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;

Colin Groves • School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia.

Primates of Western Uganda, edited by Nicholas E. Newton-Fisher, Hugh Notman, James D. Paterson, and Vernon Reynolds. Springer, New York, 2006.

- 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 fieldwork. 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* (Lönnberg, 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.

Allochrocebus *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, Allochrocebus 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 tesselatum*, 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 in 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*, *Piliocolobus 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 *Piliocolobus foai* (and *Galagoides demidoff*) enter Uganda only in the Semliki valley, while the others all have substantial Ugandan populations.

A number of authors, notably Colyn (1991), have noted that there is an odd hiatus within the range of two species of colobus in the Kivu region. The southern boundary of *Colobus angolensis cottoni* is the Lindi River; there are no black-and-white colobus in the Kivu lowlands until the Ulindi is reached, and south of this *C. a cordieri* occurs. The southern boundary of *Piliocolobus foai ellioti* is the Maiko River, south of which there is again a hiatus (though smaller than that within *C. angolensis*), until the Ulindi, south of which *P. f. foai* is found (there is one questionable record of red colobus north of the Ulindi, south of the Lowa). It is especially interesting that the hiatus in the range of red colobus is precisely the area where *Gorilla beringei graueri* extends into the lowlands, toward the Lualaba, and what makes this even more intriguing is that almost the entire western (West Central region) range of gorillas also fills a hiatus within the range of red colobus.

In western Uganda there is a strong north–south division in primate faunas, but it is uneven (Table 1). The Savannah Biome has markedly distinct Northern and Southern savannah mammalian faunas, and some groups of primates have a northern and a southern vicar, but the patas monkey is northern only. Forest primates are mainly southern in distribution; this is not—or not entirely—due to the way the forests themselves change from true rainforest in the south to a drier semievergreen formation to the north, because in two cases there are specifically northern forest representatives: *Colobus guereza*, replacing *Colobus angolensis*, and *Cercopithecus mitis stuhlmanni*, replacing (and, apparently, hybridizing with) *Cercopithecus doggetti*. The colobus is not part of the East Central fauna, but a (mainly forest-edge) species widespread along

Table 1. The north–south division in the primate fauna of western Uganda

Northern	Southern
Savannah species	
Galago senegalensis senegalensis	*Galago senegalensis sotikae*
Chlorocebus tantalus	*Chlorocebus pygerythrus*
Erythrocebus patas	–
Forest species	
–	*Otolemur monteiri*
Cercopithecus (mitis) stuhlmanni	*Cercopithecus doggetti*
–	*Piliocolobus tephrosceles*
Colobus guereza	*Colobus angolensis*
–	*Gorilla beringei*
–	*?Pan troglodytes marungensis*

the margins of several faunal regions. Only the blue monkey is a genuine East Central taxon.

Superimposed on this is a montane element. The Rwenzoris have no endemics, but appear in some instances to be the conduit for entry of species into Uganda, and at least three species—*Galagoides demidoff*, *Piliocolobus foai*, and *Cercopithecus denti*—got no further. *Colobus angolensis* got no further along this route, but evidently found a second, more successful, southerly route of entry. On the other hand, the Virungas developed two endemics, *Gorilla beringei beringei* and *Cercopithecus kandti*; the former was able to spread into Bwindi when there was a forest connection, but the latter was unable to do so, blocked by the presence of a closely related species, *C. doggetti*.

Three species of primates in the western Uganda forests are not part of the East Central faunal region at all. These are *Piliocolobus tephrosceles*, which does not occur in the DRC at all; *Cercopithecus doggetti*, which perhaps occurs there in the form of hybrids with *Cercopithecus mitis stuhlmanni*, and their recombinants; and *Colobus angolensis ruwenzorii*, which is restricted to the Kahuzi highlands and the Ruzizi River. The ranges of all three extend well south through Rwanda, Burundi, and western Tanzania (*Piliocolobus tephrosceles* extends south to Lake Rukwa). The two colobus—but perhaps not the Silver Monkey—actually belong to Eastern Region sections of their respective genera.

The forests of western Uganda have undergone alternate episodes of contraction and expansion over the past few hundred thousand years. The periods of contraction seem to have been accompanied by lowering of vegetation zones in mountainous areas, most lately during the Last Glacial Maximum (LGM), peaking at about 18,000 bp (Hamilton, 1988). The drying was intense; for example, Lake Victoria apparently dried out completely during the LGM, filled at 14.5 ka during an ultra-wet phase, and, after a reversal in the refilling trend corresponding to the Younger Dryas, finally established a continuous outflow into the Nile at 11.2 ka. The Rift lakes probably did not actually dry out, but certainly rose and fell, and around Lake Albert the evidence of drying, with arid grasslands, was patent (Beuning *et al.*, 1997). These two phenomena have presumably had considerable effects on primate ranges in recent times.

A much older geological phenomenon that would have affected primate distributions was uplift along the Western Rift, which went on throughout the Pleistocene (Andrews & van Couvering, 1975). Some of the cichlid fishes of Lake Victoria show affinities not with those of the Nile, as one would predict from present-day river patterns, but with those of the Congo (Seehausen *et al.*,

2002), indicating a former connection. The lake itself is said to be only about 400,000 years old, formed by blockage and back-ponding of rivers that had once flowed from East Africa into the Congo, and now obtained their headwaters in the Rift mountains. This may relate to the renewed Middle Pleistocene uplift of the Rwenzoris, which, as described by Krafft (1990), was the event that split Lakes Albert and Edward into separate basins.

Vulcanism in the Virunga region goes back to the Late Oligocene, but the formation of the present chain is much more recent: the oldest of the group, Mikeno and Sabinyo, formed between the Late Pliocene and Early Pleistocene, while Muhavura, Mgahinga, Visoke, and Karissimbi were formed as recently as the Late Pleistocene, or even later (Krafft, 1990:10). The Toro-Ankole volcano region has a not dissimilar history; Kiyambogo has an age of 450 ka, and the latest volcanic activity in the region is only 6.5 ka.

These dramatic changes imply a history of continual depopulation and repopulation of western Uganda by primates. Prior to the uplift of the Rwenzoris and Virungas, and the onset of Toro-Ankole vulcanism, continuity between present-day Uganda and the forests of the Congo basin was complete; gradually, this continuity was rendered intermittent. Meanwhile climatic fluctuations saw forests periodically withdrawn from Uganda, then reestablished across the southwest reaching as far as Lake Victoria and severing the northern from the southern savannahs. With each spread of the forests, the East Central fauna spread as far as it could, whether not quite to Uganda, just across the Uganda border (in the Semliki region), or far into Ugandan territory. At the same time, continuity was reestablished with the forests of the Eastern region along the eastern edge of Lake Tanganyika, and two taxa of colobus and one of Cercopithecus (see above) spread north into Uganda. The spread of the two colobus may be what prevented *Piliocolobus foai* and *Colobus angolensis cottoni* from spreading further into Uganda than the Semliki forest; the spread of *Cercopithecus doggetti*, and the further spread of *Colobus angolensis*, however, were checked by *Cercopithecus* (*mitis*) *stuhlmanni* and *Colobus guereza* coming the other way, having apparently entered Uganda around the northern end of Lake Albert.

Most recently, human deforestation of southwestern Uganda has left "orphan" populations of several forest species clinging to the shores of Lake Victoria, isolated from the western forests, and has brought northern and southern savannah populations of *Chlorocebus* and of *Galago senegalensis* into contact, resulting (in the former case at least) in a belt of hybridization.

In summary, the primate fauna of the forests of western Uganda is a unique blend of East Central and Eastern and of montane and lowland forest faunas. Only here do they meet, interact, and overlay. A multitude of questions arise as a consequence. What determines which species shall exist where? Is it chance, or is it competition? Why have some species not spread further than the Semliki? Why have the species from the south apparently spread faster than their sister species from the west? What blocks the further northward spread of red colobus? Or gorillas? Is it lack of time; is it human interference; or is it unsuitable ecological setting? There is a rich research field here, for Ugandan and expatriate primatologists alike.