron's Red Colobus (*P. waldronae*) from the border area between Ghana and Cote d'Ivoire, which has not been seen in the wild by primatologists in several decades. The last of the African colobine genera is *Procolobus*, the Olive Colobus, a monotypic species found only in the forests of Upper Guinean West Africa. It is smaller than other colobus monkeys, weighing only 3–5.7 kg.

The seven genera of Asian colobines are more diverse than their African counterparts, and their taxonomy has also been in a state of flux over several decades. There are four less diverse genera, sometimes referred to as the "odd-nosed monkeys," all of them having unusual pointed, upturned, or even pendulous noses. Their taxonomy has been relatively stable over the past few decades, although there has been some lumping and some splitting. The most famous is the Proboscis Monkey (*Nasalis*) from Borneo, a monotypic genus found in the *Nipa* palm and mangrove swamps around the coast of Borneo and sometimes extending inland along the larger rivers. This unusual animal is characterized by a long pendulous nose in the males, which is used as a resonating chamber for loud, honking vocalizations. A large species, with males weighing as much as 24 kg, it is also an adept

swimmer and regularly crosses rivers and even swims out in the ocean to reach nearby islands. There has been much discussion as to whether the smaller genus *Simias*, the Pig-tailed Langur endemic to the tiny Mentawai Islands off the west coast of Sumatra, should be included as a member of the genus *Nasalis* or as a separate genus, as has been the case for most of the last few decades. Not even the authors of this book are in agreement as to where *Simias* should be placed. Although genetically close to *Nasalis*, it occupies a different niche, being found in tropical rainforest, has a short tail (unlike the long tail of the Proboscis Monkey), exhibits an unusual color dimorphism, and is not markedly sexually dimorphic in size. It is also much smaller, the males weighing only 8.5–8.8 kg (females a little less at 7.0–7.2 kg). For the present, we have taken a conservative position, leaving the one species and two subspecies of Pig-tailed Langur in the separate genus *Simias*.

The other two odd-nosed Asian colobines are found in China and Indochina. The five species and seven taxa of snub-nosed monkeys (*Rhinopithecus*) are found mainly in isolated montane habitats in temperate and subtropical China (four species and six taxa), with one species found in the montane forests of northern Vietnam, and the last, the recently discovered *R. strykeri*, also being found in Myanmar and across the border in China. These are quite large monkeys, with males weighing 14–19 kg, and the females 6–10 kg. They live in some of the most extreme conditions occupied by non-human primates. Yunnan Snub-nosed Monkeys (*R. bieti*), for example, live at altitudes above 4000 m where it snows for a month at a time; in winter they feed largely on pine needles, lichens and bark. The doucs (*Pygathrix*) are found only in Vietnam, Cambodia and Laos. There are three species, they live in tropical rainforest, and are somewhat smaller than the *Rhinopithecus*, males weighing in at 8 kg to 12.5 kg, females 4.7 kg to 11.7 kg. All of the odd-nosed monkeys are diurnal and arboreal, with the Chinese *Rhinopithecus* occasionally going to the ground to forage.

The three larger genera of Asian colobines have undergone much taxonomic revision over the past three decades, and there is still no final consensus among taxonomists. Initially these animals were all included in the genus *Presbytis*. *Presbytis* was then divided into four genera or four subgenera: *Presbytis*, *Trachypithecus*, *Semnopithecus*, and *Kasi*. The species within them were moved around as well, some shifting from one genus to another depending on the opinion of the experts involved. The latest arrangement, which we present here, recognizes three genera, *Presbytis*, *Trachypithecus*, and *Semnopithecus*, with the two species previously in *Kasi* now being included under *Semnopithecus*.

The genus *Presbytis* is very diverse, with 16 species and 28 taxa. They are the langurs, sometimes called surilis, of tropical South-east Asia, both on the mainland and on the islands of Sundaland, west of Wallace's line. They are medium to large monkeys, ranging in weight from 4.3 kg to 8.2 kg, and the sexes are generally not dimorphic in size. The genus *Trachypithecus*, the species sometimes referred to as lutungs, is even more diverse, with 18 species and 32 taxa, and is found from North-east India, Bhutan, and Bangladesh through mainland South-east Asia and onto the same islands as *Presbytis*. Langurs of the genus *Presbytis* are now restricted to Malaysia and western Indonesia. *Presbytis* differs from *Trachypithecus* by a number of dental and cranial features (thick enamel, short faces, no supraorbital ridge, and relatively small larynx), and they are distinct genetic clades. *Trachypithecus* infants have distinct bright-orange-colored infants. The langurs of these two genera are all diurnal and arboreal, and occupy a wide range of forest habitats.

Last we have the genus *Semnopithecus*, which is found in South Asia, including India, Nepal, Bhutan, Bangladesh and Sri Lanka. At one time, all the gray langurs were subspecies of *Presbytis entellus*, the Hanuman or Bengal Sacred Langur, but this wide-ranging group has now been divided into a number of different species and subspecies, with each taxonomist working on them having a somewhat different breakdown of taxa. The arrangement that we follow here follows the molecular genetic studies of K. P. Karanth and colleagues, who recognize eight species and 15 taxa. The Nilgiri Langur (*S. johnii*) from southern India, and the Purple-faced Langurs (*S. vetulus*) from Sri Lanka that have been placed in a separate genus *Kasi* in the past, are now lumped with the Hanuman or gray langur group in *Semnopithecus*. For the most part, the *Semnopithecus* species are large monkeys. The Hanuman or gray langurs exhibit size dimorphism, with males of the Himalayan species reaching nearly 21 kg in weight and females ranging from 9.5 kg to 17.7 kg. So does the Nilgiri Langur of the Western Ghats, with males weighing c.12 kg to nearly 14 kg, and females 10–11 kg. *S. vetulus* from Lanka, however, is a smaller species with no dimorphism (males and females weigh 3.8–9.4 kg). All the *Semnopithecus* species are diurnal. The Hanuman group spends a lot of time on the ground whereas *S. johnii* and *S. vetulus* are largely arboreal. Many of the taxa of the Hanuman group are also very adaptable and often live in close proximity to humans and even in cities and temples.

The apes are divided into lesser and great apes. The gibbons of the family Hylobatidae constitute the lesser apes, and are found mainly in continental and insular South-east Asia as far east as Java and Borneo, and in North-east India, Bangladesh, Myanmar, Indochina, and extreme southern China. Four genera, 19 species and 24 taxa are currently recognized, and they include some of the most endangered primates on Earth, best symbolized by the Hainan Crested Gibbon, which is restricted to a very small area of the island of Hainan, China, and is down to about 20 individuals in the wild. Largely frugivorous, pair-living, diurnal and arboreal, all gibbons lack tails and are the ultimate brachiators among the primates, moving from tree to tree by swinging by their arms. The three smaller genera can also move by “ricochetal brachiation,” a rapid form of brachiation that has them literally flying through the trees, and is among the most spectacular of all forms of animal locomotion. The much heavier Siamang (*Symphalangus*) brachiates, but does not display ricochetal brachiation.

The genus *Hoolock* is composed of two small species (c.6–7 kg) found in northeastern India, Bangladesh, and Myanmar. *Nomascus* has seven species and eight taxa, and is restricted to mainland South-east Asia and extreme southern China (including Hainan). *Nomascus* gibbons range from 5 kg to 10 kg. *Hylobates* is the largest genus ranging from southern China through mainland South-east Asia to the islands of Java, Sumatra, and Borneo. There are nine species and 13 taxa, and they range in size from 4 kg to 7.5 kg. The fourth genus, *Symphalangus* (the Siamang), is monotypic and restricted to Malaysia and Sumatra. It is by far the largest member of the family, weighing in at 9 kg to nearly 13 kg.

Last we have the great apes of the family Hominidae—three genera, six species, and 13 taxa—and our own species, *Homo sapiens*, with just one genus and species and a wide range of variation

around the world. The Chimpanzees and the Bonobo (*Pan*), the gorillas (*Gorilla*), and the orangutans (*Pongo*) are by far the best known primates, and are among the world's most important flagship species. The Bonobo (*P. paniscus*), also sometimes called the Pygmy Chimpanzee (although it is not a pygmy in any sense of the word), is also becoming very well known. The Chimpanzees (*P. troglodytes*) and the Bonobo are our closest living relatives, sharing with us roughly 98% of our DNA, and the gorillas and the orangutans are not far behind.

The gorillas are by far the largest living primates, with males reaching 209 kg and females 98 kg, and are divided into two species and four taxa. They are found in two widely separated parts of Africa, one in the eastern part of the DR Congo (*G. beringei graueri*) and in the Virunga Volcanoes of extreme eastern DR Congo, Rwanda, and in the Bwindi (Impenetrable) Forest of Uganda (*G. beringei beringei*), and the other in western equatorial Africa in Gabon, Equatorial Guinea, Cameroon, Republic of the Congo, DR Congo, and the Cabinda enclave of Angola (*G. gorilla gorilla*), with an isolated subspecies on the Cameroon/Nigeria border (*G. gorilla diehlii*). Gorillas are diurnal and largely terrestrial, although they are capable of climbing into the trees.

The one species of Chimpanzee is divided into four subspecies and occurs from western Uganda and Tanzania across Central and western equatorial Africa, up into the Guinean forests of West Africa and even into drier habitats in Senegal and Mali. Males range in size from 28 kg to 70 kg and females 20–50 kg. The Bonobo, by contrast, is restricted to the “Cuvette Centrale” of DR Congo, south of the bend of the Congo River, and is found only in tropical rainforest. Though sometimes referred to as a “Pygmy Chimpanzee,” it is comparable in size to the Chimpanzee, males weighing from 37 kg to 60 kg and females 27–38 kg. Chimpanzees and Bonobos are diurnal, and are equally at home in the trees and on the ground.

The orangutans are found only on the islands of Sumatra and Borneo, with the Sumatran populations belonging to the species *P. abelli* and the Bornean populations being divided into three subspecies of *P. pygmaeus*. Males weigh up to 85 kg and females up to 45 kg. They are found only in tropical rainforest, are largely frugivorous, and are the largest arboreal animals on Earth, although they periodically move on the ground.

Last, but certainly not least, we have ourselves, *Homo sapiens*, a single species that occurs on all continents except Antarctica, and is the most adaptable, successful, and destructive mammal on Earth. Given that we would need volumes to describe the amazing behavioral, ecological, cultural, and technological diversity of our own species, we have decided to exclude it from this volume, and to focus instead only on the non-human members of the Order of which we are a part.

What should be obvious to the reader after he or she has pored through this extensive text is that it is no longer easy to make generalizations about behavior and ecology, nor to easily categorize primate species and genera into discrete categories, monogamous vs. polygamous, permanently pair-bonded vs. opportunistic, one male vs. multimale groups, folivore vs. frugivore, frugivore vs. omnivore, nocturnal vs. diurnal... and the list goes on. The more we learn about different species in different habitats, and even different populations of the same species, the more we see that there is a great deal of flexibility in their behavior and ecology and the ways in which this fascinating Order of mammals adapts to different environmental conditions. Perhaps this is not surprising, given the great adaptability of our own primate species, *Homo sapiens*, but it only adds to the overall appeal of the primates. Much of primatology in the early days was based on a desire to learn more about our own evolution by studying our closest living relatives, and certainly such research has provided many extraordinary and exciting results and insights. But as we have progressed in primate studies over the decades, we have found that these animals are extremely interesting in their own right, and worthy of study beyond their value as surrogates for our early ancestors. We hope that this book gives you at least some understanding of how exciting and interesting the primates are, and that it stimulates you to become more involved in their study and their conservation.

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