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The Endemic Uganda Mangabey, *Lophocebus ugandae*, and Other Members of the *albigena*-Group (*Lophocebus*)

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Abstract: Revising the grey-cheeked mangabeys (*Lophocebus albigena* group) in the light of the Phylogenetic Species Concept reveals more taxonomic diversity than was formerly suspected. The three subspecies recognized by Groves (1978) are diagnosably distinct, and are here upgraded to species rank. Most significantly, the mangabeys of Uganda, not recognized as distinct at all in the 1978 revision, are now shown to constitute a fourth species, *Lophocebus ugandae* (Matschie, 1912), which is apparently confined to Uganda, and as such probably Uganda's only endemic primate

Key Words: Mangabey, *Lophocebus albigena*, *Lophocebus osmani*, *Lophocebus johnstoni*, *Lophocebus ugandae*, Uganda endemicity

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Introduction

Mangabeys of the genus *Lophocebus* are allied to baboons (*Papio*) and geladas (*Theropithecus*), whence Kingdon (1997; p.47) calls them "baboon-mangabeys." According to Goodman *et al*. (1998), the three groups diverged only in the mid-Pliocene, some 4 million years ago, which would be too recent to support generic separation under their preferred model (which requires two clades to have diverged at least 7 million years ago in order to merit separate genera). Despite the fact that genera (and families, and orders) are currently recognized in a fashion that is still quite arbitrary (except that they must be monophyletic), the proposal by Goodman *et al.* (1998) to introduce this objective criterion has still not achieved wide acceptance. As such, I here continue to recognize *Lophocebus* as a genus.

Groves (1978) recognized five taxa, which he classed as subspecies of a single species, *Lophocebus albigena* (Gray, 1850). The five subspecies were as follows:

L. a. albigena (Gray, 1850)
L. a. osmani Groves, 1978
L. a. johnstoni (Lydekker, 1900)
L. a. aterrimus (Oudemans, 1890)
L. a. opdenboschi (Schouteden, 1944)

The last two admittedly stand apart from the other three, and this was given expression in Groves (2001), where *Lophocebus aterrimus* and *L. opdenboschi* were given status as separate species. The three resulting species are certainly diagnosably and geographically distinct, and can be instantly recognized by characters of the crest on the crown, cheek whiskers, and pelage in general. *L. opdenboschi* is particularly poorly known, from only a few localities, along the Kwilu and Kwango rivers in southwestern DRC, and is a prime candidate for future field surveys. Grubb *et al.* (2003) continued to separate *L. aterrimus* specifically, but relegated *opdenboschi* to the status of a subspecies of it; they also expressed some misgivings about the status of the subspecies of *L. albigena*. In the present brief report, I restrict myself to the *L. albigena* group, i.e., the first three 'subspecies' listed above, commonly known as grey-cheeked mangabeys.

The three 'subspecies' remaining in *L. albigena*, after the removal of *L. aterrimus* and *L. opdenboschi*, are briefly described in Groves (2001), but for further details see Groves (1978); beautiful paintings of them will be found in Gautier-Hion *et al.* (1999). The most noticeable distinctions are in the colour of the mantle of elongated hair over the foreparts:

L. a. osmani – rusty-brown,
L. a. albigena – light grey, sometimes with faint straw tones,
L. a. johnstoni – from dark grey-brown to very pale, whitish-grey to chocolate.

In *L. a. osmani* and *albigena*, there is usually a black patch on the nape and withers, but this is rare in *L. a. johnstoni*. The underside is yellow-grey in *L. a. osmani,* but not noticeably

lighter than the upper side in the other two. The cheek-whiskers are long and bright grey or golden-white in *L. a. osmani*; more creamy in *L. a. albigena*; and light grey-brown, passing to white lower down in *L. a. johnstoni,* but the lower cheeks are so thinly haired that this is hardly noticeable. In *L. a. albigena* and *johnstoni*, the crown hair is long and scruffy, often forming two little 'horns' above the brows. The crown hair is 'neater' in *osmani*, and never forms 'horns'.

The distribution of *L. a. osmani* extends from the Cameroon Plateau (Batouri district) northwestward across the Sanaga River to Mamfe on the border of Nigeria; mostly it seems to occupy higher altitudes, 600 m and more, except in the Edea district which is on the coast to the north of the Sanaga River. The range of *L. a. albigena* extends along the coast south of the Sanaga, then west via northern Gabon to the Ubangi River, skirting that of *osmani* to the southwest, south and east, apparently in low-lying, often swampy forests. *L. a. johnstoni* is found in the DRC from Lisala District (2°57'N, 20°07'E) east to the Ituri and Semliki Forests, and from Kabambare (4°13'S, 27°07'E) in the south to Uele District in the north, and southeast to Rwanda and Burundi. These distributions have been mapped in Groves (1978: reproduced here, Fig. 1) and in Gautier-Hion *et al.* (1999).

I have, for some years now, argued for the so-called 'Phylogenetic Species Concept' (PSC): a species must be 'diagnosable', meaning that it must possess consistent differences, in any apparently heritable character, from others. This offers objectivity and repeatability; recognition of species, the units of biodiversity, should not depend on hypotheses of relatedness or that they "might perhaps" interbreed. I will not repeat the arguments here; they have been set out in Groves (2001) and elsewhere. The first observation that needs to be made about what I previously regarded as subspecies of *Lophocebus albigena* is that they are consistently different: under the PSC, they would all rank as distinct species.

For a symposium on mangabeys at the International Primatological Congress in Entebbe, June 2006, Michele Hawkins and I returned to the data which had formed the basis of the revision by Groves (1978). Very little material has accumulated since then; I have not studied the *Lophocebus* material in the North American collections, but the European collections are so copious and have such a wide geographic coverage that they are adequate. It is desktop computers and statistical packages that have in the meantime made all the difference; it is now possible to perform, in a fraction of a second, the sorts of calculations which used to take weeks of preparation, hours of repetitive (and potentially inaccurate) keystrokes, and the need to book time on a central computer system. The gain in flexibility alone makes it all worthwhile! When you are able to try all sorts of ways to analyze the data, all in a single afternoon, you inevitably discover things which you had no inkling of before.

Material and Methods

The material studied, and the methods, and the 17 measurements taken on each skull, are described in Groves (1978), and need not be repeated here. What is new is that the skull measurements were entered in a data file in SPSS version.14.0. Adult male and female variables were entered, separately and in different combinations, both as raw variables and log-transformed, into Discriminant Function Analyses (Direct method), based on geographically constrained samples, which were then grouped as far as the preliminary results warranted. In any given analysis, an attempt was made to avoid Type I Errors ('false positives') by ensuring, where possible, at least as many specimens per group as there were variables in the analysis: the different available sample sizes account for the 'different combinations' mentioned above.

It should be acknowledged right away that, as one referee has pointed out, because Discriminant Analysis 'is very good at distinguishing groups', one must consequently be on the alert for possible circularity. This is why one cannot start by taking 'accepted' taxa for granted: initial samples must be as geographically circumscribed as possible, as if no species/subspecies had ever been described (if samples are large enough).

Results

I first tested the homogeneity of two of the three 'subspecies' by separating them into geographic samples and entering each as a separate group into a Discriminant Analysis (the sample of *L. a. osmani* was not large enough to divide into geographic samples). This was done for males and females separately; only the results for males are shown here.

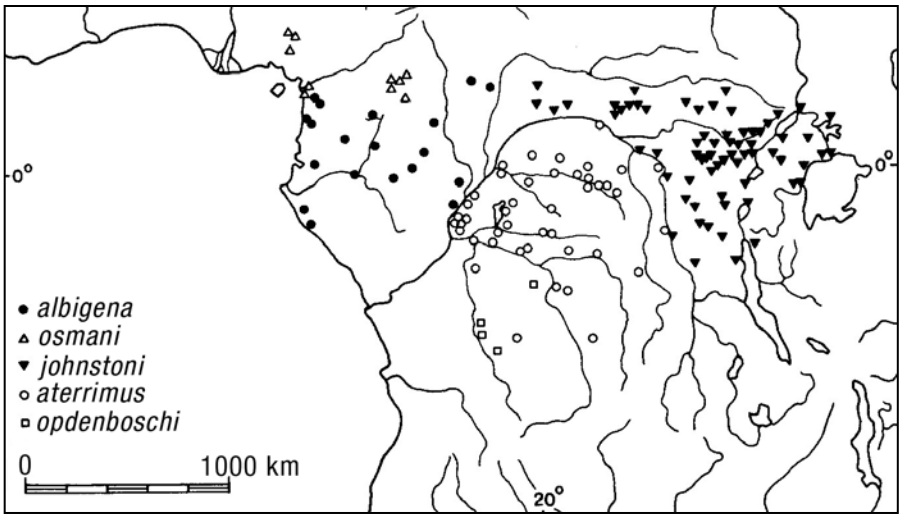

Figure 1. The map of Central Africa showing localities for five taxa of *Lophocebus* that was published in Groves (1978). All were given as subspecies of *L. albigena* at that time.

Figure 2 shows the results for what Groves (1978, 2001) called *L. a. johnstoni*, using nine variables. The Uganda sample stands out strikingly from all the others; no other sample is at all well differentiated, and all the individual specimens, including the one from Burundi, fall well into the range of those from the non-Uganda ones (i.e., Democratic Republic of Congo). Only a skull from Yangambi (Kisangani District) approaches the Uganda sample somewhat. Inspection of the coefficients shows that Function 1, which separates Uganda from DRC, is heavily weighted positively on Basal Length and Facial Length, and negatively on Palate Length; this means that Uganda skulls are small with short faces but relatively long palates (large masticatory apparatus). The table of classification results (which calculates what proportion of each sample is closer to the mean of that sample than of others) records that all of the 10 Uganda skulls are closest to their own mean, whereas the nine Uele, 28 Ituri, and six PNV (Parc National du Virunga) skulls are intermixed with each other but never closer to the Uganda mean.

Figure 3 compares the western Central African samples allocated by Groves (1978, 2001) to *L. a. albigena* and *osmani*, using this time only six variables, as available sample sizes are smaller. Samples ascribed to *L. a. albigena* separate on average but, even given the relatively small sample sizes, there is in no case anything like a complete separation. The subspecies *zenkeri* has sometimes been recognized (Schwarz 1910; Napier 1981) from the Cameroon coast south of the Sanaga River—and these mangabeys do tend to have the greyest mantles—but this sample (n = 9) is also not strongly distinct (the others are Gabon [n = 3] and Sangha region [n = 7]). Whereas these samples are intermixed, 100% of the *L. a. osmani* sample (n = 6) is correctly classified, indeed it is completely distinguished from any sample ascribed to *albigena*; DF1 is strongly positive on both basal length and bicanine breadth, and strongly negative on palate length. A skull (lacking a skin) from Akouafim, just south of the Batouri region from which some of the *osmani* specimens come, identifies itself clearly as *osmani*.

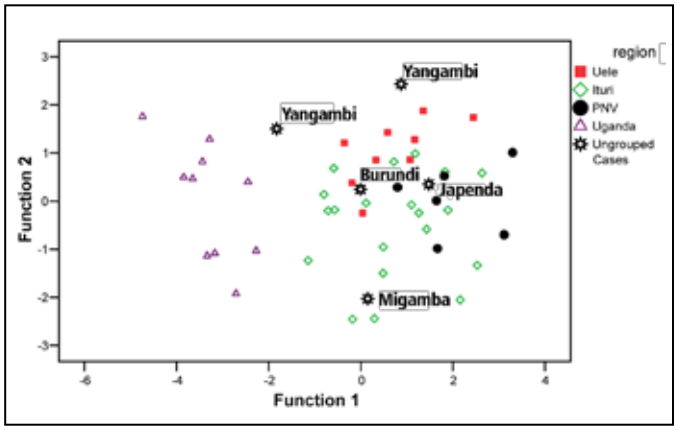

Figure 2. Canonical Discriminant Functions 1 and 2 in samples and individual specimens of males of *Lophocebus albigena johnstoni* (as recognized in Groves 1978 and 2001), utilising nine cranial variables. Function 1 accounts for 86.4% of the total variance, Function 2 for 8.4%.

Figure 5 includes all male skulls of the *L. albigena* group; on the evidence of the results of the first two analyses, all the samples of *L. a. albigena* are combined into one, and the same with *johnstoni* with the exception of the Ugandan sample, so as to give just four groups. Seven variables are used. The Uganda sample (n = 10) still stands out, and again does not overlap with the *johnstoni*-DRC sample (n = 40). The difference between *albigena* (n = 20) and *osmani* (n = 7: the Akouafim specimen has now been added to the original six) has now been to some extent overwhelmed by the separation of Uganda, and they both overlap extensively with the DRC sample. As before, DF1 is strongly positive on Basal Length and Facial Length, and strongly negative on Palate Length.

As just noted, the inclusion of too many groups may 'swallow up' some of the discrimination; so a new analysis was made excluding the Uganda sample (Fig. 6). The three remaining taxa remain incompletely separated; *L. a. johnstoni* is somewhat better differentiated from the two western Central Africa taxa than these are from each other. Recall, however, that when *L. a. osmani* and different geographic groupings of *L. a. albigena* are analysed together, the two taxa separate well, and of course all three are absolutely different in external features.

The analyses using females are not reproduced here, because discrimination is less and sample sizes are less. The sexes are significantly different ($F = 211.614$, $p<0.0001$), but degrees of sexual dimorphism may differ in the different taxa. Individual measurements were plotted out separately to test this. In Total Skull Length (Fig. 7), *L. a. osmani* is by far the most sexually dimorphic: males average somewhat larger than other taxa, whereas females average noticeably smaller than

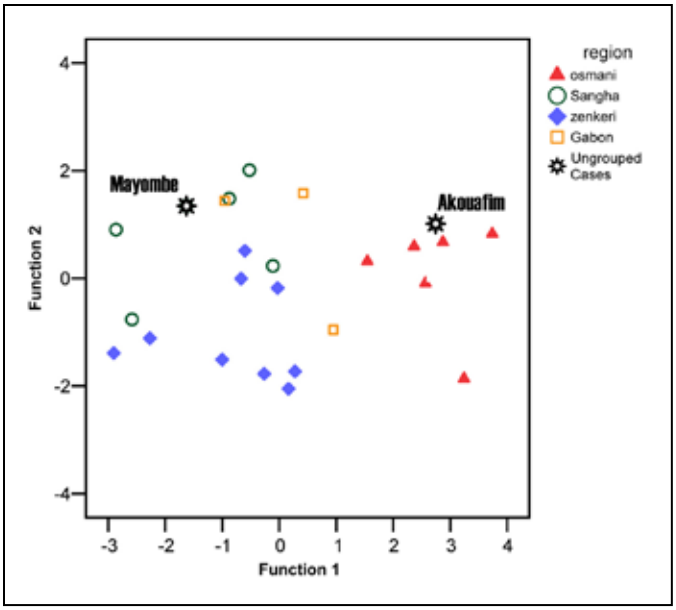

Figure 3. Canonical Discriminant Functions 1 and 2 in samples and individual specimens of males of *Lophocebus albigena albigena* and *osmani*, utilising six cranial variables. Function 1 accounts for 77.1% of the total variance, Function 2 for 21.1%. The name "*zenkeri*" denotes a sample, sometimes recognised as a distinct subspecies, from the Kribi/Bipindi district of the Cameroon coast, south of the Sanaga River.

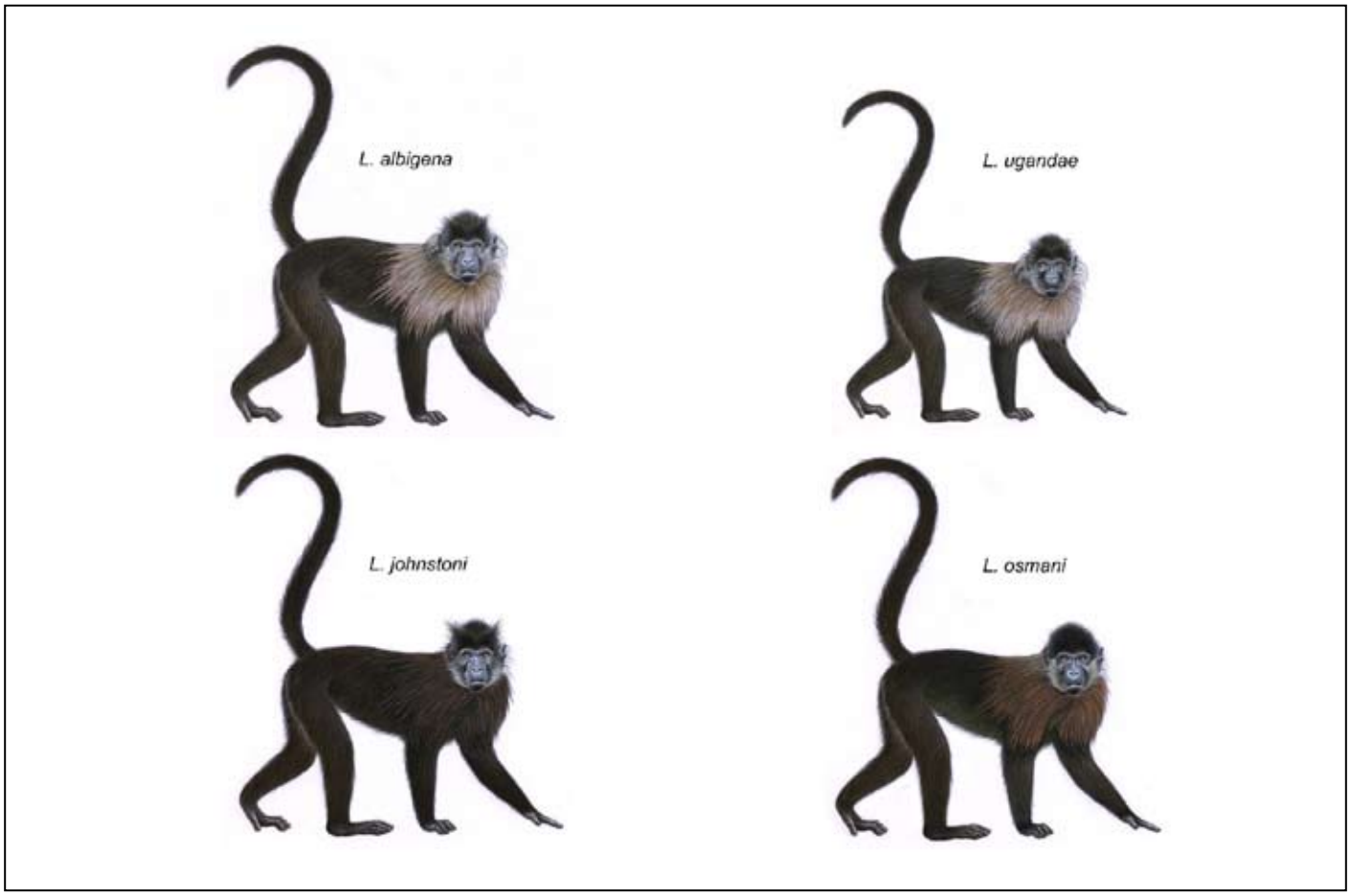

Figure 4. The grey-mantled grey-cheeked mangabey (*Lophocebus albigena*), Ugandan grey-cheeked mangabey (*L. ugandae*), Johnston's grey-cheeked mangabey (*L. johnstoni*), and Osman Hill's grey-cheeked mangabey (*L. osmani*). Illustrations by ©Stephen D. Nash / CI.

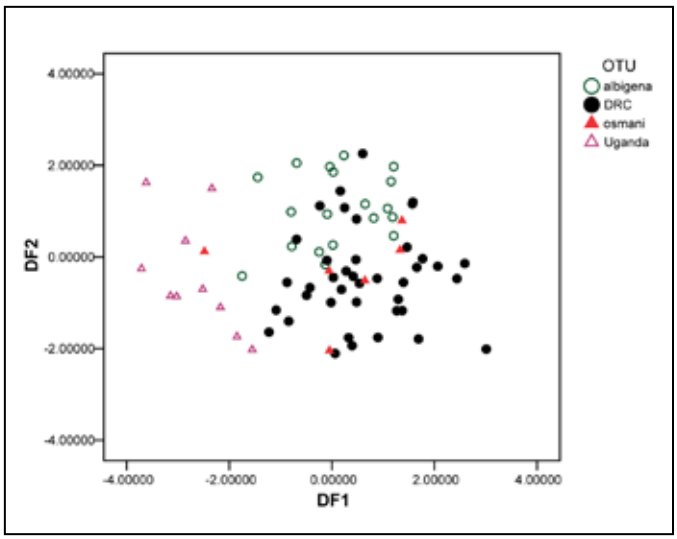

Figure 5. Discriminant Functions 1 and 2 in samples and individual specimens of males of all members of the *Lophocebus albigena* group, utilising seven cranial variables. Function 1 accounts for 56.5% of the total variance, Function 2 for 24.4%. DF3 accounts for the remaining 19.1%, but adds nothing to the discrimination.

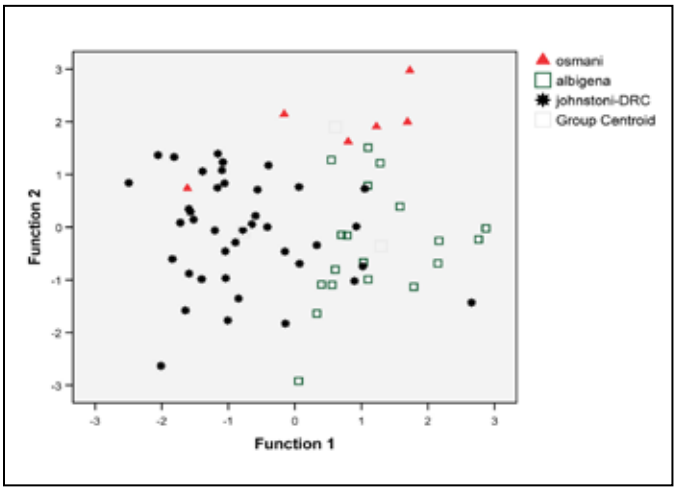

Figure 6. Discriminant Functions 1 and 2 in samples and individual specimens of males of all members of the *Lophocebus albigena* group except for the Uganda form, utilising 10 cranial variables. Function 1 accounts for 71.3% of the total variance, Function 2 for the remaining 28.7%.

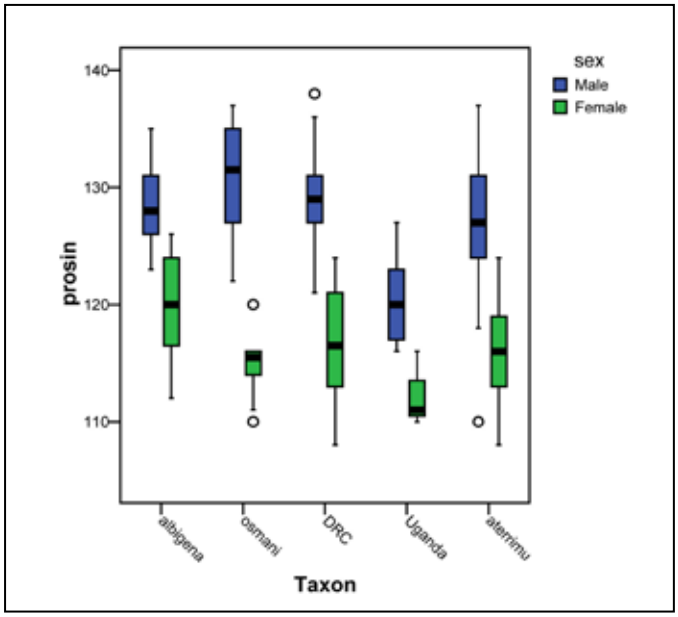

Figure 7. Prosthion-to-Inion distance (=greatest skull length) in adult males and females of the *Lophocebus albigena* group.

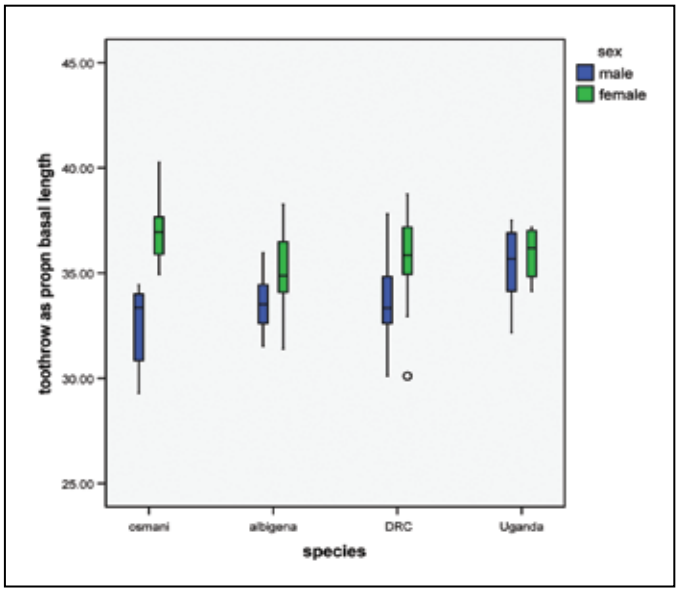

Figure 8. Maxillary toothrow length (premolars and molars) as a percentage of basal skull length (Prosthion to Basion) in adult males and females of the *Lophocebus albigena* group.

all others except for Uganda. Skull size of both sexes is small in Uganda, males being very much smaller than other taxa, females less so.

It is implied by the multivariate analyses that the Uganda taxon, though small in size, has relatively large masticatory apparatus. This is tested by an index relating the length of the maxillary postcanine dentition to basal skull length (Fig. 8). Again, *L. a. osmani* is extremely dimorphic (teeth in females are relatively larger than in males), whereas the Uganda taxon shows no sexual dimorphism at all, as the teeth are relatively enlarged in males as well as females.

Discussion

It is clear from these results that, as far as cranial measurements are concerned, *johnstoni*-Uganda differs more from the taxa *albigena, osmani* and *johnstoni*-DRC than these three do from each other. To a somewhat lesser degree, but still absolutely (without overlap), the taxon *osmani* differs from *L. a. albigena*. We have here four diagnosably distinct taxa, i.e., four species. Three of these are already recognized as distinct subspecies by Groves (1978), and all that needs to be done is to raise them to specific rank: *Lophocebus albigena*, *L. osmani* and *L. johnstoni*. But this analysis has shown that "*johnstoni*" actually consists of two diagnosable entities: one in DRC, Rwanda and Burundi, the other confined to Uganda. Which is the true *Lophocebus johnstoni*, and what is the correct name for the other?

Semnopithecus albigena johnstoni was described by Lydekker (1900) from a living specimen in the London Zoo, said to have been "brought from the country Barundi, at the north end of Tanganyika". Schwarz (1910) fixed the type locality as present-day Burundi; as noted above, a skull from Burundi falls well within the sample from DRC, which is therefore the species that takes the name *Lophocebus johnstoni*. Groves (1978) lists four junior synonyms for *johnstoni*, of which one has its type locality within Uganda: *Cercocebus* (*Leptocebus*) *albigena ugandae* Matschie, 1912 (type locality 'Chagwe'). The available name for the Uganda mangabey is therefore *Lophocebus ugandae* (Matschie, 1912).

The location of Chagwe was given by Groves (1978) as "Nbondo, Nile mouth at Lake Albert", but it is in fact "a large area north of Lake Victoria, east of Kampala, west of the Nile and Jinja, and a little northwards towards Bugerere" (Robert Kityo, pers. comm.), approximately 00°17'– 00°33'N, 32°40'–33°11'E, and more correctly called Kyagwe (Fig. 9). The main forest block in this district, hence probably the restricted type locality, is Mabira Forest.

As we have seen, the skull of *Lophocebus ugandae* differs from other species of the *L. albigena* group in its small size, especially in the males, reduced sexual dimorphism and relatively large masticatory apparatus. Multivariate analysis separates the species 100% from others of the group, although in any one skull measurement there may be a slight overlap.

Matschie (1912) described *ugandae* as having a pale chocolate mane and breast, contrasting with the dark grey-brown mantle of the mangabey of the Ituri Forest. Groves (1978, p.26) described the mantle as "darkish brown, often not too much lighter than body colour": this had reference mainly to the very large Ituri Forest series in the Tervuren Museum. Allen (1925: p.344) likewise described 35 adults from the upper Uele District and Ituri lowlands as varying "but little in colour tones, but considerably in the extensive brownish areas", the mantle being "brown (light seal-brown to pale sepia)". Consistent with this, the type of *johnstoni* (in the Natural History Museum, London) has a mantle which contrasts comparatively little with the body colour. Skins from Uganda in this Museum are more variable, but tend to be somewhat

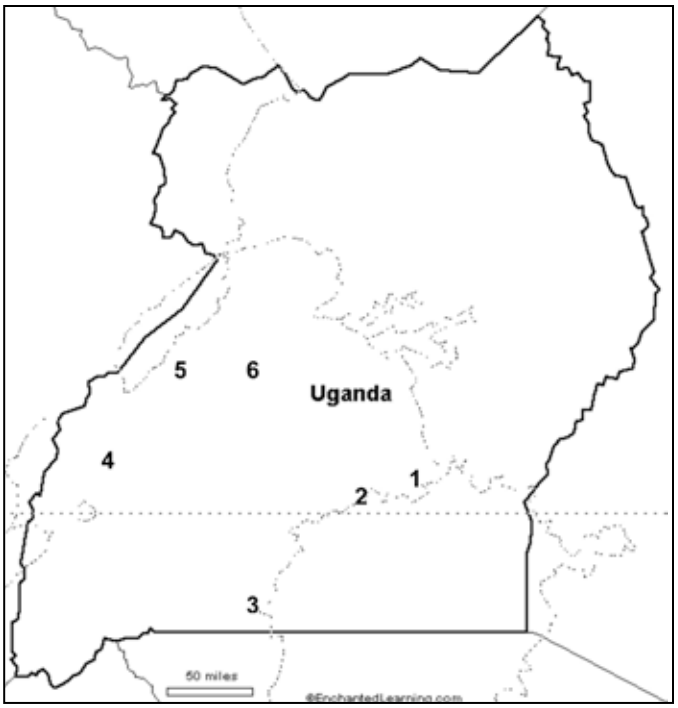

Figure 9. Known distribution (based on museum records) of *Lophocebus ugandae*. 1. Mabira forest (= Kyagwe; type locality). 2. Bujuko and Bukasa forests. 3. Sango Bay forests. 4. Kibale and Mpanga forests. 5. Bugoma forest. 6. Budzi.

more contrasted, the more easterly specimens (Mabira, Bujuko, Kampala District) being light yellow-brown, whereas some of those from Bunyoro, Toro and Sango Bay are somewhat darker grey-brown. Photos published on the web from Kibale forest (see <www.shunya.net/Pictures/Uganda/Kibale/Kibale.htm, www.msnbc.msn.com/id/13421030/, en.wikipedia.org/.../fridge_door>) are also grey-brown, varying from medium to rather light. In summary, the pelage characters need to be restudied, but the evidence to date indicates that the mantle in *Lophocebus ugandae* contrasts more with the general body colour than that in *johnstoni*.

Lophocebus ugandae seems most numerous in the forests along the northern and northwestern shores of Lake Victoria, including Mabira Forest (the type locality), Bujuko and Bukasa Forests, and Sango Bay; and it also occurs in the forests along the eastern side of the Albertine Rift, especially Kibale (Fig. 9). *Lophocebus ugandae* is not known from DRC or Rwanda, but only within Uganda; as far as we know, it is Uganda's only endemic primate.

Acknowledgments

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