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Cover illustration: (clockwise from top left): blue monkey *Cercopithecus mitis* (© T. Furuichi), mountain gorilla *Gorilla beringei* (© J. Rothman), chimpanzee *Pan troglodytes schweinfurthii/marungensis* (© N.E. Newton-Fisher), red colobus *Piliocolobus tephrosceles* (© A.J. Plumptre).

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PREFACE

From galagos to gorillas, the primates of western Uganda comprise a very diverse collection of species. Western Uganda has a long history of primatological research extending back to the publications of the Uganda Virus Institute in 1947 and even to the notable first encounters of Count Beringe with mountain gorillas in 1913. Many forested areas of Uganda (Figure i) have been the focus of research continuously since 1970, and thus western Uganda has a central place in primatology that it maintains to the present day. In this book, we present a series of new, unpublished scientific accounts of a selection of the species in the region, each chapter focusing on one or more particular characteristics of the species concerned. The book falls naturally into four sections. First, we introduce the primates of western Uganda, with a chapter on their taxonomy. We have left authors to follow the taxonomic terminology with which they are most comfortable, but present this first chapter to reflect recent developments in the understanding of taxonomic relationships among the Ugandan primates. Second, we present a section with an ecological focus, followed by a collection of chapters on behavior and physiology. Finally the focus shifts to conservation.

Chimpanzees and gorillas have always attracted a lot of interest both among the general public and among researchers; consequently, this interest is reflected in the present volume. This book contains 12 chapters on chimpanzees, 4 chapters on gorillas, 6 chapters on monkeys and prosimians, and 1 general chapter on taxonomy. The chimpanzee bias is unfortunate in a book on “primates,” but is an unavoidable reflection on the recent research that has been conducted in western Uganda. Studies of other primate species have been made in the past, but this volume is not a compilation of past studies; every study is new and is here published for the first time.

If there is a message emerging from this book, it is that western Uganda provides an excellent area for future studies of primates. In the modern setting of population increase, depletion of primate habitats, hunting with snares and



Figure i. Map of Uganda showing the major forested areas.

traps, and other challenges to the forests and their natural inhabitants, scientific projects can provide havens of security for wildlife. Scientific research needs to be more widely recognized as a primary mechanism for conservation, and its importance needs to be spelled out to wildlife NGOs and governmental authorities. All those who work with primates, whether in research or in conservation, must assist in the effort to bring their work to the attention of the Uganda National Forest Authority and the Uganda Wildlife Authority, in particular, as well as to local authorities. It is thus with great pleasure that we publish here the work of a number of Ugandan primatologists. They will be the stewards of Uganda's primates in the years to come.

Finally, a word of thanks. The idea of putting together a book about the primates of western Uganda first arose after a very successful meeting of the Primate Society of Great Britain held in London on December 5, 2001. The meeting attracted a large audience and it was clear that there was a lot of interest in the primates of western Uganda, nowadays sometimes referred to as the Albertine Rift, although technically most of the study areas here are outside of the Rift itself. We are therefore very grateful to the Primate Society of Great Britain for making possible the meeting, which led to the present book.

Nicholas E. Newton-Fisher
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SECTION ONE

Taxonomy



Figure ii. Red colobus *Piliocolobus tephrosceles* (above, photo: A.J. Plumptre) and chimpanzee *Pan troglodytes schweinfurthii/marungensis* (below, photo: N.E. Newton-Fisher).

CHAPTER ONE

Taxonomy and Biogeography of the Primates of Western Uganda

Colin Groves

INTRODUCTION

In this brief survey, I will list the species (and subspecies) of nonhuman primates that have been recorded from western Uganda, with an outline of their known ranges within Uganda and in neighboring countries, and use this to try to assess the biogeographic affinities of the region as a whole.

I adopt the following definitions, paraphrased after Groves (2001):

- A species is a population (or group of populations), distinguished by the possession of one or more consistent (fixed, absolute) heritable differences from other such populations;
- A subspecies is a geographic segment of a species, distinguished by the possession at high frequencies, but not as much as 100%, of one or more heritable differences from other such segments;

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- A genus is a monophyletic group of species (or a single species), which separated from other such groups earlier than the Miocene–Pliocene boundary;
- A family is a monophyletic group of genera (or a single genus), which separated from other such groups before the Oligocene–Miocene boundary.
- Species-groups, tribes, subfamilies, and superfamilies are best taken as further convenience categories, set up to assort an otherwise unwieldy group of families or genera into monophyletic clusters.

The number of taxa is still uncertain. In some cases, especially in that of the *Cercopithecus mitis* group, there are problems that accurate field records, by experienced observers, can easily untangle. In other cases, especially involving the genus *Galagoides*, solution of the problems will take more specialized field-work. In no case is further collecting necessary, which is not to say that pick-up specimens (including bones from owl pellets and from the ground below eagles' nests) should be ignored.

In what follows, the taxonomic outlines presented in Groves (2001) will be followed, except where indicated. I may be forgiven for reiterating the guiding principle laid down in that book: “I hope that the classifications in the book will be taken as a starting point, not as a solution to problems. I hope that others will take up some of the propositions and test them” (Groves, 2001:viii).

STREPSIRRHINI: LORISIFORMES

Galagidae Gray, 1825

Jenkins (1987) reinstated the original spellings “Loridae” and “Galagonidae” for the lorises and bushbabies, and was supported in this change by Groves (2001). The previously better known forms of the names have recently, however, been officially sanctioned (International Commission on Zoological Nomenclature, 2002). This means that all names of superfamilies, families, subfamilies, and tribes based on these two names take the stem form Loris- and Galag-, respectively. Also, the higher-category name should preferably be Lorisiformes, not Loriformes, although ranks above the family-group are not actually covered by the rules of nomenclature.

How many genera there are in the Galagidae is unclear. Groves (2001) recognized three, while noting that one of them, *Galago*, was probably not

monophyletic; Grubb *et al.* (2003) provisionally increased the number to five genera, separating *Galagoides* from *Galago* but noting that it, too, may not be monophyletic.

Galago E. Geoffroy St. Hilaire, 1796

Two species live in western Uganda, one in tree-savannah and thorn-bush, the other in rainforest.

Lesser or Senegal bushbaby, *Galago senegalensis* E. Geoffroy St. Hilaire, 1796. These are the common small bushbabies of the nonforested regions. There are two quite distinct subspecies in western Uganda (Groves, 2001):

- *Galago senegalensis senegalensis* E. Geoffroy, 1796: from the northern part, grey in color with creamy yellow limbs, a grey-brown tail, and yellow-white underparts.
- *Galago senegalensis sotikae* Hollister, 1920: from Ankole and south into Tanzania, more brownish grey and noticeably larger in size (mean skull length 48.3 mm [$n = 4$] as against 43.6 mm [$n = 21$]).

Eastern needle-clawed bushbaby, or Spectacled galago, *Galago matschiei* Lorenz von Liburnau, 1917. A rainforest species, whose main distribution is the eastern Democratic Republic of Congo (DRC). In Uganda, according to Kingdon (1971), it lives mainly in the southwest, north perhaps to the Victoria Nile, and is characteristic of medium-altitude *Parinari excelsa* forest and along forest margins. It is dark in color, with large yellow eyes ringed with black, and has sharp needle-pointed nails. Vocalizations are distinctive (Bearder *et al.*, 1995).

Galagoides A. Smith, 1833

The genus may or may not include the “rolling callers” and “incremental callers” listed in Grubb *et al.* (2003)—the species that are central to the genus being the “crescendo callers.” While Bearder *et al.* (1995) recognized only two crescendo-calling species, their taxonomic diversity is probably far greater than this (Groves, 2001; Grubb *et al.*, 2003), and the two species of Bearder *et al.*

(1995) probably actually represent species-groups. The two groups are widely sympatric across the Central and West African rainforest belt.

Thomas's bushbaby, *Galagoides thomasi* (Elliot, 1907). The common small rainforest bushbaby of western Uganda, it extends at least from Bwindi in the south to the forests east of Lake Albert in the north, and in DRC at least to Idjwi island in Lake Kivu. Vocalizations resembling it, but not necessarily identical, have been recorded by Bearder *et al.* (1995) as far west as Cameroon, Gabon, and Bioko island.

This is the largest of the Central African crescendo callers, the skull length being always above 40 mm. It is larger and more blackish grey than others, with a more conspicuous median facial white stripe.

Demidoff's bushbaby, *Galagoides demidoff* Fischer von Waldheim, 1806. On the evidence of vocalizations, Bearder *et al.* (1995) recorded *G. demidoff* in the Ugandan sector of Semliki forest. Vocalizations attributed by them to this species are rather uniform across the West and Central African rainforests, but physical phenotypic diversity is considerable (Groves, 2001), so that it is probable that there are several species in the group rather than one.

Otolemur Coquerel, 1859

The generic distinctiveness of the greater galagos or thick-tailed bushbabies has been acknowledged for many years. They live in forested regions, but not strictly rainforest. The number of species is still unclear; two are generally recognized, but Kingdon (1997) added a third, *Otolemur argentatus*, citing several differences, in particular the structure of the penis. Groves (2001:105) noted that externally the Lake Victoria *Otolemur* “can barely be distinguished” from those from Angola, and that the name *monteiri* (given to the Angolan form) has 50 years' priority over the name *argentatus* (given to the Lake Victoria form).

Silvery Greater galago, *Otolemur monteiri* (Bartlett, 1863). This is a large, usually silvery-white, bushbaby, with dark hands and feet, and is creamy yellow on the midline of the underparts. The tail is often nearly white. Melanistic individuals are common.

The Uganda subspecies is *Otolemur monteiri argentatus* (Lönnerberg, 1913). It reaches Uganda only in the far southwest, on the borders of Tanzania and Rwanda.

Lorisidae Gray, 1821***Perodicticus* Bennett, 1831**

Grubb *et al.* (2003) predict that this genus will prove to contain several valid species, but until further research is done only one can be recognized.

Potto, *Perodicticus potto* (Müller, 1776). This is a rainforest species, extending from DRC through Uganda as far east as the Kakamega forest in Kenya. The “eastern subspecies” is designated *Perodicticus potto ibeanus* Thomas, 1910; as noted above, this may turn out to be a distinct species. The names *arrhenii* and *nebulosus* were given to pottos from eastern DRC (Masisi and Ukaika, respectively), near the border with western Uganda.

HAPLORRHINI: SIMIIFORMES**Cercopithecoidea Gray, 1821: Cercopithecidae Gray, 1821**

Both subfamilies of Cercopithecidae occur in western Uganda.

***Cercopithecinae* Gray, 1821**

Groves (2001) divided this subfamily into two tribes, whose validity and content have recently been confirmed by molecular studies (Tosi *et al.*, 2003).

Cercopithecini Gray, 1821. The number of genera in this family has recently been thrown into question by the finding of Tosi *et al.* (2004) that the genus *Cercopithecus*, as traditionally recognized, is nonmonophyletic. It turns out that the *Cercopithecus lhoesti* species-group is part of a clade containing *Chlorocebus* (vervets) and *Erythrocebus* (patas). The postcranial skeleton of the *Cercopithecus lhoesti* species-group shows similarities to that of patas monkeys and, to a lesser extent, to that of vervets (Gebo & Sargis, 1994), but the skull does not (Verheyen, 1962).

The question is how to recognize this taxonomically? Tosi *et al.* (2004) list the options: transferring both the lhoesti group and the patas monkey to the genus *Chlorocebus*, or splitting up the clade into three different genera—*Chlorocebus* for vervets only, *Erythrocebus* for patas, and *Allochrocebus* for the lhoesti group. They indicate that they marginally prefer the first of these two options.

Preliminary determinations indicate that the divisions between the three subclades are deep, probably late Miocene (T. Disotell, personal communication). If this is so, the time criterion recommended by Goodman *et al.* (1998) is amply met, and even more so the modified one of Groves (2001). Therefore, it is appropriate to recognize three separate genera among the terrestrial cercopithecins:

Chlorocebus Gray, 1870. These are predominately wooded savannah monkeys, not rainforest. There are several species in the genus, although they may well not be precisely as delimited by Groves (2001), and a full revision is needed. Western Uganda has two species that are parapatric and hybridize.

Tantalus monkey Chlorocebus tantalus (Ogilby, 1841). This species extends into Uganda from Sudan, and extends as far south as the latitude of Entebbe, and west into the DRC (Mawambi in the north, Rutshuru plains in the south), east into Kenya. The dorsum is grizzled olive brown, the limbs grey with blackish digits, the underparts white, the tail greyer with a white tip and a white basal tuft, the scrotum sky blue surrounded by a long orange tuft. There is a black line from eye to temple, separating the sinuous, tapered brow-band from the long, stiff whitish yellow, black-tipped cheek whiskers. The subspecies in Uganda is *Chlorocebus tantalus budgetti* (Pocock, 1907).

Vervet monkey Chlorocebus pygerythrus (F. Cuvier, 1821). This is the southwestern Ugandan species, whence it extends into Rwanda and round the southern and eastern shores of Lake Victoria to Entebbe. The dorsum, limbs, and tail are fawn to orange yellow, the hands, feet, and tail-tip darker, the underparts whitish often infused with reddish, the tail base red but without tufts, the scrotum turquoise blue. There is no black line, so the white face ring is complete; the cheek whiskers are shorter and speckled. The Ugandan subspecies is *Chlorocebus pygerythrus rufoviridis* (I. Geoffroy St. Hilaire, 1843).

Where this species meets the last, there are hybrids along with the parent forms. The hybrid zone has been described in some detail by Dandelot (1959), who maps it as extending approximately from the Kazinga Channel southeast to the Tanzanian border.

Erythrocebus Trouessart, 1897. There is a single species in this genus:

Patas monkey, Erythrocebus patas (Schreber, 1774). The patas monkey in Uganda is found only north of the latitude of Lake Albert, and north of the Victoria Nile.

Allochocebus Elliot, 1913. As explained above, what has hitherto been called the *Cercopithecus lhoesti* group is here recognized as a distinct genus. They are robustly built monkeys, with distinct terrestrial adaptations in the postcranial skeleton (Gebo & Sargis, 1994).

L'Hoest's monkey, Allochocebus lhoesti (Sclater, 1899). This mainly terrestrial monkey is known from several rainforest areas, predominately in montane forest regions: Bwindi, Kalinzu, and Kibale. It is black with an orange, speckled dorsal saddle, and has bushy white cheek whiskers.

Cercopithecus Linnaeus, 1758. With the expulsion of the lhoesti group, the genus *Cercopithecus* becomes a homogeneous group of agile, generally brightly colored, short-faced arboreal rainforest monkeys. Four of the seven species-groups have representatives in western Uganda. These groups are the *cephus*, *mitis*, *mona*, and *neglectus* groups; three of these are taxonomically simple, but the *C. mitis* group is diverse and somewhat controversial.

Red-tailed monkey, Cercopithecus ascanius (Audebert, 1799). This species, widespread in Central Africa, extends into western Uganda as far north as Budongo, to the shores of Lake Victoria (including Buvuma Island) and into Kenya (Kakamega Forest). It is distinguished by its white heart-shaped nose spot, white ear tufts and red tail. The subspecies in Uganda is *Cercopithecus ascanius schmidti* Matschie, 1892, which is so strikingly—and, apparently, consistently—different from other members of the species that it should probably be ranked as a distinct species.

Blue monkey, Cercopithecus mitis Wolf, 1822. Blue monkeys, like Redtails, are found in all the western forests of Uganda and across it into Kenya, where the range is much wider than the Redtail and it extends to the Rift Valley (and is represented east of it by a related species, *Cercopithecus albogularis*), and north into Ethiopia. In Uganda it reaches higher altitudes than the Redtail.

The subspecies in western Uganda is *Cercopithecus mitis stuhlmanni* Matschie, 1893, which is not closely related to *Cercopithecus mitis mitis* (Grubb *et al.*, 2003), and may not in fact be conspecific. Outside Uganda it occurs in the Ituri and Semliki districts of DRC to west of Lake Kivu, and west as far as the Lualaba. In Uganda, it is found in all the western forests from Budongo south to about Lake George, including Kibale (where it is rare), Semliki, and the Rwenzoris. It was recorded by Kingdon (1971) in Bugoma, but appears no longer to occur there. It is characterized by the dark speckled blue-grey color, with dark (sometimes partly black) legs, paler underparts, and black crown, which contrasts strongly with a light speckled grey frontal diadem.

Silver monkey, *Cercopithecus doggetti* Pocock, 1907. This monkey replaces the Blue monkey, to which it is very closely related, in the southwest, from the Virungas and Maramagambo and Bwindi forests, east to Sango Bay; south of the border it extends into Rwanda, Burundi, and the mountains bordering Lake Tanganyika. Darker animals, presumed to be hybrids with *Cercopithecus mitis stuhlmanni*, are known from some areas of the eastern DRC, in the Rift mountains on the western side of Lakes Edward, Kivu, and Tanganyika as far as 4° S. It is light silvery grey-brown, with black feet and arms, dark grey legs, long grizzled cheek whiskers, and black crown corresponding with a pale buff-speckled frontal diadem. In some respects it is a paler (more silvery) version of a Blue monkey, but the respective distributions of the two are complex, and need elucidation by careful field observations.

Golden monkey, *Cercopithecus kandti* Matschie, 1905. This is the third presumptive species of the *C. mitis* group to occur in Uganda. It is bright golden colored, with black limbs and tail, and black crown contrasting with the golden cheeks and frontal diadem. In the field, females appear distinctly more brightly colored than males (Twinomugisha *et al.*, 2003).

The distribution centers on the high altitude forests of the eastern Virungas (not the Hagenia forests of the western Virungas), but is also claimed to occur in Bwindi and in the Nyungwe forest of southern Rwanda. In all these areas, *Cercopithecus doggetti* has also been recorded, but Twinomugisha *et al.* (2003) did not encounter it in Mgahinga although they cite an unpublished thesis by Werikhe (1997) that recorded few *C. doggetti* there in the past. There are also

grey-olive monkeys that may be hybrids between them; to this color type the name *schoutedeni* has been given. There are two explanatory models for this situation: *Cercopithecus kandti* is a high altitude species whose range has been progressively invaded by *Cercopithecus doggetti* until it is now restricted to the highest altitudes; or it is not a separate taxon at all, but simply a high-altitude morph of *Cercopithecus doggetti*.

I prefer the first explanation, because the pelage pattern is not simply a golden variant of that of *Cercopithecus doggetti*, and because of the existence of the “*schoutedeni*” intermediates. In fact, the latter may constitute a different taxon yet again, as they are reputed to form the entire population on Idjwi and Shushu islands in Lake Kivu. This may be a case where mtDNA and Y chromosome DNA could help to untangle potential ancestral strands.

Dent's mona, *Cercopithecus denti* *Thomas, 1907*. This representative of the *Cercopithecus mona* group is widespread in eastern DRC and enters Ugandan territory only in the Semliki forest, where, according to Kingdon (1971), it lives in high canopy mixed forest. It also occurs in Rwanda. It is dark brown with blackish limbs and white underparts sharply demarcated from the dark upper side. The head is yellowish, set off with black lateral crown stripes.

De Brazza's monkey, *Cercopithecus neglectus* *Schlegel, 1876*. A heavy-bodied, short-tailed largely terrestrial monkey favoring swamp forests. Its distribution in western Uganda is curiously restricted to the Lake Albert region; it is found again at Sango Bay, and then again on Mt. Elgon in the far east.

Papionini *Burnett, 1828*

Papio Erxleben 1777. Baboons are widespread in western Uganda; here and in the neighboring northeastern DRC they penetrate more deeply into rainforest than is usual for baboons. Of the five species, one occurs in Uganda:

Olive or Anubis baboon, *Papio anubis* (*Lesson, 1827*). A sort of “patchwork” morph, described as *Papio tessellatum*, of this species predominates in rainforest habitats. The light and dark bands of the hairs in this morph happen to coincide over wide areas to give the patches of dark and light colors.

Lophocebus Palmer, 1903

These arboreal mangabeys were formerly included with the true “white-eyelid” mangabeys in *Cercocebus*, but they are nowadays universally separated from them. *Lophocebus* are closely related to baboons, while *Cercocebus* are related to mandrills. Molecular clock estimates (Goodman *et al.*, 1997) suggest that *Mandrillus* separated from *Cercocebus* only in the Pliocene, and if this rather shallow time depth is corroborated then it would be appropriate to combine them into a single genus; it is unclear when *Lophocebus* separated from *Papio* and *Theropithecus*.

Gray-cheeked mangabey, *Lophocebus albigena* (Gray, 1850). Mangabeys are widespread from the DRC border to Sango Bay, and are especially common in swamp forests. They are absent from Budongo but occur in Kibale; in Bugoma, according to Kingdon (1971), they are “almost the only monkey.”

The Uganda mangabey was included by Groves (1978) in the subspecies *Lophocebus albigena johnstoni* (Lydekker, 1900), which elsewhere was distributed in northern and eastern DRC; but, to judge by the skull, Ugandan mangabeys are noticeably smaller, and may rate a different subspecies, in which case the name *ugandae* Matschie, 1913 is applicable.

Colobinae Jerdon, 1867

Colobus monkeys, both red and black-and-white, are presently numerous in the forests of western Uganda. Their high biomass masks a disconcerting vulnerability; it is as well to remember that the only primate taxon that seems to have been exterminated during the 20th century was a red colobus (Oates *et al.*, 2000b).

Piliocolobus Rochebrune, 1887

Although all red colobus have been traditionally included in one single species, it is very clear that this is an oversimplification. There are several species, distinguished by characters of pelage and skull, vocalizations, and other features (Groves, 2001; Grubb *et al.*, 2003). The Ugandan red colobus, therefore, is not to be referred to as *Piliocolobus* (or *Procolobus*, or *Colobus*) *badius*; that name denotes a West African species.

Ugandan red colobus, *Piliocolobus tephrosceles* (Elliot, 1907). This species has long, loose glossy black dorsal pelage, with a red crown, light to white underparts, dull light grey forearms and legs, and light tufts at the tail base. There are also prominent tufts at the base of the ears, and a prominent dark red-brown forehead crest bordered by a black stripe that runs back to the temporal region.

The distribution is patchy; it is abundant in Kibale, but absent from Bugoma and the Kagombe–Matiri forest complex, and it does not reach Budongo. South of Uganda, the species occurs in suitable habitats along the whole eastern shore of Lake Tanganyika, to Lake Rukwa in far southern Tanzania. Ugandan examples tend to be more red-tinged, with a lighter grey-brown rump than of those from further south.

Central African red colobus, *Piliocolobus foai* (Pousargues, 1899). This diverse species, hard to define, includes a diversity of forms mostly from northern and eastern DRC. All have dark to black hands and feet, red crown, black brow-band, and light-colored cheeks. One population enters Uganda, where it occurs in the Semliki forest. The subspecies is *Piliocolobus foai semilikiensis* (Colyn, 1991). It is distinguished from *P. tephrosceles* by having legs blackish to reddish grey, and arms red-brown, with black hands (instead of all four limbs being dirty grey); throat reddish, and rest of underparts and inner aspects of limbs grey (instead of white or whitish); and pelage short and dull-colored (instead of long and shiny) (Colyn, 1991).

Colobus Illiger, 1811

Black-and-white colobus are represented in Uganda by two species, about whose distinctness there is no doubt. While, overall, *C. guereza* has a more northerly range and *C. angolensis* a more southerly one, they overlap in the Ituri forest.

Mantled guereza, *Colobus guereza Rüppell, 1835*. In western Uganda, this species is found west of the Nile, in all forested areas as far north as Budongo. The subspecies is *Colobus guereza occidentalis* Rochebrune, 1887, in which the white flank-veil or mantle is shorter than in other subspecies, and the white tail tuft occupies only a third of the length of the tail. It extends north into southernmost Sudan and west through northern DRC into Congo, Cameroon, and northeastern Gabon.

Angola colobus, *Colobus angolensis Sclater, 1860*. This species has a restricted distribution in Uganda. It occurs in the Semliki region, where it replaces *C. guereza* in the montane forests of the Rwenzoris (Kingdon, 1971); and in the forests of Mt. Kakuka, Maramagambo, Kaiso, Katera, and Sango Bay. The subspecies in Uganda is said to be *Colobus angolensis ruwenzorii* Thomas, 1901, which ranges south into Rwanda, Burundi, and northwestern Tanzania, and in DRC it occurs on Mt. Kahuzi and along the Ruzizi River. A different subspecies, *Colobus angolensis cottoni*, is widespread in the northern DRC, and extends at least to the borders of the Semliki valley according to Colyn (1991). It is very different in appearance from *C. a. ruwenzorii*, having much thinner white shoulder tufts (“epaulettes”), a longer grey terminal zone on the tail, and no white in the pubic region. The two possibly should be regarded as different species. *C. a. ruwenzorii* is closely related to an East African form, *C. a. palliatus*.

Hominoidea Gray, 1825: Hominidae Gray, 1825

There are two subfamilies in this family: Ponginae (of which the only living representative is the Asian orangutan) and Homininae, which includes *Gorilla*, *Pan*, and *Homo*.

Homininae Gray, 1825

Of the three genera, *Gorilla* is more divergent from *Pan* and *Homo* than these are from each other. A strong case has recently been made that *Pan* ought to be sunk into *Homo*, in effect making chimpanzees a kind of human being (Goodman *et al.*, 1998; Watson *et al.*, 2001; Wildman *et al.*, 2003).

Gorilla I. Geoffroy St. Hilaire, 1853

Groves (2001) divided the genus into two species: *Gorilla gorilla*, found in West Central Africa; *G. beringei*, found in Uganda, Rwanda, and DRC.

Eastern gorilla, *Gorilla beringei Matschie, 1903*. In Uganda, Eastern gorillas occur in Mgahinga (the Uganda sector of the Virunga Volcanoes) and in Bwindi. The Virunga population belongs to the subspecies *Gorilla beringei beringei*, the Mountain gorilla. According to Sarmiento *et al.* (1996a,b), the

Bwindi gorillas differ in several respects from those in Virunga. The possibility that they are different is intriguing, and can be resolved only by larger samples, especially from Bwindi. The problem must be approached by assessing whether there are heritable differences between them, such that most (presumably not all) individuals can be correctly sorted; ecological differences are not strictly relevant, except as possible explanations for why they may differ.

Pan Oken, 1816

Common chimpanzee, *Pan troglodytes Blumenbach, 1775*. This species is no longer “common,” but is declining throughout its range. Uganda is guardian to one of the relatively few populations that is both substantial and stable. Chimpanzees occur in all the western forests, north as far as Budongo (A recent survey reported a small number of chimpanzees further north, in the Otzi Forest Reserve; see Plumptre *et al.*, 2003).

Hitherto, all common chimpanzees from Uganda, Sudan, Rwanda, Burundi, Tanzania, and the northern and eastern parts of DRC have been regarded as belonging to a single subspecies, *Pan troglodytes schweinfurthii* (Giglioli, 1872). Recently (Groves, 2005), I compared measurements of different geographic samples of skulls, and concluded that not one but two subspecies are represented, as follows:

- *Pan troglodytes schweinfurthii* (Giglioli, 1872): northern and eastern DRC into southernmost Sudan, east to the Ituri region and Lakes Edward and Albert, and southeast to Lake Kivu. Large size, with relatively long and wide upper face, and wide braincase.
- *Pan troglodytes marungensis* (Noack, 1887): Rutshuru district to western Uganda south to Rwanda, Burundi and northwestern Tanzania; Kivu district south through Maniema and the Itombwe Mountains to Marungu. Small size, with relatively broad muzzle and fairly long palate.

The Ugandan subspecies would therefore be *marungensis*, not *schweinfurthii*. I am confident that this would apply to those from the southern part of western Uganda, but my Ugandan sample included mainly skulls from the far southwest (bordering Rutshuru and Rwenzori). I had only a single skull from Budongo and one from Toro, so their allocation to the newly resurrected subspecies *marungensis* must be provisional only.

BIOGEOGRAPHY OF UGANDA'S PRIMATES

The primates and other fauna of the western Ugandan forests are generally regarded as “overspills” from the northeastern rainforests of DRC, the “East-Central Primate Zone” of Grubb (2001). Within this zone, Grubb distinguishes two Centers of Endemism: an Ubangui-Uele and a Kivu centre. Some discussion of the East-Central Primate Zone, placed in the context of African mammal zoogeography in general, seems necessary to put Uganda’s primates into some perspective.

The African Forest Biome is divided into five faunistic regions: Western, West Central, East Central, South Central, and Eastern (Grubb, 1978). These have substantially different subsets of the general forest mammal fauna, with different duikers, dwarf antelopes, squirrels, genets, and so on, as well as primates. The East Central region is divided from the South Central by the great bend (Cuvette Centrale) of the Congo/Lualaba; to the west, it may be divided from the West Central by the Oubangui (Ubangui), but where detailed distributions are known the divider actually turns out, in some cases at least, to be a much more easterly tributary of the Congo, the Itimbiri, which marks the boundary between *Cercopithecus mitis* and *Cercopithecus nictitans*, and between *Cercopithecus denti* and *Cercopithecus pogonias* (Colyn, 1991). It is plausible that in the Middle Pleistocene the Oubangui flowed west into Lake Chad, and it was the Itimbiri that carried most of flow that is now carried by the Uele, the major tributary of the Oubangui; it would then be only rather recently that the Oubangui was captured by the Congo.

There is no doubt, certainly, that the area of highest diversity of primates in the East-Central region is the Kivu area. Here are found not only apparently widespread (perhaps only because poorly studied) species like *Galagoides demidoff*, *Galagoides thomasi*, and *Perodicticus potto*, but all the taxa that are characteristic of the region, and wholly or partly endemic to it: *Galago matschiei*, *Gorilla beringei*, *Lophocebus albigena*, *Cercocebus agilis*, *Allochrocebus lhoesti*, *Cercopithecus (ascanius) schmidti*, *Cercopithecus denti*, *Cercopithecus hamlyni*, *Cercopithecus (mitis) stuhlmanni*, *Ptilocolobus foai*, and the *Colobus cottoni/cordieri/prigoginei* group. These have spread varying distances to the east; *Cercocebus agilis* and *Cercopithecus hamlyni* have not reached Ugandan territory at all, *Cercopithecus denti* and *Ptilocolobus foai* (and *Galagoides demidoff*) enter Uganda only in the Semliki valley, while the others all have substantial Ugandan populations.