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The taxonomic diversity of the Colobinae of Africa

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Summary - *The colobine monkeys of Africa are much more diverse than is often realized; in the case of Red Colobus (genus* Piliocolobus*), this is because the species replace each other geographically, and there is even some interbreeding where their ranges meet. It is not possible to make a modern taxonomic revision of Black-and-white Colobus (genus* Colobus*), in the absence of a thorough modern study to determine consistency of the differences between the taxa deemed to be subspecies of the two polytypic species,* C. angolensis *and* C. guereza*. Red Colobus, in particular, are by their behaviour extremely vulnerable, and one species is presumed extinct, and another has not been seen for some years.*

Keywords - *Colobus, Taxonomy, Biogeography, Piliocolobus, Procolobus, Africa, Cercopithecoidea.*

Introduction

The Old World monkeys are divided into two subfamilies: Cercopithecinae and Colobinae. The Colobinae are commonly known as 'leaf eaters', but this is too sweeping: while it is true that they are capable of subsisting on leaves to a much greater degree than probably any other primate, detailed field study has shown that many species are in fact specialized seed eaters as much as leaf eaters. The stomach has been described by Kuhn (1964). In all of the Colobinae it consists of three (or four) parts. The most conspicuous part is the Saccus Gastricus, an enormous blind sac in which symbiotic bacteria attack (and possibly detoxify) solid ingesta, fermenting cellulose and hemicellulose, releasing short-chain fatty acids which are directly absorbed into the bloodstream. The bacterial pap, now enriched in protein, moves into the next part, the Tubus Gastricus, where pH gradually drops until the final part, the Pars Pylorica, which corresponds to the simple stomach of other primates and where proper digestion begins. Some genera, including *Procolobus* and *Piliocolobus*, have a fourth stomach compartment, the Praesaccus, at the mouth of the Saccus, but its exact function is unknown. Liquid ingesta, especially fruit juices, bypass the fermentation chamber, going directly via a groove (which is closed off into a tube by longitudinal muscle bands) into the Pars Pylorica. The colobine multipartite stomach has been likened to the ruminant stomach, although structurally and probably functionally the stomach of Macropodidae (kangaroos and wallabies) is probably a better comparison. In all three cases, however, the system enables the animal to extract much more energy from its food than can other herbivores, by making complete use of the structural carbohydrates in cellulose and hemicellulose. This is the secret to 'leaf eating'.

The stomach, when full, extends the belly and accounts for between 10.8 and 24.9% of the body weight in records of 14 specimens (10 *Colobus guereza*, three *C. angolensis*, one *Piliocolobus tephrosceles*) in the Kenya National Museum, Nairobi. The molar and premolar teeth of Colobinae are distinguished from those of Cercopithecinae by their high crowns and occlusal relief, and the shortened trigonids. Skeletally, they are characterised by thumbs being short or absent, and somewhat

shortened second toes on the foot. Strasser (1994) detailed other specialisations of the foot morphology. In the skull, mandibular corpus deepens posteriorly, and generally the interorbital pillar is very broad, although in two Asian genera, *Nasalis* and *Simias*, it is narrow as in the Cercopithecinae. The African genera of the Colobinae (which are all known popularly as colobus monkeys) can be distinguished from the Asian genera (which are broadly known as langurs) by lacking a thumb (Fig. 1). In some individuals, a tiny nubbin of a thumb is present, but there is never more than a rudimentary proximal phalanx. In the past, all colobus were commonly put together in a single genus, *Colobus*; Verheyen (1962) retained Black-and-white and Red Colobus together in this genus but split off Olive Colobus into a separate genus *Procolobus*; Kuhn (1967), followed by Grubb et al. (2003), transferred Red Colobus to *Procolobus*, but kept them apart from Olive Colobus in a separate subgenus, *Piliocolobus*; while Groves (2001) recognised all three as separate genera. I continue to regard all three as separate genera.

Systematic account

Colobus. Black-and-White Colobus.

Diagnosis: Skull prognathous but supraorbital torus not strongly developed; sagittal crest hardly ever developed; no suborbital fossa; borders of pyriform aperture rounded; no anterior nasal spine; posterior palatal canals not in deep fossae; choanae and pterygoid fossa narrow, basisphenoid crested, laterally guttered.

In mandible, digastric fossae poorly imprinted; lower margin of jaw curved upward especially at anterior end; ascending ramus upright; coronoid process hooked backward; no symphyseal foramen.

Maxillary incisors elongated, narrow, with no lingual cingulum or tubercle; tips of lateral pair point mediosagittally. Postcanine dentition heavy. The larynx is enlarged, measuring in a male *C. vellerosus* 59mm long by 36mm dorsoventrally and 34mm wide (Hill & Booth, 1957). External nose convex, its septum extending onto upper lip. Ischial callosities in male fused across midline. No perineal swellings. Fur black, with white areas in four out of the five species; infant coat white.

Fig. 1 - African colobines, such as this* Colobus polykomos, *lack thumbs (photo S. Gippoliti).

Procolobus. Olive Colobus.

Diagnosis: Skull not very prognathous, premaxillae vertical; supraorbital arcades thin, curved; sagittal crest develops in adult males; suborbital fossa present; pyriform aperture with sharp margin, often an incipient anterior nasal spine; posterior palatal canals in deep fossae; choanae and pterygoid fossa broad, basisphenoid flat. In mandible, digastric fossae deep, well separated; upper and lower margins of mandible straight, parallel; ascending ramus slopes back; coronoid process rounded; a labial symphyseal foramen.

Maxillary incisors relatively broad, low, with a lingual cingulum and tubercle; lateral incisors somewhat caniniform, their points directed downward. Postcanine dentition not as massive as *Colobus*, but M3 with a tuberculum sextum. The larynx is not enlarged: 20 x 12 x 14 mm (Hill & Booth, 1957). External nose simple. Ischial callosities separate in both sexes. Perineal swellings developed periodically in adult females and temporarily in subadult males. Pelage predominately phaeomelanic; infant coat not strikingly different from adult's.

Piliocolobus. Red Colobus.

Skull generally prognathous, with good supraorbital development; supraorbital arcades straight, robust; sagittal crest develops in adult males; suborbital fossa present; borders of pyriform aperture rounded; no anterior nasal spine; posterior palatal canals not in deep fossae; choanae and pterygoid fossa narrow, basisphenoid crested, laterally guttered. Mandible more as in *Procolobus* but with no symphyseal foramen.

Dentition more as *Colobus* but with no incisor cingulum or tubercle; no tuberculum sextum.

Larynx is barely larger than in *Procolobus*: 24 x 16 x 15mm (Hill & Booth, 1957). External characters in general as in *Procolobus*.

As for species, I employ the Phylogenetic Species Concept (Cracraft, 1983), as argued in detail in Groves (2001). In this view, species are units essentially diagnosed by the possession of fixed heritable differences from other such units. This avoids classifying according to whether one thinks that two distinguishable populations would or would not interbreed were their ranges to meet, or according to one's hypothesis of interrelationships: we should classify species according to how things are observed to be, given the available evidence, not according to how we think things ought to be! There are two drawbacks to this way of viewing species, both of them illustrated by colobus taxonomy. First is that different species may indeed interbreed where their ranges meet, and even form an inextricable hybrid swarm. We just have to acknowledge this as a fact of nature, and we must treat hybrid swarms as valuable populations for conservation purposes in their own right, as illustrating the operation of natural processes. The second drawback is that the state of research in different genera may be at very different stages of understanding; this is the case for the African Colobinae. I have myself carefully studied available specimens of Red Colobus in European and some other museums, and feel confident that I have identified the units, whereas such study as I have made on Black-and-white Colobus is incomplete (with the exception of the West African taxa), and I have no option but to accept the revisions made, using different species concepts, by Colyn (1991) and by David Hull (personal communication). If this results in a rather unbalanced treatment, it is to be regretted but I feel I have no option, as I have no evidence as to what diagnosable units (phylogenetic species) might exist within *Colobus angolensis* or *Colobus guereza* as presently recognised.

Genus COLOBUS Illiger, 1811.

Colobus Illiger, 1811, *Prodr. Syst. Mamm. Avium,* 69.
Colobolus Gray, 1821, *London Med. Repos.* 15: 298.
Guereza Gray, 1870, Cat. Monkeys, Lemurs & Fruit-eating Bats, *Brit. Mus.*, V and 19.
Stachycolobus Rochebrune, 1887, *Faune de Senegambie*, Suppl., Vert., 1: 96.
Pterycolobus Rochebrune, 1887, loc. cit., 96.

Genotype of *Colobus* and *Colobolus*, *Simia polycomos* Schreber; of *Guereza, Guereza ruppellii* Gray; of *Stachycolobus, Colobus satanas* Waterhouse; of *Pterycolobus, Colobus vellerosus* I.Geoffroy.

Oates & Trocco (1983) studied the loud-call (roaring) vocalisations of Black-and-White Colobus, and divided them into three groups: (1) *C.guereza* and *C. vellerosus*, with low-pitched pulsed calls; (2) *C.satanas*, with higher-pitched, fast-pulsed modulated calls, preceded by an endearing cough; (3) *C.angolensis* and *C.polykomos*, with roars of high or indeterminate pitch and pulse rate. This arrangement, though of course it does not necessarily identify all the units in the genus, makes sense phyletically. *C.guereza* is both externally and cranially the most highly derived species, and *C. vellerosus* shows its diagnostic features in incipient form. *C. satanas* is sister-group to the other species.

COLOBUS POLYKOMOS
King colobus (Zimmermann, 1780).

Cebus polykomos Zimmerman, 1780, *Geogr. Gesch.*, 2: 202. Sierra Leone (probably Sherbro Island).
Simia (Cercopithecus) regalis Kerr, 1792, *Linnaeus Anim.Kingd.*, 74. Sierra Leone (probably Sherbro Island).
Simia tetradactyla Link, 1795, *Beytr. Naturgesch*. 62. Locality unknown.
Simia polycomos Schreber, 1800, Saugethiere, pl.10D. Lapsus (?) for *polykomos.*
Simia comosa Shaw, 1800, *Gen. Zool. Mamm*., 1: 59. Sierra Leone (probably Sherbro Island)
Col[obus] ursinus Ogilby, 1835, *Proc. Zool. Soc.* 98. "Algoa Bay" (this locality is in South Africa, and the species obviously does not occur there!).

Diagnosis: front of crown and sides of head and neck with long grey-white hairs, becoming gradually intermingled with black on sides of neck and shoulders where hair forms long epaulettes; white gradually disappears on flanks and inner side of humerus. Rest of body, crown and limbs black; tail completely white, untufted; tail relatively long; area ventral to ischial callosities white, in male continuous, in female in two separate crescentic zones along callosities' ventral margins. No whorl on crown (Fig. 2). Cranium with low rounded orbits, weakly developed rounded supraorbital torus with no concavity at glabella; pyriform aperture low, narrow.

Distribution: Guinea Bissau, possibly The Gambia (Gippoliti & Dell'Omo, 2003) to Ivory Coast. The boundary between this species and *C. vellerosus* is essentially the Sassandra River, east of which occurs a hybrid population ("*dollmani*"); hybrids occur between the Sassandra River and the Bandama River and its eastern tributary, the Nzi. Groves *et al.* (1993) hypothesise that formerly this species extended as far east as the Nzi-Bandama, but has been largely displaced from the region east of the Sassandra by a westward spread of the more derived *C. vellerosus*.

COLOBUS VELLEROSUS
White-thighed colobus (I. Geoffroy, 1834).

Semnopithecus vellerosus I. Geoffroy St Hilaire, 1834, in Bélanger, *Voy. aux Indes Orientales*, *Zool.*, 37. "Afrique".
Semnopithecus bicolor Wesmael, 1835, *Bull. Acad. Roy. Sci. Belles-Lettres Belg.*, 2: 236. "Côtes d'Afrique".
Colobus leucomeros Ogilby, 1838, *Proc. Zool. Soc.* 1837: 69. Supposedly from Gambia River.
Colobus polykomos dollmani Schwarz, 1926, *Ann. Mag. N. H.,* (9) 9:155. Bouaké, Bandama River, Ivory Coast. Groves *et al.* (1993) showed that, strictly speaking, *dollmani* (known from specimens from between the Bandama and Sassandra rivers) is a hybrid swarm between *Colobus vellerosus* and *C. polykomos*, although more resembling *C. vellerosus*, perhaps because the female hybrids preferentially backcross with males of this species.

Diagnosis: tail wholly white, with a slight tuft; tail relatively short; no white epaulettes or flank veil, but elongated black hairs on flanks; the body being entirely black; bushy pure white cheek whiskers continuing back, covering ears and along sides of neck, from a complete white face ring; white forms a broad band along forehead, but does not extend back onto crown; white ends cleanly in mid-throat region, not extending onto sternum; upper thigh white, this zone continuous with white of perineum in male. In female, white does not extend to perineum, but is restricted to immediate margin of ischial callosities, except their upper rims (whereas in male white does extend to upper rims of callosities). No whorl on crown.

Distribution: from the Bandama River, Ivory Coast, to Ghana and Togo. The population west of the Bandama, as far west of the Sassandra River, the so-called *dollmani,* is essentially of this species but somewhat hybridised with *C. polykomos* (Groves *et al.*, 1993).

COLOBUS SATANAS
Black colobus (Waterhouse, 1838).

Colobus satanas Waterhouse, 1838, *Proc. Zool. Soc.* 58. Fernando Poo (=Bioko).
Semnopithecus anthracinus Leconte, 1857, *Proc. Acad. Nat. Sci. Philad.*,10. Gabon.
Stachycolobus municus Matschie, 1917, *Sber. Ges. Natwf. Fr. Berlin,* 155. Wurminsog, south of Rio Muni, west of Noya.
Stachycolobus limbarenicus Matschie, 1917, loc. cit. 156. Lambaréné, Gabon.
Stachycolobus zenkeri Matschie, 1917, loc.cit. 157. Bipindi, Cameroon.
Colobus metternichi Krumbiegel, 1942, *Arch. Naturgesch.*, NF, 11:305. Fernando Poo (=Bioko).

Diagnosis: wholly black; a whorl on front of crown, with an occipital crest rising from behind and an upright brow fringe in front; hairs long, somewhat elongated on shoulder; no tail tuft. Braincase with a saddle-shaped depression.

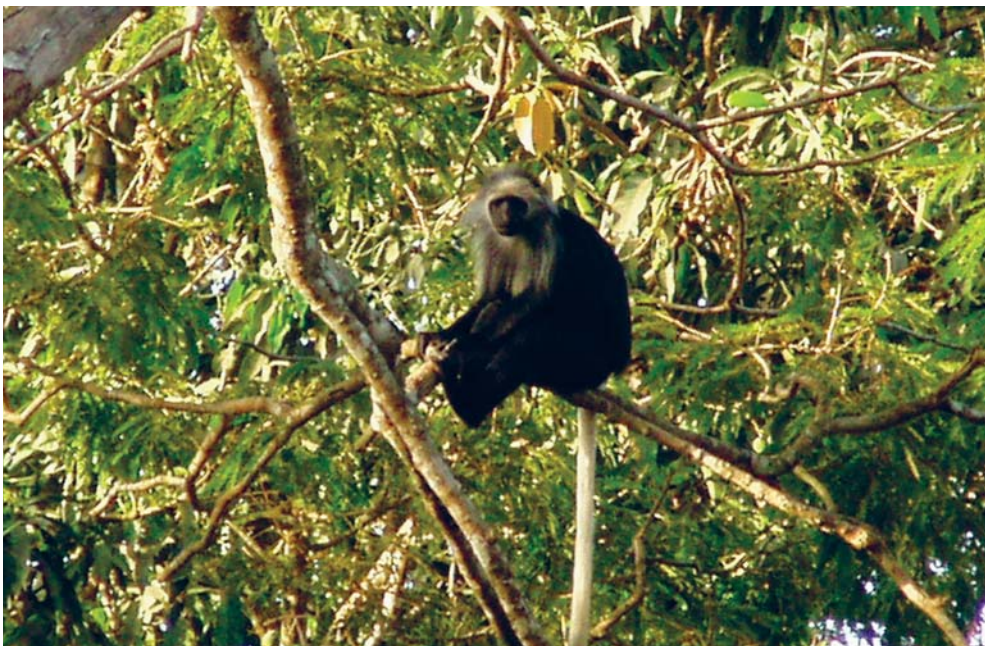

Fig. 2 - Colobus polykomos in the coastal forest of southern Guinea-Bissau (photo C. Sousa)

Distribution: Bioko Island; coastal districts of Gabon, Equatorial Guinea, and southern Cameroun, inland as far as Batouri; a single hunter-shot specimen was recorded from NW Congo near the borderline with NE Gabon (Carpaneto, 1995). In the inland parts of its range it appears to be sympatric (or parapatric?) with *C.guereza*, but is rarer: the Powell-Cotton Museum has four specimens from the Batouri and Lomie districts, against 11 of *C. guereza*.

COLOBUS ANGOLENSIS
Angola colobus (Sclater, 1860).

Diagnosis: prominent white cheek-whiskers; a long bilateral shoulder mane ("epaulettes"), not or only slightly connected along side of neck with cheek-whiskers; tail not or moderately tufted, white or grey-yellow for a varying amount of its terminal part; a whorl in centre of crown, giving rise to a brow fringe in front and often a crest behind.

Distribution: this species is found in a broad swathe from Angola across central Africa to Tanzania and the Kenya coast, mainly south of the Congo River but extending northeast to the Ituri forest. The subspecies are well marked, and further study is needed to determine whether the difference between some of them may be fixed (i.e. they may rank as distinct species).

Colobus angolensis angolensis Sclater, 1860.

Colobus angolensis Sclater, 1860, *Proc. Zool. Soc.* 245. Inland from Bembe, northern Angola
Colobus angolensis sandbergi Lonnberg, 1908, *Ark. F. Zool.,* 4,15:1. Lusiji River, between 10.07°S, 22.27°E and 10.08°S, 22.54°E, Southern DRC (Ansell, 1959).
Colobus (Colobus) palliatus weynsi Matschie, 1913, *Rev. Zool. Afr.*, 2:207. "Lower Congo".
Colobus maniemae Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 336. Between Kisangani and Kassongo, Lualaba R.
Colobus benamakimae Matschie, 1914, loc.cit., 337. Bena Makima, Sankuru R.

Diagnosis: tail untufted, white for one to two thirds of its length, with a gradation zone to the black of the proximal half of the tail; white epaulette-hairs 175-210mm long, often much yellowed, broadly joined to the well-developed white cheek-whiskers. A white pubic strip present.

Distribution: northeastern Angola and DRC, south of the Congo River, into northern Zambia. From the data of Colyn (1991), it would seem to extend west to about 15°E and south to about 11°50'S. It has much the widest distribution of any of the subspecies of this species.

Colobus angolensis cordieri Rahm, 1959.

Colobus polycomos cordieri Rahm, 1959 (June), Folia scient. Africae centralis, 5,1:34. Kampungu, Pangi territory, DRC.
Colobus polykomos prigoginei Verheyen, 1959 (September), *Rev. Zool. Bot. Afr.,* 60:120. Mt Kabobo, 5.06 S, 29.01 E, 2400m., DRC.

Diagnosis: tail base black, with a short transition zone to the yellow-white to light greyish-brown colour which occupies five-sixths of its length; no tail brush; cheek-whiskers greyer, less developed than other races; no white forehead band; white shoulder-fur reduced to a thin brush, weakly joined to cheek-whiskers by grey-white hairs. Fur long, 20cm in anterior part of dorsum. No white pubic band.

Distribution: southeastern Democratic Republic of Congo (DRC), south of the Ulindi River to about 4°30'S in the lowlands, but to nearly 6°S in the highlands, from the Lualaba River to Lake Tanganyika.

It is probable, but not certain in the present state of knowledge, that the two synonyms really are just a case of the same taxon being described in ignorance of one another in the same year.

Colobus angolensis ruwenzorii Thomas, 1901.

Colobus ruwenzorii Thomas, 1901, *Proc. Zool. Soc.* 2:85. Bwamba country, northwest flank of Mt Ruwenzori, DRC.

Colobus adolfi-friederici Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin*, 337. Rugege Forest, northeast of L. Kivu, Rwanda.

Diagnosis: tail black, becoming grey-white only on its extreme end, if at all, with no terminal brush; a broad grey or white median pubic band present; cheek-whiskers long, broadly connected with epaulettes, which are 210mm long; crown hairs evenly long, not or only slightly elongated into a crest behind; white brow-band narrow.

Distribution: from the north end of Lake Tanganyika (about 4°S on the west side, and 5°S on the east) via the mountains of Burundi and Rwanda to the Ruwenzoris. According to Colyn (1991), intermediates between this subspecies and *cottoni* occur in DRC, along the left bank of the Semliki River, and between it and *cordieri* on the Elila River at 3.35 S, 28.40 E, although he notes that a specimen from Luemba, 7 minutes further south, is typical for *ruwenzorii*.

In Bwamba, both this form and *C. guereza occidentalis* occur. According to the maps in Kingdon (1971), they are not strictly sympatric, but *C. angolensis* lives in the montane forest on the slopes of Mt Ruwenzori, at about 4000m, while *C. guereza* is in the *Cynometra* forest, mainly below 2500m. At a few points they appear to approach each other, especially at about the 4000m contour along the River Tokwe, where they would seem to come within 1/2 km of each other.

Colobus angolensis cottoni Lydekker, 1905.

Colobus palliatus cottoni Lydekker, 1905, *Ann. Mag. N.H.,* 16:432. Zokwa, between Mahagi and Irumu, DRC.

Colobus (Colobus) palliatus mawambicus Matschie, 1913, *Rev. Zool. Afr.,* 2:205. Northern Pemba, between Irumu and Mawambi

Colobus mawambicus nahani Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 335. Panga, Aruwimi R.

Diagnosis: epaulettes small; no white pubic band; distal 30-60% of tail grey-whitish, with no terminal brush. Crown whorl modified into a parting; there is no occipital crest.

Distribution: Democratic Republic of Congo, northeast and north of the Congo River west to the Itimbiri River, east to Lake Albert, south to the Lindi River, north to nearly 4°N. There are no Black-and-white Colobus between the Lindi and Ulindi Rivers.

Colobus angolensis subsp.
"Nkungwe's Angolan Colobus", Nishida *et al.*, 1981.

Diagnosis: has large epaulettes like the *angolensis-palliatus-ruwenzorii* group, but unlike them lacks a white pubic band, in which character it resembles the *cottoni-prigoginei* group. No white forehead band. Tail greyish-coloured only at tip, with slight brush in males but not in females.

Localities: western Tanzania, Mt Nkungwe, and the ridges of the northern Mahale Mountains as far as Mt Pasagula to the north and Mt Kahoko and Mt Sibindi to the south, a distance of 7 km, in wet upland forest. These areas are more than 300km from the nearest localities of other subspecies.

Colobus angolensis palliatus Peters, 1868.

Colobus palliatus Peters, 1868, Monatsber. K. Preuss. Akad. Wiss. Berlin, 637. East African coast opposite Zanzibar (probably Pangani River, Tanzania).

Colobus sharpei Thomas, 1902, P. Z. S. 1: 118. Nkuka forest, Rungwe Mountains, Tanzania, 33.38°E, 9.08°S (Ansell, 1959).

Colobus langheldi Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 337. Locality unknown (purchased at Ujiji, Tanzania).

Diagnosis: epaulettes large; a white pubic band, broad and oval in males, narrow in females; tail tip white, bushy, occupying about a third of tail length. White forehead band fairly broad, broadly connected via full cheek-whiskers with epaulettes; no well-marked crown whorl; occipital hairs lengthened. Coat long, thick, soft; a whorl on withers.

Distribution: East African parts of the range; discontinuously distributed, wherever there is sufficient forest cover. The

southwesternmost localities are the Rungwe Mts. (9.08 S, 33.38 E) and Lake Rukwa, Tanzania (±8°S, 32°E); they occur in the montane forests of the Southern and Eastern Highlands of Tanzania - Ulugurus, Ngurus, Usambaras - and some coastal and riverine lowland forests, some little more than a ribbon of scrubby trees, in the northeast, and into extreme southeastern Kenya: Diani Beach, Shimba Hills, Mrima Hill.

COLOBUS GUEREZA
Mantled guereza. (Ruppell, 1835).

Diagnosis: a long white veil of hairs along either flank, extending variably up on to lower part of back; a white stripe on upper thigh; complete white face-ring, developed on chin and throat into a full, rather woolly beard; a long, full, white tail-brush; no whorl on crown, all hairs being directed backwards, short in midline, developed on either side into bushy tufts.

This species has a more northerly distribution than *C. angolensis*. It is found in lowland forests from the Yabassi region of Cameroon, as far south as the Makokou district in Gabon, and across the Oubangui River into the Democratic Republic of Congo, always north of the Congo River, east through the Ituri forest into Uganda, east into the highlands east of the Rift Valley in Kenya, southeast to the Serengeti and Ngorongoro, and northeast into the Ethiopian Highlands. On the Kenya coast and in the Usambara Mountains, and further south in Tanzania, it is replaced by *C. angolensis*.

The subspecies of *Colobus guereza* are less strikingly different than those of *C. angolensis*. The southeasternmost one, *C. g. caudatus*, is very different from the northwestern *C. g. occidentalis*, but there is a string of geographically and morphologically intermediate forms.

Colobus guereza guereza Rüppell, 1835.

Lemur abyssinicus Oken, 1816, *Leheb. Naturg.*, 3 (2):1182. Abyssinia Unavailable (Opinion 417, 1956).

Colobus guereza Rüppell, 1835, Neue Wirbelthiere z.d.F auna Abyssinien gehörig, Saugeth.,l, pl.l. Damot region, Gojjam, Ethiopia (Mertens, 1925).

Colobus abyssinicus poliurus Thomas, 1901, *Proc. Zool. Soc.* 1900: 800. Omo River.

Colobus (Guereza) poliurus managaschae Matschie, 1913, *Ann. Soc. R. Zool. Malacol. Belg.,* 47: 54. Managasha Forest, Ethiopia.

Diagnosis: proximal half of tail generally grey, distal half with long white tuft, forming about half the total length; white mantle relatively long, extending onto dorsum, shorter on flanks but long behind, covering a fifth of the length of the tail; thigh-stripe somewhat diffuse. Tail longer than head and body.

Distribution: Ethiopian Highlands, west of the Rift Valley, and extending down into more lowland forests along the Omo River to the south, and the Blue Nile to the west. The more thinly furred lowland colobus of the Omo River perhaps should be separated as *C. g. poliurus*, first re-evaluated by de Beaux (1943) on craniometric considerations.

Colobus guereza gallarum Neumann, 1902.

Colobus gallarum Neumann, 1902, *Sber. Ges. Naturf. Fr. Berlin,* 49. Arussi Mountains, Webi Shebeyli headwaters, Ethiopia.

Diagnosis: tail tuft very bushy, white, extending for 40% of its length; proximal tail black, not grey-white as in *C. g. guereza*. White sprinkling on thighs, but not on shoulders. Hair on loins under 300mm long; mantle relatively thin, short, but more developed on shoulders than *C. g. guereza*, and covering base of tail.

Distribution: this taxon is commonly supposed to be found in the Ethiopian Highlands, to the east of the Rift Valley. Carpaneto & Gippoliti (1994), however, saw guerezas in the Harenna Forest (Bale Mts, in the southern part of the highlands east of the Rift Valley) and

noted their striking difference from *gallarum*. They have short tails, black basally with a bushy white tuft occupying at least half the total length. Spartaco Gippoliti (personal communication) saw the type of *gallarum* in the Berlin Museum and confirmed the considerable difference from the Bale Mt. guerezas

Colobus guereza percivali Heller, 1913.

Colobus abyssinicus percivali Heller, 1913, *Smithson. Misc. Collect.* 61, 17:6. Mt Gargues (= Varagess), Matthews Range, Kenya.

Diagnosis: white tail tuft extends over nearly two-thirds of tail length; tail approximately as long as head and body, usually slightly shorter; flank veil very long, creamy-yellow, extending well up onto flanks and loins but shortened posteriorly, so only just reaches tail base; no white sprinkling on thighs or shoulders. Hair very long, more than 400mm long on loins.

Distribution: restricted to the Matthews Range, Kenya.

Colobus guereza kikuyuensis Lonnberg, 1912.

Colobus abyssinicus kikuyuensis Lonnberg, 1912, *Ann. Mag. N.H.,* 9: 63. Escarpment Station, Kenya.
Colobus (Guereza) caudatus thikae Matschie, 1913, *Ann. Soc. Roy. Zool. Malacol. Belg.*, 1912, 47:56. Western slope of Mt Kenya.
Colobus (Guereza) caudatus laticeps Matschie, 1913, loc. cit. 57. Western slope of Mt Kenya.

Diagnosis: white tail-tuft very bushy, extending over 72% of tail length on average; tail proximally grey; tail short, about equal to head-and-body length; flank veil very long, extending well up on back, and beyond base of tail-tuft; hair very long, over 400mm on loins; thigh stripe short.

Distribution: Kenyan Highlands, east of the Rift Valley, from the Ngong Escarpment north via the Aberdare Range to Mt.Kenya.

Colobus guereza caudatus Thomas, 1885.

Colobus guereza caudatus Thomas, 1885, *Proc. Zool. Soc.* 219. Useri, northeast slope of Mt Kilimanjaro, 3000ft.
Colobus albocaudatus Lydekker, 1906, *Proc. Zool. Soc.* 1905, 2: 328. Renaming.

Diagnosis: flank-veil and tail-tuft even longer than in *C. g. kikuyuensis*; the tuft makes up 80% of the length of the tail, only extreme proximal part of tail black; fur on underside less woolly.

Distribution: confined to northern Tanzania, in the montane forests of Mt.Kilimanjaro and Mt.Meru, and adjoining forests at slightly lower altitudes (Kahe; Momela Lakes in Arusha National Park).

Colobus guereza matschiei Neumann, 1899.

Colobus matschiei Neumann, 1899, Sber.Ges. Naturf.Fr. Berlin, 15. Kwa Kitoto, near Kisumu, Kenya.
Colobus abyssinicus roosevelti Heller, 1913, S*mithson. Misc. Collect.,* 61, no. 17:5. Mau Forest, near Njoro.
Colobus abyssinicus elgonis Granvik, 1925, Ac*ta Univ. Lundensis,* 21 (2), no.3:5. East slope of Mt Elgon.

Diagnosis: white tail-tuft short, occupying only 45% of tail length; rest of tail black; tail much longer than head and body; flank veil much yellowed, not extending up onto back, but covering base of tail; white hairs sprinkled on upper thighs, and over shoulders nearly (or just) linking veil to white of throat. Hair short, on loins less than 300mm long.

Distribution: western Kenya (forests west of the Rift Valley, and some forests within the Rift itself) to the Uganda border (Mt.Elgon) and extreme northwestern Tanzania (Ngorongoro Crater; Grumeti River).

Colobus guereza dodingae Matschie, 1913.

Colobus (Guereza) matschiei dodingae Matschie, 1913, *Ann. Soc. Roy. Zool. Malacol. Belg.,* 1912: 52. Southwestern Didinga Hills, 4.10 N, 33.42 E, Sudan.

Diagnosis: tail tip (which is not bushy) white for only 40% of its length; tail much longer than head and body; flank-veil slightly creamy, not extending up onto back, but longer and thicker than neighbouring forms, and covering part of tail behind; hair relatively short, but somewhat longer, coarser than *C. g. matschiei*; some white sprinkling on thighs, but not on shoulders.

Distribution: Didinga Hills, southeastern Sudan.

Colobus guereza occidentalis (Rochebrune, 1887).

Guereza occidentalis Rochebrune, 1887, *Faune de Senegambie,* Suppl., Vert., 140. Noki, Congo Republic.
Colobus (Guereza) matschiei uellensis Matschie, 1913, *Ann. Soc. Roy. Zool. Malacol. Belg.*, 1912, 47: 47. Uele River, DRC.
Colobus (Guereza) matschiei ituricus Matschie, 1913, loc. cit. 48. Ituri Forest, DRC.
Colobus (Guereza) matschiei dianae Matschie, 1913, loc. cit. 49. Kisenge, northeast of Lake Albert, DRC.
Colobus (Guereza) matschiei brachychaites Matschie, 1913, loc.cit. 53. Modi, between Kaya and Dufile, Lado district, Sudan-Uganda border.
Colobus abyssinicus terrestris Heller, 1913, *Smithson. Misc. Collect.,* 61, no. 17: 7. Rhino Camp, Uganda.
Colobus (Guereza) escherichi Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 342. Gombe, below Ikelemba, Sanga R., Congo Republic.
Colobus occidentalis ituricus Lorenz, 1914, *Anz. K. Akad. Wiss. Wien*, Math.-Nat.Kl., 51: 508. Mawambi, Ituri Forest, DRC.
Colobus occidentalis rutschuricus Lorenz, 1914, loc.cit., 508. Ishasha River, southeast of Lake Albert,DRC-Uganda border.

Diagnosis: white tail tuft occupying only one-third of tail length; tail longer than head and body; flank veil creamy, not extending onto back, long on shoulders but covering only root of tail; white sprinkling on thighs and on shoulders. Hair under 300mm long on loins.

Distribution: Uganda, west of the Nile, and southwestern Sudan; north of the Ubangui River, Democratic Republic of Congo (about as far as 1°25'S, in the Ituri Forest), west into Cameroun. In Cameroun it is found as far west as Batouri and Lomié, where apparently sympatric with *C. satanas*, and the Yabassi/Ndokyam district (4°N,10'E), where apparently sympatric with *Piliocolobus preussi*. In Gabon it reaches the Belinga/Makokou district of the northwest.

Genus *PROCOLOBUS* Rochebrune, 1887.

Procolobus Rochebrune, 1887, *Faune de Sénégambie,* Suppl., Vert., 1:95.
Lophocolobus de Pousargues, 1895, *Bull.Mus. H. N. Paris,* 1:98.

Genotype of *Procolobus*, *Colobus verus* Van Beneden; of *Lophocolobus, Colobus verus* Van Beneden.

The organ and the sexual swellings of females are as well-developed in *P. verus* as they are in *Piliocolobus* (Fig.3). Because more is known about the sexual swellings in Red Colobus, I will leave discussion of them to be treated under *Piliocolobus*. Again, as in *Piliocolobus*, the infants are not contrastingly coloured, unlike *Colobus* and most other colobines. Welker (1981) drew attention to the relative helplessness of the newborn: initial mouth-transport, followed by belly transport (there is no mouth transport in *Piliocolobus*). He regarded the contrast of this genus and *Piliocolobus* with other colobus sufficient to erect a separate subfamily, Procolobinae. Unique features of the skull and dentition include the presence of a labial symphyseal foramen on the mandible, the presence of a lingual cingulum,

with a distinct tubercle, on upper incisors, the upper incisors being reduced and vertically implanted, the sharp margin of the pyriform aperture with often an incipient anterior nasal spine, and the presence of a tuberculum sextum on the posterior lower molar. In many of its features, this genus appears superficially to be more primitive than most other colobines; but in other respects it seems so obviously to form a clade with *Piliocolobus* that features such as the simple agouti pelage are probably best explained as secondary simplifications in the interests of its bizarre cryptic way of life .

PROCOLOBUS VERUS
Olive Colobus (Van Beneden, 1838).

Colobus verus Van Beneden, 1838, *Bull. Acad. Roy. Sci. Belles-Lettres Belg.*, 5: 347. "Africa".
Semnopithecus (Colobus) olivaceus Wagner, 1840, *Schrebers Säugethiere*, Suppl.1: 309. "Africa".
Colobus ?? chrysurus Gray, 1866, *Ann. Mag. N.H.* 17 (3): 77. "West Africa".
Colobus cristatus Gray, 1866, loc.cit.77. "West Africa".

Fig. 3 - A female* Procolobus verus *showing sexual swelling (photo S. MacGrew).

Distinguished by its olive colour, with agouti (many-banded) hairs; limbs slightly lighter, tail greyer; a longitudinal crest above each ear, extending forward to corner of eye; an asymmetrical whorl on crown, sometimes a symmetrical pair, balanced by another on occiput. Second and fourth fingers shortened, the former with a claw-like nail. On the basis of hunter-shot specimens and museum records, Oates *et al.* (1990) gave the following body weights, in kg., for this species: males (n=20) 4.7 (4.0-5.7), females (n=14) 4.2 (2.8-5.4).

Distribution: Oates (1981) mapped the distribution as from Sierra Leone to just east of the Niger, south of the Niger-Benue confluence. It has a large gap in its distribution between Togo and eastern Nigeria. It is probably restricted by mountains more than by the distribution of large forest blocks. It lives in groups of 5-20 (but usually under 10), with 1 or 2 males and the same number of females; it is especially common in riparian forest (Oates, 1981). It is commonly found in company with *Cercopithecus* spp., to whose alarm calls it responds, according to Hill & Booth (1957); Oates & Whitesides (1990) and Korstjens & Noë (2004) specified that, both on Tiwai Island (Moa River, Sierra Leone) and in Tai Forest (Ivory Coast), this association with other species is invariable, and is most particularly with *Cercopithecus diana*. Each Olive Colobus troop follows "its" Diana Monkey troop around, and the Dianas' territorial encounters bring their associated Olive Colobus likewise into proximity, resulting in (territorial) countercalling by adult males, and extra-troop matings. Females carry conspicuous sexual swellings for about half of their menstrual cycle, and this makes them conspicuous to males; females are strongly proceptive, and mate overwhelmingly with the dominant male in a troop (Korstjens & Noë, 2004). On Tiwai, group size averages 6; at 1.1 to 1.3 groups per km^2, this gives a biomass of 21-25 kg/km^2, the lowest of any primate on the island and far less than the Black-and-White or Red Colobus there. This odd social system may

account for the species' restricted distribution, and indeed it seems common only where Diana monkeys are found. What species it associates with in Nigeria is unknown; its very occurrence there was long unsuspected, and the absence of Diana monkeys may well be the cause of its apparent rarity there, although of course its dull, apparently cryptic colouration was also a factor. Much remains to be learned about the species.

Genus *PILIOCOLOBUS* Red Colobus. Rochebrune, 1887.

Tropicolobus Rochebrune, 1887, loc.cit., 96.
Piliocolobus Rochebrune, 1887, loc.cit., 96.

Genotype of *Tropicolobus, C. rufomitratus* Peters; of *Piliocolobus, Simia (Cercopithecus) badius* Kerr.

The skull has a few characters in common with *Procolobus*, but in general in its more prognathous form, the development of a sagittal crest, and other features, it much more resembles *Colobus*. This contrasts with the common possession of female and subadult male sexual swellings with *Procolobus.* Kuhn (1967) and Hill (1958) described the genitalia of female red colobus as having (1) a pubic cushion, a ventral prominence from which the clitoris projects, (2) paravaginal cushions, and (3) a transverse perineal cushion, dorsal to the vaginal opening and extending to (but not involving) the anus. At times the whole region swells: it is an ovulatory swelling like that of some Cercopithecines. It consists of loose oedematous connective tissue and engorged subepidermal vessels. The degree of swelling seems to vary in different taxa within the genus; it is especially enormous in *P. preussi*, and is very reduced, even absent, in some eastern taxa according to Korstjens & Noë (2004). An exact mimic of the female genital arrangement is found in juvenile males, the Perineal Organ of Kuhn (1972). There are a Pseudo Pubic Cushion bearing a Pseudo-clitoris; Pseudo Paravaginal Cushions; and a Pseudo Transverse Perineal Cushion, bearing a narrow median raphe which unites ventrally with the Pseudo Pubic Cushion. This arrangement, already developing in the foetus at term, reaches its maximum in juveniles. In a several-month-old male of *P. badius* (crown-rump length 230mm), studied by Kuhn, the paravaginal cushions were 35mm apart and almost completely covered the ischial callosities (which they did totally in the term foetus); a deep fold between the pseudo paravaginal and pseudo transverse cushions mimicked the vaginal opening; the pseudoclitoris was not as long as in the foetus; the pseudo transverse cushion incorporated the anus. In the juvenile the pseudoclitoris and surrounding skin, the pseudo transverse cushion, and the circumanal skin were bright blue; the rest of the organ, bright red. Meanwhile, the scrotum was undeveloped, the preputial opening inconspicuous. With maturity the preputial organ decreases in size; it no longer overlaps the ischial callosities; the pseudo vaginal opening becomes inconspicuous and variable; the pseudoclitoris may become a mere wart; and the colours fade, the blue to bluish-black, the red to grey yellow-red. Thickened skin dorsal to the anus may, however, develop into a cushion of its own. Histologically, the dermal-epidermal junction is unusually flat, with almost no papillae on the red parts and only somewhat more papillated on the blue parts. The perineal organ is mainly filled out with adipose tissue, quite contrary to the swelling of the female. The area is rich in apocrine glands (Kuhn, 1967). Kuhn suggested that the perineal organ serves as an optical signal analogous to the contrasting infant fur colour of most other colobus; that is to say, its function is to reduce aggression from the adult males, apparently at a time when the subadult is preparing to disperse from the natal troop. Kuhn described how young males "present" to adult males, exactly like adult females: the presence of the perineal organ, analogue of the female's sexual swellings, is therefore correlated

with pseudo-female behaviour. Marler (1970, 1972) found that red colobus have a graded system of vocalisations, while black-and-white colobus have a discrete system; he correlated this with emphasis on intratroop communication rather than intertroop communication.

Verheyen (1962) distinguished red colobus from black-and-white as follows:

1) The pterygoid fossa is deep, narrow and perforated at the bottom, going through into the floor of the orbit; in Black-and-White it is shallow, broad, and not perforated.
2) The base of the medial pterygoid plate is separated from the side of the basisphenoid by a deep channel, instead of being smoothly joined to it.
3) The lateral pterygoid plate is entire, instead of being perforated at the base by one or more foramina.
4) The choanae are high and narrow, not broad and low.
5) The posterior processes of the vomer surround a narrow presphenoid, covering the greater part of it and extending past the pre/basisphenoid suture; not, as in black-and-white, united in the middle to form a bony convex plate which covers only a small part of the (broader) presphenoid, and never extending as far as the suture.
6) The apex pyramidis of the basisphenoid is acute, with lateral crests; not acute, without crests.
7) The orbits are angular, not oval; with very heavy superior and lateral tori, with well-marked foramina or notches; black-and-white colobus have lighter tori, with no foramina and very occasional notches.
8) There is a pronounced suborbital depression.
9) There is usually a sagittal crest in adult males (as in *P.verus*).
10) The medial incisors, in both jaws, are short and broad; the lateral are caniniform with the points directed laterally; the cheekteeth, narrow. In black-and-white, the medial incisors are long, the laterals caniniform withe the points directed proximally and rather obtuse; the cheekteeth, broad.
11) The canines are more sexually dimorphic, those of females being about one-third the length of males', while in black-and-white they are one-half (in *C. angolensis*) to 70% of males' (in *C. guereza*).

Not all these characters hold when samples from the full range of both genera are examined; in effect, Verheyen was characterising Central African taxa (*P. oustaleti, P. foai, P. elliotti, P. tholloni*), and the West African and East African species show greater and or lesser degrees of difference. In particular, the perforation of the pterygoid fossa varies in frequency from place to place.

Taxonomic notes. The members of this genus have in the past mainly been referred to a single species, *Piliocolobus* (or *Procolobus,* or *Colobus*) *badius*. In the main, this seems to be because the taxa are all allopatric, although they are in fact about as morphologically distinct from one another as are those of *Colobus*. Schwarz (1928), Allen (1939) and others recognised "subspecies groups", an ultimately unsatisfactory arrangement; we feel that it is time to formalise a full species arrangement. Dandelot (1968) has already made some suggestions in this regard.

PILIOCOLOBUS BADIUS
Western Red Colobus (Kerr, 1792).

Diagnosis: broad skull, broad palate, narrow across canines, short face, little sexual dimorphism. Nostrils are raised on a prominent fleshy base; face slaty black, wrinkled, depigmented around eyes and mouth; colour glossy black or deep grey on back and outer sides of proximal limb segments, forehead, crown and tail; red on underparts, inner aspects of limbs, lower limb segments and cheeks; white on hind part of thigh; tail red in proximal part, becoming darker towards the tip. Perineal

organ of male conspicuous; clitoris small; sexual swelling of female varies somewhat. Infant grey, lighter than adult, with reddish tints on tail and extremities, whitish ventrally. Measurements in mm from museum records (n=16) reveal some difference in size between males and females (Fig. 4), but not apparently between the two subspecies (N.B. limited evidence for *temminckii*). Oates *et al.* (1990) however gave the following weights (in kg.) for Sierra Leone specimens: males (n=9), 8.3 (6.4-9.6); females (n=14) 8.2 (7.0-10.0); sexual dimorphism may thus be greater in Ivory Coast populations than in Sierra Leone. Museum records vary from 6.1 - 9.1 kg (females only, n=6).

Piliocolobus badius badius (Kerr, 1792)

Simia (Cercopithecus) badius Kerr, 1792, *Linnaeus' Animal Kingdom*, 74. Sierra Leone (probably Sherbro Island).
Simia ferruginea Shaw, 1800, *General Zoology, Mammals,* 1, pt 1: 59. Sierra Leone.
Colobus ferruginosus E.Geoffroy, 1812, *Ann.Mus. H.N. Paris,* 19: 92. Sierra Leone
Colobus rufoniger Ogilby, 1838, Library of Entertaining Knowledge. The Menageries, Natural History of Monkeys, etc., 1: 273. Locality unknown.

Diagnosis: dark areas intense glossy black, red parts deep maroon-bay. Female's sexual swelling large.

Distribution: southern Guinea, Sierra Leone, Liberia, to the Nzi-Bandama system, Ivory Coast. Localities are from 9.00°N, 12.58°W (Rokupr, Sierra Leone) to the Bandama River.

Piliocolobus badius temminckii (Kuhl, 1820).

Colobus temminckii Kuhl, 1820, *Beitr. Zool.* 7. Locality unknown.
Colobus fuliginosus Ogilby, 1835, *Proc. Zool. Soc.,* 97. Gambia.
Colobus rufofuliginus Ogilby, 1838, *Library of Entertaining Knowledge*, 1: 345. "Guinea Coast".

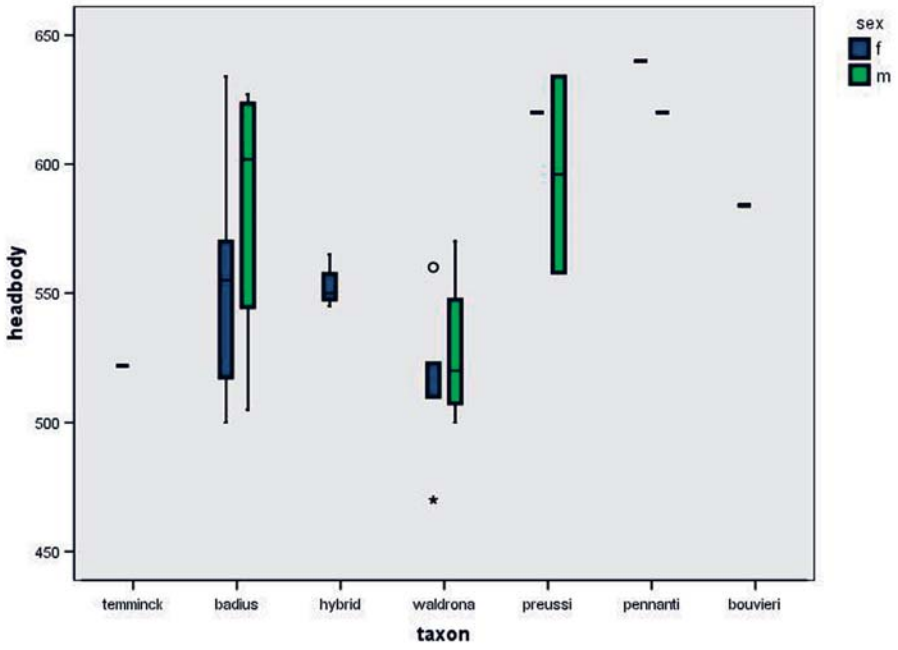

Fig. 4 - Sexual dimorphism: Red Colobus Western group (head plus body lenght in millimeters) .

Diagnosis: scrotum appears less pendulous; perineal organ of male small, knoblike; Female's sexual swelling apparently smaller. Dark areas slaty or ashy grey, red areas orange, becoming whitish on underparts; fingers and toes darkening to rufous (Fig. 5). Palate shorter, teeth smaller.

Distribution: Senegal, Gambia, northern Guinea; Guinea Bissau. Localities are from Gambia to the Upper Senegal, Kopulau Camp, 12.4°N, 13.58°W, and Massirali and Marsassoum, Senegal.

Notes. Specimens from Bignona, Casamance, tend towards the nominotypical race, as to a lesser extent do some from 10 miles south of Cape St Mary, Gambia, and from Guinea-Bissau. The three Bignona skins were examined on my behalf by Dr Peter Grubb in Dakar (Institut Fondamental de l'Afrique Noire); they are blacker than *temminckii* but not as black as *badius*, becoming grey on the outer aspects of the thighs, this grey not quite extending to the knees. The reddish tone of the underside is not quite as pale as in *temminckii*; the tail is all reddish. The skin (BM 46.133) from Gambia is just slightly blacker than usual in *temminckii*, with very red arms, and the red collar is nearly obsolete; very similar, but with better marked red collars, are two skins (nos. 1905.420 and 421) in Paris, labelled merely "French Guinea". Skins from Guinea-Bissau (Powell-Cotton Museum) are rather darker than usual in *temminckii*.

It would appear, therefore, that typical *temminckii* is confined to areas of Gambia and Senegal north of the Gambia River, and that south of this river there is a gradual darkening, loss of the red collar and of the white strip on the underside. There seems to be a fairly gradual transition between this pale coloured dry forest form and the typical deeply coloured rainforest form.

PILIOCOLOBUS WALDRONAE
(Hayman, 1936) Miss Waldron's Red Colobus.

Colobus badius waldroni Hayman, 1936, *Proc. Zool. Soc.* 1935: 915. Goaso, Ashanti, Ghana.

Diagnosis: nose flat without raised fleshy base; face slaty, with a pale trace on lips, but no circumocular depigmentation; crown, nape, shoulders and back glossy black as in *P. badius badius*, but this colour does not extend to forehead nor onto limbs; tail virtually black; forehead, whiskers, lower half of flanks, chest, belly and whole of limbs bright deep maroon-bay; hind part of thighs, and scrotum of male, white. Face is broad across canines. The head plus body length (n=9) is smaller than in *P. badius*; there is no sexual

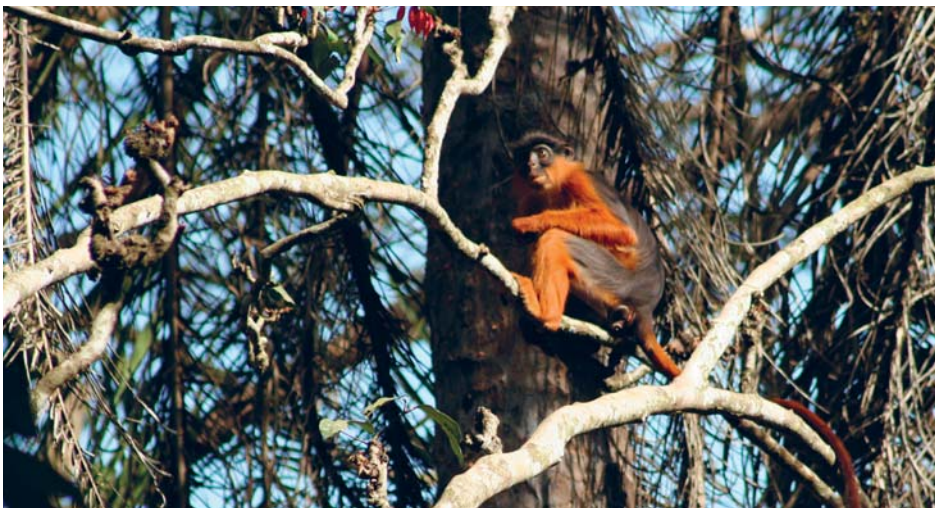

Fig. 5* - Piliocolobus badius temminckii *in southern Guinea-Bissau (photo C. Sousa).

dimorphism (Fig. 4); and the tail is shorter (Fig. 6). Two museum weights are 5.5 and 6.3 kg, which would make it much lighter than *P. badius*.

Distribution: from Nzi-Bandama system, Ivory Coast, east to the Volta River in Ghana. There are no red colobus east of the Volta until the Nigeria/Cameroon border is reached. Localities are from the Bandama River east to Bibianha, Ghana (6.30°N, 2.08°W). This species and *P. badius* meet at the Bandama River, Ivory Coast, and appear to interbreed across the headwaters of the Bandama and its tributary, the Nzi (Pont de Nzi, between the Bandama and Nzi Rivers); of the presumed hybrid specimens one resembles *badius* but the tail has only a slight tinge of maroon, and the other two (a mother and her infant) resemble *waldronae* but have almost no maroon on the front of the crown or the lower thigh. A fourth specimen from Pont de Nzi is typical *waldronae*. All three adult specimens, however, are large and long-tailed like *P.badius* (Figs. 4, 6). The skulls from Pont de Nzi are intermediate between *badius* and *waldronae* in size, broad-faced as in *waldronae* but excessively long-faced as *badius*. It was the peculiar nose shape of *badius* (and *temminckii*) which led Dandelot (1968) to propose separating them specifically from all other red colobus, including *waldronae*. Although the differences in pelage between *waldronae* and *badius* seem rather slight, they are quite consistent; the hybrid zone is very restricted. Separation at species level is almost certainly warranted, but detailed investigation is no longer possible since *waldronae* is probably extinct (Oates *et al.*, 2000) or nearly so (McGraw, 2005). The name *waldroni* is here corrected to *waldronae*, as required by Art.31.1.2 of the International Code of Zoological Nomenclature, 4th. ed., 1999.

PILIOCOLOBUS PREUSSI
Preuss's Red Colobus (Matschie, 1900).

Piliocolobus preussi Matschie, 1900, S*ber. Ges. naturf. Fr.*, Berlin, 183. Barombi, Elephant Lake, Cameroun.

Diagnosis: biorbital breadth is very great. Fur dense, more frizzy than other species. Forehead black; crown, nape, shoulders, back, rump and base of tail dark brown to blackish, with fawn bands or tips to hairs; flanks and limbs deep orange-rufous, becoming dark brown-black on hands, and distal part of tail; underparts pale red-gold, this colour going very narrowly up throat to chin; inner sides of limbs white. Clitoris large, prominent, but perineal organ of male is not as conspicuous as

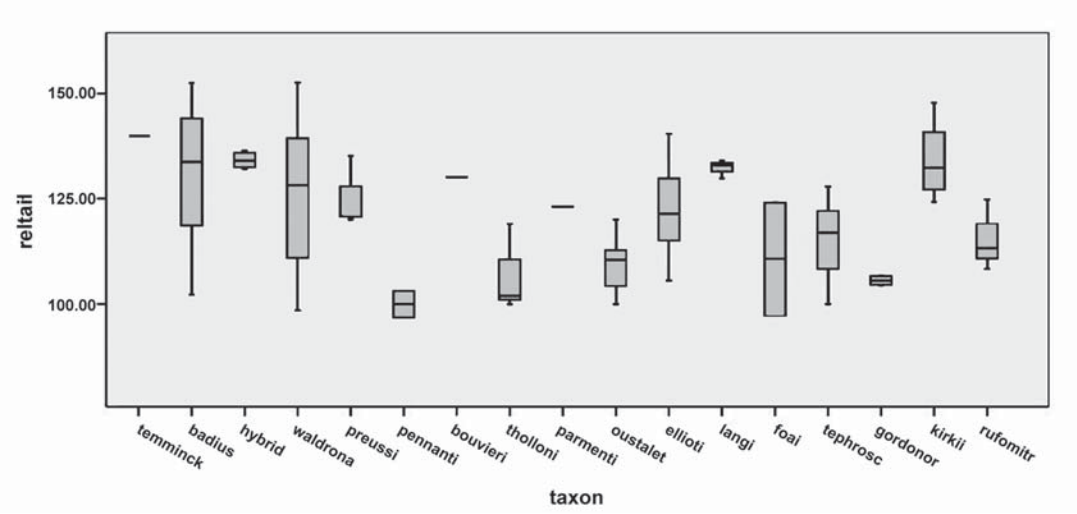

Fig. 6 - Relative tail length in Red Colobus taxa (tail as percentage of head plus body).

in *P. badius*. Sexual swelling of female enormous, affecting the anus and circumanal skin. A whorl above brows, but no whorls above ears. Neonate black above, light grey below. Proportionally, this species (n=3) seems to resemble *P.badius* in being long-tailed (Fig. 6), but it is large in size (Fig. 7).

Distribution: known only from a small area of Cameroun; today probably restricted to Korup Reserve (100,000 ha), 5º to 5º25'N, 8º40' to 9°05'E, and Ebo forest (4°30'N, 10°30'E).

PILIOCOLOBUS PENNANTII
Bioko Red Colobus (Waterhouse, 1838).

Colobus pennantii Waterhouse, 1838, *Proc. Zool. Soc.* , 57. Fernando Po (Bioko) Island.

Diagnosis: skull narrow across zygomata and palate, broad across canines; teeth relatively small; face long; no suborbital fossa; black from crown along back to haunches, upper thighs, base of tail, and hands and feet, this colour extending partway up limbs; flanks bright red, limbs dark red, somewhat blackened on arms; tail black above, deep red below; underside creamy white, this colour extending to inner surface of limbs, cheeks, and sides of neck. Face black. Hair whorls are present above ears, and a whorl above brows. Scrotum not conspicuous; clitoris prominent; perineal organ small in size; sexual swelling of female fairly small. Neonate black, grey below, with no red anywhere. Skull sutures close relatively early, before third molars become worn. Seems a rather large species (Fig. 7), on the evidence however of only two museum specimens; weight of a female is given as 5.8 kg, but of a male, 9 kg. It is relatively very short-tailed (Fig. 6).

Distribution: Island of Bioko, Equatorial Guinea.

PILIOCOLOBUS EPIENI
Delta Red Colobus (Grubb & Powell, 1999).

Procolobus badius epieni Grubb & Powell, *J. Zool. Lond.,* 248: 68. Sampou-Apoi, 4°55'N, 6°.00'E., 12km SW of the junction of Sagbama and Egbedi Creeks, Niger Delta, Southern Ijaw Local Government camp area, Bayelsa State, Nigeria.

Diagnosis: blackish from crown to rump as in *P. pennantii*; rest of upper side orange-brown; whitish of underside extends onto outsides of arms, replacing the orange-brown tones or restricting them to a narrow band; hands and feet black, this colour not extending part way

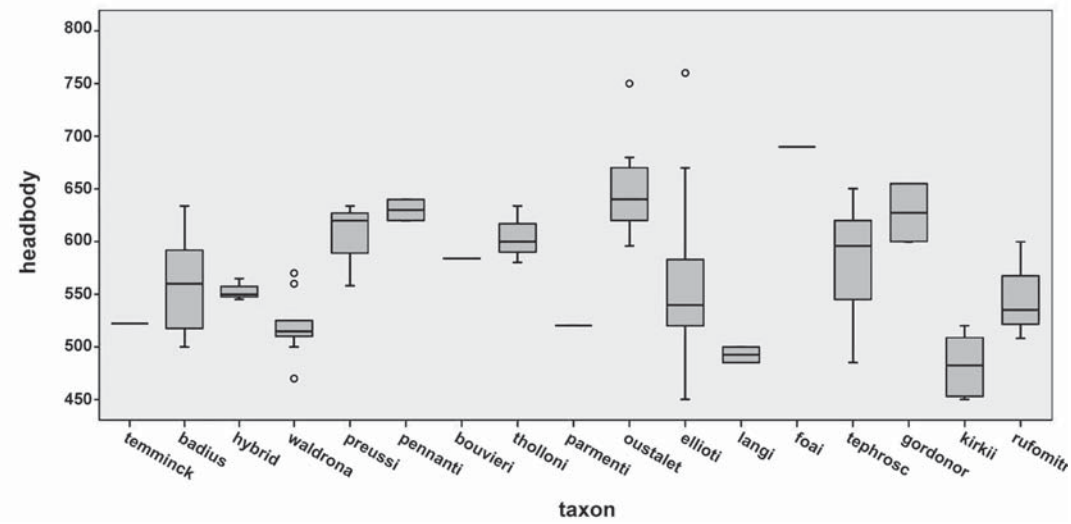

Fig. 7 - Head plus body length in Red Colobus taxa (millimeters)

up limbs; tail dark red-brown above with a median dark brown dorsal band, chestnut or maroon below, terminal third to two thirds of tail becoming black-brown; conspicuous black whorls above ears. No measurements are available.

Distribution: western part of Niger Delta, approximately the area south of 5°09'N and west of 6°07'E.

PILIOCOLOBUS BOUVIERI
Bouvier's Red colobus (Rochebrune, 1887).

Piliocolobus bouvieri Rochebrune, 1887, *Faune de Sénégambie,* Suppl., Vertébrés, pt 1: 108. "Gambia" (selected by Allen, 1939), but apparently "Mongo, right bank of the Congo, two days' journey by boat above the mouth of the Alima River" (Moreau *et al.*, 1946).
Colobus (*Piliocolobus*) *likualae* Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 346. Sanga River, near mouth of R. Likuala aux Herbes.

Diagnosis: lighter than *P.pennantii*, the black tending to chocolate-brown, and more restricted and less sharply bordered; chin covered with white hairs; whiskers white; a black brow-band bordering forehead whorl, extending laterally on temples; thighs rufous like flanks, not brownish as in *P.pennantii*; tail dark at root, turning to brownish rufous distally; underparts paler, partly brown and rufous; face light slaty, with large pink eye-rings; callosities pink; sexual swelling very large.

To judge by measurements of a single specimen, this is fairly small but very long-tailed (Figs. 6, 7).

Distribution: apparently, in swampy forest on the right bank of the Congo River, between the mouths of the Alima and Oubangui Rivers, and a short distance along the major tributary in this region, the Likouala-aux-Herbes. F.Petter and F.Vincent both told me that they had seen what seemed to be this species at Inoni, near Boembe, Lefini Reserve, at 3°S, 15°30'E, a long way south of the previously known distribution. The status of this extremely poorly known monkey needs urgent investigation. Quite unique appears to be the light face of this species, which varies from flesh-coloured with blackish cheek-bones and brows, to darker with only nose and lips light. F.Vincent (personal communication) and others who have seen this form in the wild agree as to the distinctiveness of the light face. Rochebrune (1887) described it as "rosy-flesh" with blue-black cheekbones and eye-rings, and pale, rosy-tinted ears and black brows.

PILIOCOLOBUS THOLLONI
(Rivière, 1886).

Colobus tholloni Rivière, 1886, Revue Scientifique (8) 12:13. Lower Congo.
Colobus (*Piliocolobus*) *lovizettii* Matschie, 1913, *Rev. Zool. Afr.,* 2: 207. Kutu, L. Léopold II (now L.Mai Ndombe), DRC.

Diagnosis: skull is distinctively long and narrow, small-toothed, very prognathous, with a big sagittal crest which is more extensive than in other forms. Hairs at sides of tail-base developed into a long "panache" or curtain; face slaty, with trace of pale eyelids and lips; a black browband, extending to temples, blending with whiskers which are smoky rufous; crown light bay to mahogany; upper parts bright orange-rufous, often with black intermixture on nape and forepart of back; tail darker; underside creamy white; legs orange rufous, paler than arms; hands and feet dark to black. Ischial callosities pink or slaty. On the basis of only 3 specimens, it seems a rather large species (Fig. 7), very short-tailed (Fig. 6).

Distribution: DRC, south of the "Grande Cuvette" of the Congo River, south to Dumba, 6.10°S, 19.35°E, and bordered in the east by the R. Lomami.

PILIOCOLOBUS PARMENTIERI
(Colyn & Verheyen, 1987).

Colobus rufomitratus parmentieri Colyn & Verheyen, 1987, *Rev. Zool. Afr.,* 101:125. Mabobi (0.01°N, 25.19°E), left bank of Lualaba (=upper Congo) River.

Diagnosis: no "panache"; facial skin dark, with narrow depigmented zones along lips, at base of nose, on chin, and upper eyelids; a black browband extending to temples and thence to nape, middorsal region, shoulders and upper arms; crown agouti brown-red, sharply separated from the surrounding regions, and lacking a crest; a long black tuft at base of ears; rest of upper surface of body and outer surfaces of limbs reddish; hands and feet black, contrasting with the colour of the rest of the limbs; underside, inner surfaces of limbs, and "epaulette" on front of shoulders greyish-white, contrasting sharply with red and black tones of rest of pelage; tail reddish basally, darkening distally but never becoming quite black. Size (Fig. 7) among the smallest of the Central African species; longer-tailed than *P.tholloni* (Fig. 6).

Distribution: central DRC, between the Lomami and Lualaba Rivers. The describers (Colyn & Verheyen, 1987) suggested that that the distribution is probably limited to the south by the rivers Ruiki and Lutanga.

The describers note that this subspecies differs strongly from *tholloni* in its contrasted colouration, the ear-tuft and the absence of the "panache". In some respects it more closely resembles the species east of the Lualaba, *P. foai*. Groves (2001) argued that this subspecies was named after Monsieur et Madame F.Parmentier, and that consequently the form of the name had to be altered to *parmentierorum* in accordance with the *International Code of Zoological Nomenclature*, 4th.ed., 1999, Art.31.1.2. Grubb *et al.* (2003), however, suggested that this cumbersome alteration is unnecessary if one adopts a strict interpretation of Colyn & Verheyen's (1987:129) phrase "dedié à" – a rather semantic point, but one which at least leaves the name pronounceable!

PILIOCOLOBUS OUSTALETI
(Trouessart, 1906).

Colobus oustaleti Trouessart, 1906, *Bull. Mus. Hist. Nat. Paris,* 12:443. Youmba, right bank of lower Oubangui, 0.30°N, 17.50°E (Moreau *et al*., 1946).

Colobus nigrimanus Trouessart, 1906, loc. cit., 444. Liranga, right bank (see Moreau *et al*., 1946) of Congo, south of Youmba.

Colobus (*Piliocolobus*) *powelli* Matschie, 1912, *Ann. Soc. Roy. Zool. Malacol. Belge,* 47: 61. Zakwa, between Mahagi and Irumu.

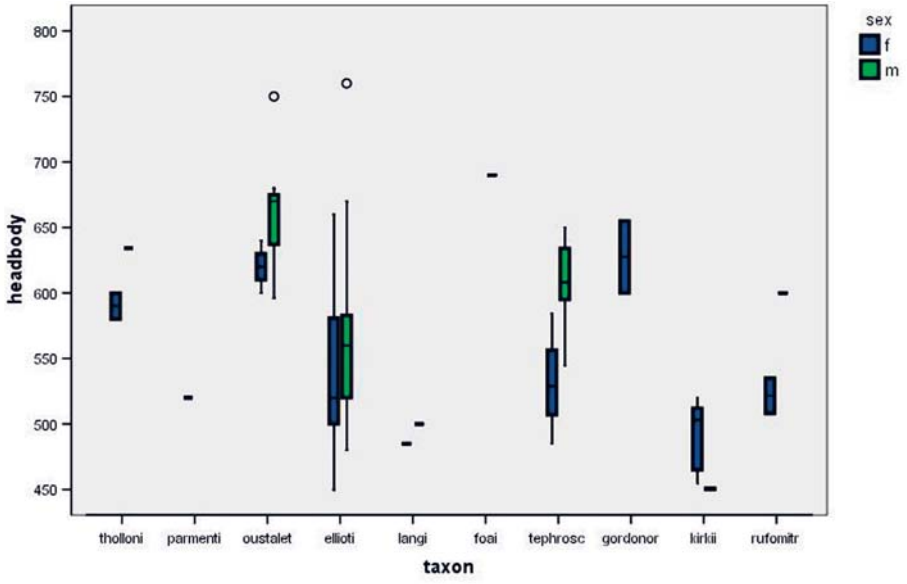

Fig. 8 - Sexual dimorphism: Red Colobus Central and Eastern groups (head plus body length in millimeters) .

Colobus (*Tropicolobus*) *umbrinus* Matschie, 1914, *Sber. Ges. naturf. Fr. Berlin,* 342. Bungi, Sangha River, between Ouesso and Ikelemba.

Colobus (*Tropicolobus*) *schubotzi* Matschie, 1914, loc. cit., 345. Koloka, between Likati and Bima Rivers, Uele basin.

Colobus (*Piliocolobus*) *brunneus* Lonnberg, 1919, *Rev. Zool. Afr.,* 7: 112. Sili, upper Uele.

Diagnosis: "panache" present, though shorter than in *tholloni*; robust build; dorsal colour fur speckled, dark smoky brown to raw sienna, brownish-fawn or deep reddish; underparts paler (buffy to whitish or pale red); hands and feet dark. Crown not, or hardly, contrasting with back; whiskers greyish. Skull with relatively broad zygomata and small teeth; differs from *tholloni* and resembles *ellioti, foai* and *tephrosceles* (*parmentieri* being unknown in these respects) in lack of concavity behind supraorbital torus, a distinctive downturn of the zygomatic arches, earlier closure of vault sutures, angular orbits and constriction below orbits. Large in size (Fig. 7), sexually dimorphic (Fig. 8), short-tailed (Fig. 6). A museum record gives the weight of a female as 12 kg. Cranially, this species and *P. ellioti*, *foai* and *tephrosceles* form a group; all have an unusually long palate, ending well behind M^3, early-closing sutures (closed by the time M^3 becomes worn), and angular orbits. The cranial characters of *P. parmentieri* are as yet unknown.

Distribution: from Pombo (1.22°S, 16.16°E), Sangha region, across the Oubangui (north of the Congo River) east to Lake Albert. Evidently it intergrades with next race in Epulu region (1.15°N, 28.21°E). Northernmost localities are Sili, Uele district (4.04°N, 27.11°E), Dedegwa, Garamba (4.35°N, 29.43°E), Mongoumba (3.40°N, 18.35°E) and Bakota, south bank of the Lobaye, 3.38°N, 17.34°E. There is a skin in Tervuren labelled "Sudan". The southwesternmost locality, Pombo, is very close to Butando where *bouvieri* is found. There is enormous variation, partly of a clinal nature, partly polymorphic, in skull characters and in colour, in this species. In the southwest of the range, a red form (*nigrimanus*-type) occurs alongside the normal brown form, with every intermediate between. Red specimens again occur in the east of the range; here it seems probable that they reflect introgression from *ellioti*, so their occurrence in the southwest may possibly indicate gene-flow from *bouvieri*. In the west, too, occurs an extremely dark morph, typified by the type of *umbrinus*. The Congo Republic sample (mainly from the Sangha River) is unusual in generally lacking the interpterygoid perforation usual in the Central African red colobus, but there is no other character distinguishing them. Colyn (1987) mapped *powelli* as a northeastern subspecies, replacing *oustaleti* approximately in the Uele district and east to Lake Albert, but gave no distinguishing features; the basic similarity of of these populations was recognised as long ago as 1914 by Matschie, who noted the very close likeness between his *umbrinus* (from the Sangha) and *schubotzi* (from the Uele). The distinction between *powelli* and *brunneus* in the eastern part of the range (Allen, 1925) is in some ways real enough: the former represents the normal dark (red-) brown type, indistinguishable from topotypical *oustaleti*; the latter is a gallery-forest form of light brown colour with no red tones. The difference is, however, on average only, and some of the characters ascribed to *powelli* would perhaps be due to gene flow from *ellioti*. Overall, four main colour types can be described:

1) Dark brown type (*oustaleti, powelli* and, most extreme, *umbrinus* and *schubotzi*), the common morph all over the range: whole body is dark smoky brown above, a little paler below. Hands and feet darker, purplish black. Some eastern specimens have a wash of chocolate, and whitish underparts.

2) Raw sienna type, occurring only in Oubangui/Lobaye area: warm, raw sienna brown, with pale buffy or golden underparts; lower part of root of tail distinctively copper red.

3) Brownish-fawn type (*brunneus*), from the Uele gallery forest region: lighter, duller brownish-fawn, with no warm sienna wash, with paler underparts (whitish to pale buff); forearms and lower legs often lighter than arms and thighs, pepper-and-salt. speckled with greyish or pale buffy hairs, contrasting with dark hands and feet.

4) Red type (*nigrimanus*): whole body is deep ferrugineous, the underparts being lighter, reddish buff; hands and feet and tail dark purplish brown or black. Some eastern specimens vary from light chestnut to bright bay, with or without black on shoulders or with a dark brown band from shoulders to rump, and whitish underparts.

The Oubangui River seems not to be a barrier; other primates, too, as well as such mammals as squirrels and duikers, seem to be distributed across it as if it did not exist. It is noticeable that the Oubangui flows largely westward, but suddenly bends south to join the Congo, as if it formerly flowed further west (perhaps to join the Shari-Logoni system?) and had recently been captured by the Congo.

PILIOCOLOBUS LANGI
(Allen, 1925)

Colobus langi Allen, 1925, *Bull. Amer. Mus. Nat. Hist.,* 47: 443. Risimu, between Stanleyville (= Kisangani) and Bafwaboli.

Diagnosis: head, throat, chest, arms and shoulders reddish, contrasting with sepia black tone of hind parts and belly. Very small in size (Fig.7), with a very long tail (Fig.6).

Distribution: a small area of Democratic Republic of Congo, from south of the Aruwimi to about the equator, along the Congo-Lualaba, and extending east to about 27°. About this species, and its status, see under 'The *ellioti* question'.

PILIOCOLOBUS SEMLIKIENSIS
(Colyn, 1991)

Colobus badius semlikiensis Colyn, 1991, *Ann. Zool. Wet. K. Mus. Midden-Afrika*, Tervuren, 264:71. Tungula (=Kilia), right bank of Semliki River, DRC.

Diagnosis: differs from *P.oustaleti* in the unvaryingly dark to blackish mantle, arms brick-red externally, forearm bordered with dusky grey, hands black, legs blackish-grey with reddish reflections, and black tail. Size and tail length are not reported.

Distribution: *Cynometra* forests east of the Semliki River, Democratic Republic of Congo. This was said by the describer to be distinguished from other DRC forms by its fully blackish mantle (in which it approaches *tephrosceles*, from which it differs by its limbs and tail not being light smoky-grey (Colyn, 1991). The black forehead band reaches the ears; a frontal tuft is present; throat, whiskers and sides of head are reddish; the nape is brown. A small "panache" is present.

About this species, and its status, see under 'The *ellioti* question'.

The *ellioti* question

Much of the Ituri/North Kivu region (northeastern DRC) is occupied by what appears to be a three-way hybrid swarm between the three previous species, which has been commonly dubbed *Piliocolobus* (or *Procolobus* or *Colobus*) *pennantii* (or *rufomitratus* or *badius*) *ellioti*.

Colobus ellioti Dollman, 1909, *Ann. Mag. Nat. Hist.,* 4 (8): 475. 90 miles west of south end of Lake Albert (probably about the Mambasa district).

Piliocolobus ellioti melanochir Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 339. Between Beni and Irumu.

Piliocolobus anzeliusi Matschie, 1914, loc. cit., 339. "Upper Ituri province".

Colobus variabilis Lorenz von Liburnau, 1914, *Anz. K. Akad. Wiss. Wien, Math. Nat. Kl.,* 51: 383.

Ituri forest: fixed as Moera, near Beni, the first locality mentioned by the describer in his detailed study (Lorenz von Liburnau, 1917:198).

Colobus multicolor Lorenz von Liburnau, 1914, loc.cit., 385.

In this population, a "panache" is generally present, though small; large teeth, broad zygomata; face is slaty, with trace of pale eyelids and lips; a black browband extends to temples, then blends into the rufous whiskers; crown, nape, shoulders and forelimbs are always red-toned, hindparts darker, from light to dark brownish; legs are often washed with fawn, with darker zone on knees, and digits blackish-brown; underside is lighter, especially on throat and chest; tail is dark brown; callosities are slaty or pink. Colobus of this description occur more or less south of a line from Kisangani to the Luna River, 1.17°N, 29.41°E; south to Mulungu district (2.19°S, 28.48°E) (as recently confirmed by Colyn, 1991). In the Epulu district they grade into *P.oustaleti*, and indeed it is hard to avoid the impression that the frequent occurrence of the red morph in *P. oustaleti* reflects gene flow from the "*ellioti*" population. Pure "*ellioti*" first occurs at Leuda (1.20°N, 28.01°E) and at Mawambi (1.04°N, 28.34°E). Colyn (1991) proposed that "*ellioti*" is a hybrid swarm between western *P. langi* and a previously undescribed eastern taxon which he described as *semlikiensis*. In his zoogeographic model of the Congo(Zaire) basin, different lowland (riverine) and Rift Valley highland subspecies differentiated early on, then approached each other again, and today form hybrid swarms in between (he also applied this model to *P. foai*: see below). The two parent species continue to exist only at the eastern and western ends of the range of "*ellioti*", partially protected from gene flow by rivers. Colyn (1991) assigned to *P. semlikiensis* several specimens from localities west of the Semliki River (but not further west than 29.28°E) where *ellioti* is also listed: Djuma, Kisiki, Kokola, "between Moera and Beni", Nyamusonga, Teturi, Tungudu and Utuhe. In total, 18 specimens from these localities are referred by him to *semlikiensis*, 21 to "*ellioti*". To Colyn's conception, *P. oustaleti* must surely be added. There is no barrier between it and "*ellioti*", and the red morph which characterises most of the hybrid population (presumably derived from *P. langi*) penetrates deep into the northeastern end of the range of *P. oustaleti*.

PILIOCOLOBUS FOAI
(de Pousargues, 1899).

Colobus foai de Pousargues, 1899, *Bull. Mus. Hist. Nat. Paris,* 5:278. Ouroua Mountains, between southwest shore of Lake Tanganyika and Upper Congo (Lualaba).

Colobus graueri Dollman, 1909, *Ann. Mag. Nat. Hist.,* 4 (8):474. Wabembe country, 80km west of north end of Lake Tanganyika.

Piliocolobus kabambarei Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 338. Kabambare, between Baraka (northwest shore of Lake Tanganyika) and Kassongo (on the Lualaba).

Piliocolobus lulindicus Matschie, 1914, loc. cit., 338. Lulindi River, Kassongo district.

Diagnosis: "panache" present; narrow across zygomata but broad palate; small teeth; tail short; frontal crest present; crown, including crest, red, commonly contrasting with back; limbs wholly red; upper parts black, red or black-and-red; underparts smoky grey to yellowish-white; browband dark.

Distribution: from south of the Rivers Lowa and Ulindi to northernmost Zambia (Mweru Wampita), and Mulongo (7.50°S) in southeastern DRC; from the Lualaba eastward into the Itombwe Mountains on the shores of Lake Tanganyika. Rahm & Christiaensen (1963) reported that it is replaced in Irangi (1.54°S, 28.27°E) by "*ellioti*", but gave no information as to whether the ranges of the two races meet; Colyn (1987, 1991) however mapped *foai* up through the Kahuzi district to meet "*ellioti*" opposite the southern end of Lake Edward.

According to this latter author, Red Colobus are more widespread in eastern Zaire than at

one time thought; but they are absent from between the rivers Maiko and Lowa. It is remarkably interesting that this hiatus in the distribution of red colobus in South Kivu is precisely the area where gorillas spread into the lowlands; the hiatus in the distribution of red colobus in west central Africa, more or less between the Sanaga and Congo/Oubangui, is again the major area where gorillas occur.

Colyn & Verheyen (1987) and Colyn (1987, 1991) recognised *lulindicus* Matschie as a lowland subspecies separate from *foai*, which they restricted to the mountainous region west of Lake Tanganyika (and, apparently, Lake Kivu). *P.foai* (in the concept adopted in this paper) shows a certain amount of individual variability in colour, although this is much less than in "*ellioti*". Three main colour types can be distinguished:

1) Dark, "black" type (*graueri*): a dark back, mainly smoky black; crest, crown and limbs lighter, rufous to smoky fawn; underparts dark smoky grey or dusky.

2) Black and red type (*foai*): a sharply contrasting pattern, with nape, shoulders and middle of back black; rest of upperparts, crest, crown, flanks, rump, limbs and tail bright rufous; underparts creamy white.

3) Red type (*lulindicus, kabambarei*): coat shorter and glossy; crest reduced in size; whole of upperparts are intense mahogany red to bright rufous; underparts whitish buff. This type recalls a very red *P. tholloni*.

There are all intermediates between these three types; type 3 predominates in the lowlands [hence, perhaps, Colyn's (1987, 1991)] retention of *lulindicus* as a separate subspecies), the other two in the Itombwe Mountains, where the fur also tends to have a rather woolly texture. There are also variations within each type. The blackening on the shoulders may be totally absent, or strong, blending with the reddish flanks and rump or sharply set off from it. The whole underside can be grey, or only the chest, the belly being buffy or whitish. Lowland specimens simply tend to be shorter-haired, with less contrastingly-toned crown and duller colouration in general. Thus *foai* would be a subspecies proper to the Itombwe mountains west of Lake Tanganyika, and *lulindicus* a related lowland race, from between the Lowa and Luama Rivers, near the Lualaba, and all populations in between would be secondary hybrids. This model is much less well supported than Colyn's model for "*ellioti*", simply because there is much less difference between eastern and western ends of the distribution of *P. foai*, and the population (here, species) is much less variable overall. It is nonetheless noticeable that the Central African taxa of red colobus (excluding those south of the Grand Cuvette) are all curiously variable, and contrast greatly with all other taxa which are noticeably homogeneous. It may well be that Colyn's model is valid, and a great deal remains to be learned about the palaeogeography of the Congo basin and the distributional history of its fauna; but if *P. foai* does consist of two different taxa which have fused, the components cannot now readily be disentangled.

PILIOCOLOBUS TEPHROSCELES
(Elliot, 1907).

Colobus tephrosceles Elliot, 1907, *Ann. Mag. Nat. Hist.* 20 (7): 195. Ruahara River, Toro, Uganda, 4000 feet.
Tropicolobus gudoviusi Matschie, 1914, *Sber. Ges. Naturf. Fr. Berlin,* 340. Between Ussuwi and Ihangiro, SSE of Lake Burigi, west of Lake Victoria.

Diagnosis: thick-set; fur dense, long; face slaty, with trace of pale tones round eyes; a large black browband, extending to temples, where the black hairs darken the smoky fawn whiskers; two conspicuous whorls of radiating hairs behind the ears, the hairs being black-tipped; crown light chestnut to deep bay; back warm brown to chocoloate brown or nearly black, sometimes with a rufous wash on rump in lighter specimens; limbs paler, especially the legs, brownish-fawn, the upper arms often washed with rufous; hands

and feet dark brown to blackish; tail basally like the back, becoming very dark distally, but always lighter below; underparts contrastingly whitish-buff to smoky buff; callosities slaty or pink. The skull closely resembles that of *P. oustaleti* and *foai*, but invariably has a curious transverse groove across region of nasion; zygomata broad, skull base long, teeth relatively small; pterygoid perforation often lacking (about 40%); skull strongly sexually dimorphic in size. Extremely sexually dimorphic in size. Tail relatively short; "panache" present.

Distribution: montane forests of southwestern Uganda and western Tanzania, along eastern border of Rift lakes, from Kibale Forest (0.13-0.41°N, 30.19-30.32°E) to Mbisi (7.25°S, 31.41°E), Lake Rukwa. The easternmost locality in Uganda is Busesse, Ankole (0.02°N, 32.01°E). As with other Central African red colobus, there is considerable geographic and individual variation in this form, although the reddish crown and light-toned forearms and legs are always characteristic. There is in fact a north-south cline in colour:

1) Northerly specimens, from western Uganda, are dull black or brown-black with a red tinge, lighter (grey-brown) rump, and much lighter (often straw-grey) forearms and legs; underside is light grey to whitish; tail is brown, darkening towards the tip. The upper arms and part of the thigh may be invaded by an extension of the black of the back.

2) Specimens from the Uganda-Tanzania border have a black dorsum with a deep red tinge on rump and loins, lighter red-brown forearms, brown legs and tail, and a whitish underside.

3) Further south, in northwestern Tanzania, they are still blacker, in fact jet-black, this tone restricting the red-brown to the croup and haunch; arms and legs mixed with brown; the tail becomes black distally; underside is white.

4) The Lake Rukwa specimens are lighter, blackish-grey, with the shorter tail coloured like the body, the arms and legs dull straw-grey, and the underside light grey. In the field they have noticeably longer, fluffier hair, and longer cheek-whiskers; the red cap fur was noticed to extend in many individuals further down into sideburns (Rodgers *et al.*, 1984).

PILIOCOLOBUS GORDONORUM
(Matschie, 1900).

Piliocolobus gordonorum Matschie, 1900, *Sber. Ges. Naturf. Fr. Berlin,* 186. Udzungwa Mountains, Uhehe, Tanzania.

Diagnosis: dorsum deep grey-brown to shining black, sometimes with a bright red zone posteriorly; underparts white, including front of shoulders, and inner surfaces of limbs; arms black; lower legs black, mixed with silvery; tail black or mixed with ochraceous, but tending to off-white below; crown reddish, with long laterally directed hairs forming a sort of toupée; cheeks whitish; skull (as represented by females only) broad, short-faced, small-toothed; no nasion groove; "panache" weakly developed; tail short, bushy. Depigmented around nose and mouth. Sexual swelling larger than in *P. p. tephrosceles*. Somewhat larger than *P. tephrosceles*, and shorter-tailed.

Distribution: Uzungwa Mountains, and forests between Little Ruaha and Ulanga Rivers, south of Iringa, Tanzania. Struhsaker & Leland (1980) report it in the Magombero Forest Reserve, 7.47°S, 37.00°E; Mangula Forest Reserve, 7.50°S, 36.54°E; and Pala Ulanga, 7.13°S, 36.49°E. These range from 200 to 1623m; from groundwater forest to riparian forest to moist evergreen forest; the Harvard specimens were collected further south, at Dabaga, Uzungwa Mountains, 8.07°S, 35.5°E. For more recent information on skulls of this species, see Bruner *et al.* (2006).

PILIOCOLOBUS KIRKII (Gray, 1868).

Colobus kirkii Gray, 1868, *Proc. Zool. Soc.* 180. Zanzibar.

Diagnosis: skull with short face but long palate, poorly developed supraorbital torus; sutures close late in life; metopism is frequent; hindlimbs elongated. Circumnasal and circumoral depigmentation retained throughout life; rest of face is slaty black. Jaws naked, sparsely sprinkled with a few white hairs. A conspicuous raised white frontal crest; crown and nape chestnut; shoulders and outside of forelimbs black; dorsum and rump contrastingly bright bay; outer side of thighs black with long white hairs overlain, except for a black lateral strip; lower part of legs white; hands and feet black, fringed with white hairs; underparts white, including inner sides of limbs and front of shoulder; tail bay above, white below, becoming golden yellowish towards tip (Fig. 9). Callosities and skin of sparsely-haired posterior thighs dark slaty. The infant coat is white, not blackish like other red colobus. The adult facial pigmentation remains of a juvenile type. Very small in size, with a very long tail; it is possible that females exceed males in size .

Fig. 9* - Piliocolobus kirkii *is the easternmost representant of the genus (photo P. Colangelo).

Distribution: Zanzibar Island. It occurs also in the coastal scrub surrounding the groundwater forests, and Uzi Island (Struhsaker & Leland, 1980). It possibly occurred in the Pangani district of the mainland in the last century: a mounted specimen (BM 74.2.20.1) has inscribed on its wooden base "Mouth of the Pangani River, opposite Zanzibar: Kirk, 1871", and a flat skin (RML cat.d) is labelled "Pangani: Linnaea, Berlin". The skins and their associated skulls are not in any way different from those from Zanzibar. A visit to the Pangani River mouth by me in 1971 failed to find any trace or knowledge of Red Colobus; suitable habitat is nowadays lacking on the coast itself, although a few miles inland, in sparse gallery forests along the Pangani, Black-and-White Colobus are abundant. In the Handeni district, not far south, Red Colobus have, however, recently been reported (W. A. Rodgers in litt.).

PILIOCOLOBUS RUFOMITRATUS
(Peters, 1879).

Colobus rufomitratus Peters, 1879, *Monatsb. K. Preuss. Akad. Wiss. Berlin,* 829. Muniuni, Tana River, Kenya (this is at 2.04°S, 40.10°E).

Diagnosis: smoky or iron grey, often washed with chocolate tints, including arms and legs, becoming just a little lighter on hind shanks; hands a feet little if any darker; tail darker, becoming nearly black towards tip; crown bright foxy-red, this colour extending back to nape, and divided from grey of body and cheeks and from light underparts by a dark grey rim; underside whitish. A whorl on either side of crown above ears, the forehead and hairs over the ears being rimmed with black. Size very small, nearly as small as *P. kirkii*, but males larger than females; tail

somewhat shorter. The skull is distinctive: very broad across orbits, long skull base, short palate, narrow across canines; nasals triangular, prominent. Supraorbital torus interrupted by a depression above glabella; deep suborbital fossae; steep, rounded occiput; large teeth. High brachial index. Clitoris large, prominent; sexual swellings large. Neonates completely dark, blackish.

Distribution: eastern Kenya, along Tana River, from Garsen north nearly to Wenje. The habitat is in gallery forests along the river and in its flood-plain; the area inhabited, of 25 sq km, is broken into more than 70 patches (Marsh, 1978). Two-thirds of the population occur in the contiguous forest belt along either side of the Tana between Munazini and Makere ya Gwano, near the northern end of the range.

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Info on the web

http://www.iucnredlist.org

The site of the annually updated Red List of threatened species realised by the World Conservation Union (IUCN).

http://www.primate-sg.org

The site of the Primate Specialist Group of the Species Survival Commission of the World Conservation Union (IUCN). Info on threatened primates and availability of several newsletters on primate conservation.

http://www.colobustrust.org

One of the few organizations devoted exclusively to the conservation of a colobus monkey; Colobus angolensis *of the coastal forests of Kenya.*

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