
RED COLOBUS *PROCOLOBUS*,
subgenus *PILIOCOLOBUS* de Rochebrune 1887

Peter Grubb

[DRAFT SUMMARY OF SYSTEMATICS, 2002]

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This manuscript was not published prior to Peter Grubb's death in 2006, although large parts appear in Appendix 1.1 of Struhsaker (2010). Because this 2002 analysis is of scientific value, we wish to make it available to the public. We have made a small number of edits to the manuscript, corrected a few minor errors, and added several footnotes, including post-2002 references.

This manuscript appears with the permission of Peter Grubb's wife, Eileen McGrath.

See four obituaries for Peter Grubb at: <http://www.primate-sg.org/storage/PDF/PC23.grubb.obituary.pdf>

Thomas M. Butynski, John F. Oates, Thomas T. Struhsaker, and Yvonne A. de Jong (December 2019).

INTRODUCTION

The red colobus monkeys have long been one of the thorniest taxonomic problems among the African primates. There is little doubt that they are a monophyletic group, within which there is a complex pattern of variation, distributed across many allopatric forms.

DISTRIBUTION

Red colobus monkeys are distributed across the rainforests of Africa from Senegal to Kenya. They range beyond the distribution of many other forest primates into gallery forests of Senegal and Guinea Bissau; between the Lualaba River and the Albertine Rift Highlands south as far as Zambia; east of the same highlands as far south as Ufipa in Tanzania; on Zanzibar; and along the Tana River in eastern Kenya. But they are also absent from areas where they might be expected to occur. Except for the population of *epieni* in the west Niger Delta they are absent in West Africa from eastern Ghana, Togo, Benin and Nigeria west of the Cross River. They are also absent from virtually the whole forest zone south of the Sanaga River in Cameroon east to the Sanga River and south to its continuation as the lower Congo River (except for *bouvieri* on the right bank of the Congo). On the other side of the Congo River, red colobus are not found south of the Sankuru and its continuation as the Kasai. They are hence completely absent from Mbini (Equatorial Guinea), Gabon and Angola including Cabinda, and are absent from southern Cameroon, most of Congo and south-west Zaire. A much smaller distribution gap is between the rivers Maiko and Loa in eastern Zaire, and there are no red colobus in the highland forests of Ruwenzori, the Mfumbiro volcanoes, Mt Elgon, the Aberdares and Mt Kenya. Total range is less than that of other less diverse species-groups such as the *Colobus polykomos* or the *Cercopithecus cephus* species-groups. Red colobus occur in a wide range of forested habitats and from sea level to over 2000 m.

TAXA

Thirty-five taxa of red colobus were described between 1792 and 1924 and all were gathered together by Schwarz (1928) into a single species, *Colobus badius*, with 18 subspecies (Table 1). More forms were described later, *waldroni* in 1936, *parmentieri* in 1987, *semlikiensis* in 1991, and *epieni* in 1999. Different reviewers have recognised between 14 and 19 taxa. Fourteen out of Schwarz's 18 are here regarded as valid, together with *waldroni*, *parmentieri*, *epieni* and *lulindicus*. Geographical variation within several taxa (*temminckii*, *oustaleti*, *tephrosceles*, *lulindicus* and *foai*) may suggest that more subspecies could be recognised. Subspecies *badius*, *waldroni* and *tholloni* appear to be relatively uniform while *epieni*, *preussi*, *pennantii*, *bouvieri*, *parmentieri*, *rufomitratu*s, *gordonorum* and *kirkii* have such limited distributions that geographical variation within each is most improbable. There is evidence for marginal gene flow between *badius* and *waldroni*, *oustaleti* and

elliotti/semlikiensis, *lulindicus* and *foai*, and possibly between *tephrosceles* and *gordonorum*, while *langi* and *elliotti/semlikiensis* are involved in an extensive zone of intergradation.

Table 1. Eight classifications of red colobus taxa [1].

Schwarz 1928: *COLOBUS BADIUS* SECTIONS
badius section: *C. b. temminckii*, *C. b. badius*, *C. b. preussi*, *C. b. pennantii*
tholloni section: *C. b. bouvieri*, *C. b. tholloni*
*rufomitratu*s section: *C. b. rufomitratu*s, *C. b. tephrosceles*, *C. b. gudoviusi*, *C. b. oustaleti*, *C. b. nigrimanus*, *C. b. powelli* (syn.: *brunneus* and *schubotzi*), *C. b. foai* (syn.: *lulindicus*), *C. b. graueri*, *C. b. elliotti*, *C. b. langi*, *C. b. gordonorum*
kirkii section: *C. b. kirkii*

Dandelot 1974: *COLOBUS (PILIOCOLOBUS) SPECIES*
C. badius temminckii, *C. b. badius*
C. waldroni
C. preussi
C. pennantii pennantii, *C. p. bouvieri*
C. tholloni
*C. rufomitratu*s *rufomitratu*s, *C. r. tephrosceles* (syn.: *gudoviusi*), *C. r. oustaleti* (syn.: *nigrimanus*, *powelli*, *brunneus*, and *schubotzi*), *C. r. foai* (syn.: *lulindicus*, *graueri*), *C. r. gordonorum*
C. r. elliotti (syn. *langi*)
C. kirkii

Napier 1985: *COLOBUS BADIUS* SECTIONS & *C. KIRKII*
C. badius:
badius section: *C. b. temminckii*, *C. b. badius*, *C. b. waldroni*, *C. b. preussi*
pennantii section: *C. b. pennantii*, *C. b. bouvieri*, *C. b. tholloni*
*rufomitratu*s section: *C. b. rufomitratu*s, *C. b. tephrosceles* (syn.: *gudoviusi*), *C. p. oustaleti* (syn.: *nigrimanus*, *powelli*, *brunneus*, and *schubotzi*), *C. b. foai* (syn.: *lulindicus*, *graueri*), *C. p. elliotti* (syn. *langi*)
gordonorum section: *C. b. gordonorum*
C. kirkii

Groves and Dandelot ms, in Napier 1985: *PROCOLOBUS SPECIES*.
P. badius badius, *P. b. temminckii*, *P. b. waldroni*.
P. preussi.
P. pennantii pennantii, *P. p. bouvieri*, *P. p. tholloni*, *P. p. oustaleti*, *P. p. elliotti*, *P. p. foai*, *P. p. tephrosceles*, *P. p. gordonorum*, *P. p. kirkii*.
*P. rufomitratu*s

Grubb 1990: *PROCOLOBUS SPECIES*.
P. badius temminckii, *P. b. badius*, *P. b. waldroni*, *P. b. preussi*
P. pennantii pennantii, *P. p. bouvieri*
P. tholloni
*P. rufomitratu*s *oustaleti* (syn.: *nigrimanus*, *powelli*, *brunneus*, and *schubotzi*), *P. r. tephrosceles* (syn.: *gudoviusi*), *P. r. rufomitratu*s.
P. foai elliotti, *P. f. langi*, *P. f. lulindicus*, *P. f. foai* (syn.: *graueri*), *P. f. parmentieri*.
P. kirkii gordonorum, *P. k. kirkii*.

Kingdon 1997: *PILIOCOLOBUS SPECIES*.
P. badius temminckii, *P. b. badius*, *P. b. waldronae*
P. preussi
P. pennantii epieni nomen nudum, *P. p. pennanti*, *P. p. bouvieri*.
P. tholloni.
P. oustaleti oustaleti, *P. o. tephrosceles*, *P. o. semlikiensis*, *P. o. elliotti*, *P. o. langi*, *P. o. lulindicus*, *P. o. foai*, *P. o. parmentierorum*.
*P. rufomitratu*s.
P. gordonorum
P. kirkii

Groves 2001: *PILIOCOLOBUS* SPECIES*P. badius temminckii*, *P. b. badius*, *P. b. waldronae**P. preussi**P. pennantii epieni*, *P. p. pennantii*, *P. p. bouvieri**P. tholloni**P. rufomitratu*s*P. tephrosceles* (syn.: *gudoviusi*)*P. foai oustaleti* (syn.: *nigrimanus*, *powelli*, *brunneus*, and *schubotzi*), *P. f. semlikiensis*, *P. f. ellioti*, (syn.: *langi*),*P. f. foai* (syn.: *graueri*, *lulindicus*), *P. f. parmentierorum**P. gordonorum**P. kirkii*IUCN/SSC Primate Specialist Group, Orlando, Florida, February 2000 [5]: *PROCOLOBUS* SPECIES*P. badius temminckii*, *P. b. badius*, *P. b. waldroni**P. pennantii*.*pennantii* section: *P. p. preussi* *P. p. epieni* *P. p. pennantii*, *P. p. bouvieri**tholloni* section: *P. p. tholloni* *P. p. oustaleti*, *P. p. tephrosceles*, *P. p. ellioti*, *P. p. langi*, *P. p. lulindicus*, *P. p.**foai*, *P. p. parmentieri**P. rufomitratu*s,*P. gordonorum**P. kirkii*

Compromise grouping, recognising all taxa raised to species-rank by other authors (except for Dandelot's treatment of *waldroni* and *ellioti* as separate species).

P. badius temminckii, *P. b. badius*, *P. b. waldroni**P. preussi**P. pennantii epieni*, *P. p. pennantii*, *P. p. bouvieri**P. tholloni**P. oustaleti**P. tephrosceles**P. rufomitratu*s*P. foai ellioti*, *P. f. langi*, *P. f. lulindicus*, *P. f. foai*, *P. f. parmentieri**P. gordonorum**P. kirkii***ANNOTATED LIST OF TAXA**

Provisionally, all taxa are listed below as if they were subspecies of *Procolobus badius* (Kerr, 1792), prior to a discussion on species limits.[1] The subspecies are placed roughly in geographical order from west to east, but probable sister-taxa are placed next to each other. English-language names are included. Recent publications have disagreed over the status and synonymy of *langi*, *ellioti* and *semlikiensis*, and of *lulindicus* in relation to *foai*. The status of the other 14 subspecies has not recently been questioned, suggesting considerable stability at this level of taxonomy.

Procolobus badius temminckii, Temminck's Bay Colobus.

Synonymy: *Colobus temminckii* Kuhl, 1820, *C. fuliginosus* Ogilby, 1835, *C. rufofuliginosus* Ogilby, 1838.

Outside the principal forest blocks in SW Senegal, Gambia and Guinea-Bissau. Said to be absent east of the Rio Grande (Rio Corubal) in Guinea-Bissau (Maclaud 1906) except for supposed sighting at Catio, near the border with Guinea (Monard 1938). Mapped from the Fouta Djallon in Guinea (Booth 1958) from which no published records seem to be available. Reported from north-west Sierra Leone (Harding 1984) but otherwise *temminckii* is said to be geographically isolated from *badius*. Narrow black brow fringe; ochre tones on brow and on nape; upperparts from crown to tail light ashy grey extending onto upper arms and thighs; cheeks, margins of neck, limbs and margins of belly ochery; tail orange brown; midline of underlimbs and belly whitish; patch of white hairs on perineal region and inside of thighs. Geographically variable; specimens from southern Senegal and Guinea Bissau darker, grey parts charcoal and orange-ochre parts russet brown.

P. b. badius, Upper Guinea Bay Colobus.

Synonymy: *Simia badius* Kerr, 1792, *S. ferruginea* Shaw, 1800, *Colobus ferruginosus* Étienne Geoffroy Saint-Hilaire, 1812, *C. rufoniger* Ogilby, 1828.

Sierra Leone, adjacent parts of Guinea, Liberia and western Ivory Coast. Pelage bicoloured black and mahogany-brown; hands and feet not black. Black above including crown; arms, hands, legs and feet deep mahogany brown, black extends onto thigh and on arm; below deep mahogany, tail very dark brown along basal half, black distally, or all black; red-brown colour extends onto cheeks; patch of white hairs on perineal region and inside of thighs.

P. b. waldroni, Miss Waldron's Bay Colobus.

Synonymy: *Colobus badius waldroni* Hayman, 1936.

Formerly in SW Ghana and E Ivory Coast, separated from *badius* by the lower Bandama [not Sassandra] River; now probably extinct; last reliably recorded as a hunter's skin obtained in 1972. Bare face in life dark blue-black with pinkish nose and lips; pelage bicoloured black and mahogany-brown; hands and feet not black. Similar to *badius*, including white perineal patch, but tail all black, hind legs all mahogany, sharply marked off from black of dorsum, reddish tuft above ear and reddish patch behind brows.

P. b. preussi, Preuss's Red Colobus.

Synonymy: *Piliocolobus preussi* Matschie, 1900.

Known only from SW Cameroon north of the Sanaga River and marginally in adjacent SE Nigeria (Grubb et al. 2000). Blackish crown, red colour extends onto sides of neck and cheeks; blackish-grey to grey-brown dorsally extending to very base of tail but not along tail; upperparts finely agouti-speckled; reddish colour is rather orange and covers limbs, tail and flanks; hands and feet also red, not black; underparts buffy. Vocally distinct (Struhsaker, 1981).

P. b. epieni, Niger Delta Red Colobus.

Synonymy: *Procolobus badius epieni* Grubb & Powell, 1999.

Known only from a very small area in the western sector of the Niger Delta. Facial skin black to pinkish-grey, but some pink can remain on the muzzle; eyelids pinkish (field observations by J. L. R. Werre). Resembles *pennantii* in black hands and feet, blackish crown, no red colour on neck or cheeks; differs in having conspicuous hair-whorls behind ears, dorsal pelage agouti-speckled in part, whitish ventral coloration extends onto front of fore-arms. Field observations by J. L. R. Werre and study of nine preserved skins indicate a considerable range of variation (Grubb and Powell 1999).

P. b. pennantii, Pennant's or Bioko Red Colobus.

Synonymy: *Colobus pennantii* Waterhouse, 1838.

Known only from Bioko (Equatorial Guinea). Blackish colour extending onto crown and upper parts of limbs, not so dark on lumbar region, extends onto upper side of tail; rufous on limbs and along flanks but this reddish colour does not extend onto neck and cheeks; hands and feet black; underparts and cheeks white; tail on sides and below deep red-brown, darkening towards tip. There are few museum specimens, so variation in this subspecies is not well known.

P. b. bouvieri, Bouvier's Red Colobus.

Synonymy: *Piliocolobus bouvieri* de Rochebrune, 1887, *Colobus likualae* Matschie, 1914.

Between the lower reaches of the Léfini and Sangha, tributaries of the lower Congo River, in Congo. Black superciliary band extends to ear; crown deep brown without whorls; cheeks and underside of neck whitish; blackish zone down neck, shoulders and in a band down the back, becoming greyer and broadening on the rump and extending onto the tail; rest of upperparts russet, the colour extending onto arms and legs; hands and feet blackish, black colour extending up inside of lower leg; reddish colour does not extend onto throat and cheeks. This is another poorly-known subspecies. Regarded as similar to *pennantii* but lighter in colour; also resembles *tholloni* (Colyn 1991), differing mainly in pattern of blackish or grey colour on back.

P. b. tholloni, Thollon's or Tshuapa Red Colobus.

Synonymy: *Colobus tholloni* Milne-Edwards, 1886, *C. (Piliocolobus) lovizettii* Matschie, 1913.

Cuvette Central in Zaire [2] between the Congo River to the north and north-west, the Lomami to the east, and the Kasai to the south. Brow and fringe extending to ears black; crown deep brown or chestnut, without hair whorls; cheeks and underside of neck whitish; upperparts orange -russet all over, somewhat blacker on shoulders; hands blackish, feet as upperparts or dark brown; tail as upperparts becoming dark brown on distal quarter to one-third; tufts of blackish hair on either side of base of tail; underparts whitish with a yellowish tone. Skull noticeably prognathous.

P. b. oustaleti, Oustalet's or Oubangui Red Colobus.

Synonymy: *Colobus oustaleti* Trouessart, 1906, *C. nigrimanus* Trouessart, 1906, *C. (Piliocolobus) powelli* Matschie, 1913, *C. (Tropicolobus) schubotzi* Matschie, 1914, *C. (T.) umbrinus* Matschie, 1914, *C. multicolor* Lorenz, 1914, *C. (P.) brunneus* Lönnberg, 1919.

North of the Ituri River and its continuation as the Aruwimi and middle Congo Rivers and west to the Sangha River in Congo, southern Central African Republic, Zaire and marginally in southern Sudan. Variable, may constitute more than one subspecies; Colyn (1991) recognized only one taxon (*oustaleti*) north of the Aruwimi, though he had previously divided it into *oustaleti* sensu stricto and *powelli* (Colyn 1987). More recently, Gautier-Hion et al. (1999) regarded *oustaleti* as a complex of six subspecies, three west of the Oubangui (*oustaleti* sensu stricto with synonym *umbrinus*, *nigrimanus* and an undescribed form from the vicinity of the Lobaye River, a tributary of the lower Oubangui, Central African Republic) and three to the east (*shubotzi*, *powelli* and *brunneus* with synonym *multicolor*). Allocation of specimens and locality records to these nominal taxa has not yet been published. Coloration of Ituri form (*'brunneus'*): bare face blackish; black hairs along brow, the colour extending to the ears; cheeks whitish grizzled with black; crown reddish brown; whorls on crown; upperparts finely agouti-speckled (clearly evident or inconspicuous), brown grizzled with black producing the general effect of a dull chestnut pelage; nape and shoulders blacker due to black ends to hairs; arms slightly paler or streaked blackish and buff; dark to black hands and feet; underparts grey or whitish. Red morphs (two specimens) are *'nigrimanus'*. Raw sienna type with all buffy or golden underparts and coppery red under tail restricted to Lobaye area. Gallery forests of Uele tributaries lighter, brownish fawn animals with light forearms and shanks (*'brunneus'?*). Paler form (*'powelli'*) in most extreme pelage, light ochre-buff, reddish crown, ashy streaking on shoulders, hands and feet do not contrast in colour with pale limbs. Isolated population in extreme east of range, on the Lendu plateau west of Lake Albert, said to approach *tephrosceles* in characters of pelage (Colyn 1991, citing Vrydagh 1950).

P. b. tephrosceles, Ashy or Uganda Red Colobus.

Synonymy: *Colobus tephrosceles* Elliot, 1907, *Tropicolobus gudoviusi* Matschie, 1914.

Constitutes at least ten geographically isolated populations east of the mountains of the Great Rift Valley in western Uganda, Rwanda, Burundi and western Tanzania south as far as lat. 8° 17' S on the Ufipa plateau. Black brow line extends to ears, crown and nape dull reddish brown, often bushy; prominent whorls on crown partly black; cheeks greyish; upperparts including tail dark grey brown, sometimes with a reddish cast, sometimes paler on rump and base of tail; limbs, especially legs pale grey; hands blackish, feet blackish or at least somewhat darker than legs; underparts whitish to grey-white, including chin and throat. Fur long and lax, especially in males. A diagnostic cranial character of this taxon is the consistent presence of a groove across the nasion, between the orbits (Groves). There is some geographical variation. In the Biharamulu region, some skins have rich red-chocolate crown; very dark brown, almost black upperparts; rump and lower back with orangey brown suffusion; and white underparts - a colour form that is not strongly differentiated from series of Uganda skins yet is suggestive of *gordonorum*. An orangey brown lumbar patch is also recorded in Mahale Mountains skins. The Mbisi forest population has longer and thicker body hair giving a woolly or fluffy aspect, prominent cheek whiskers, fuller crown cap and shorter tail, related to colder habitat at 2200 m (Rodgers et al. 1984).

P. b. rufomitratatus, Tana River Red Colobus.

Synonymy: *Colobus rufomitratatus* Peters, 1879.

Confined to the Tana River valley in eastern Kenya. Resembles *tephrosceles* very closely in colour pattern; black brow, shading into grey cheeks; crown and nape dull orange, crown whorls with black hair tips, upperparts grey brown, darker on shoulders, paler on rump, and darker for distal three-quarters of tail; limbs, especially legs, paler brown-grey; hands and feet hardly any darker; underparts pale whitish grey. The skull is smaller and less prognathous than that of *tephrosceles* but quite similar in proportions, though it is regarded as very distinct by Groves. Vocally, it is related to *tephrosceles* and Central African forms (Struhsaker 1981).

P. p. ellioti, Semliki Red Colobus.

Synonymy: *Colobus ellioti* Dollman, 1909, *Piliocolobus anzeliusi* Matschie, 1914, *P. ellioti melanochir* Matschie, 1914, *Colobus variabilis* Lorenz, 1914, *Colobus badius semlikiensis* Colyn, 1991.

From *Cynometra* forests on both sides of the Semliki River in north-east Zaire and probably Bwamba Forest in Uganda, merging through a zone of intermediacy with *P. p. langi*. Superficially very different from *langi*, but mainly because the upperparts are blackish, black on shoulders and back becoming grey-sepia on sacral region and hind limbs; crown reddish; outside of arms dull brick red, forearm bordered dark grey between elbow and hand; hands and feet and tail blackish; throat, whiskers and sides of head reddish. Reasons for synonymy given below.

P. b. langi, Kisangani Red Colobus.

Synonymy: *Colobus langi* J. A. Allen, 1925.

Occurs in pure form in the cul-de-sac between the Lualaba and Aruwimi Rivers in north-east Zaire and extends as a variant within the population eastward to the vicinity of Lake Kivu. Fringe of black hairs on brow extends to ears; no whorls on crown; top of head, cheeks, nape, shoulders and fore limbs including hands deep orange-chestnut, darker on shoulders; rest of upperparts and hind limbs including feet dark sepia washed with black; tail from near base to tip black; underparts with foreneck and pectoral area light orange and remainder pale slate grey, lighter on inside of thighs and inguinal areas.

P. b. lulindicus, Lulindi River Red Colobus.

Synonymy: *Piliocolobus lulindicus* Matschie, 1914, *P. kabambarei* Matschie, 1914.

Zaire in lowland forest east of the Lualaba from the Lowa south to the Luama River at lat. 5° 20' S. Treated as a synonym of *foai* by Schwarz, Dandelot, Napier and Groves, but as a valid taxon by Colyn (1991) and therefore also by Grubb and Kingdon. *Lulindicus* averages smaller in skull measurements than *foai* but this may not be systematically significant. However, in a multivariate analysis of pelage scores, coordinates for 12 *lulindicus* and 19 *foai* are completely separated along Axis 2, while three geographical intermediates ('*kabambarae*') between *lulindicus* and *foai* are in intermediate positions on the plot, so a case can be made for them both being regarded as valid taxa. *Lulindicus* has shorter pelage, no crest; upperparts reddish with relatively little black pigmentation restricted to shoulders and distal end of tail; ventral parts yellowish; no black on hands and feet.

P. b. foai, Kivu Red Colobus.

Synonymy: *Colobus foai* de Pousargues, 1899, *C. graueri* Dollman, 1909.

Upland forest along the Rift highlands in Zaire south to about lat. 6° S along the western side of Lake Tanganyika. Specimens from lowland localities range much farther south (Colyn 1991), apparently in gallery forests south to lat. 9° 40' S in Zambia, and lat. 11° 27' S in Zaire (southernmost locality for red colobus monkeys). These are mostly assigned to *foai* by Colyn (1991) but are not discussed in his text, while their mapped localities are assigned to 'hybrids'. Further information on occurrence in Zambia would be desirable; it is not included in the Zambia mammal fauna by Ansell (1978). Typical *foai* characterised by long red crest sharply marked off from dark colour of crown and nape; no whorls on crown; rest of upperparts black, with orange-brown limbs, lower flanks, tail and lumbar region; whitish underneath; digits blackish. Duller and less contrasting pelage, grey below, in *graueri*. Both *foai* and *graueri* morphotypes recorded from the same locality so have been synonymised by Dandelot, Napier and Groves.

P. b. parmentieri, Lomami River Red Colobus.

Synonymy: *Colobus rufomitratu parmentieri* Colyn & Verheyen, 1987.

Restricted to the northern part of the cul-de sac formed by the confluence between the Lomami and Lualaba (= upper Congo) Rivers in Zaire. Bare face blackish with depigmented nose, philtrum and lips; crown bright red, shoulders black, rest of upperparts russet, hands and feet black, underparts whitish invading the margins of the limbs, crown whorl reduced to a forward-directed pencil of hairs.

P. b. gordonorum, Uzungwa Red Colobus.

Synonymy: *Piliocolobus. gordonorum* Matschie, 1900.

Confined to the Udzungwa and Luhombero Mountains in south-central Tanzania. Face dark grey except for depigmented area around nose and mouth; crown cap bowl-shaped, brilliant rufous to red-brown with black and longer hairs in a band just above the brow; dark charcoal to grey-brown dorsally extending to lateral surface of the arms, anterior and lateral surface of the thighs and dorsal surface of the tail, contrasting sharply with white undersides; about 2 percent have red to red-brown on the lower back; anterior edge of shoulders and entire ventral area, including medial surface of arms and legs and proximal half of the ventral surface of the tail white to greyish; long silvery grey hairs on lower legs to just above the knee.

P. b. kirkii, Kirk's or Zanzibar Red Colobus.

Synonymy: *Colobus kirkii* Gray, 1868.

Known reliably only from Zanzibar [3], but may have occurred on the Tanzania mainland in the past (Rodgers 1981). Bare face black with nose, philtrum and lips depigmented; long white hairs form fringe above eyes, sparse black hairs in front, neck and nape russet, shoulders black, arms black sprinkled with white hairs, hands black, rest of back and upper side of tail light russet; hind legs whitish but black bases of hairs show through, feet black, underparts including under surface of tail whitish though whole tail darkens towards tip. Smallest of all red colobus monkeys.

GEOGRAPHIC VARIATION - SIZE

Data on body dimensions (see below) are patchy as often they were not recorded by the collectors of museum specimens. Collectors may have differed in the way they made measurements. Size variation in body dimensions appears to be reflected in skull measurements, which are more complete (see below). For males, sequence from smallest mean skull length to largest is as follows (samples of 10 or more in CAPITALS):

kirkii < *temminckii* < *rufomitratu*s, WALDRONI < LANGI < *badius* < *epieni* < LULINDICUS < *elliotti* (*semlikiensis*) < *oustaleti* Zokwa < TEPHROSCELES Uganda < *preussi* < OUSTALETI Akenge and Oubangui < PARMENTIERI < FOAI < THOLLONI < *tephrosceles* Nyamanzi < *pennantii* < *tephrosceles* Mbizi.

For females, the sequence is similar:

KIRKII < *rufomitratu*s < *temminckii* < WALDRONI < *tephrosceles* Ruiga Bay < BADIUS < LANGI < *tephrosceles* Uganda < LULINDICUS < *preussi*, *oustaleti* Oubangui < *oustaleti* Zokwa < THOLLONI < OUSTALETI Faradje and Akenge < PARMENTIERI < *pennantii* < *bouvieri*.

The smaller subspecies are in West Africa from Ghana westward (*temminckii*, *badius*, *waldroni*), East Africa (*kirkii*, *rufomitratu*s) and parts of eastern Congo-Kinshasa (*langi*, *lulindicus*). Larger taxa include *tephrosceles*, *oustaleti*, *parmentieri*, *foai* and *tholloni*.

GEOGRAPHIC VARIATION - SKULL MORPHOMETRICS

Groves (2001) has reviewed qualitative aspects of the skull in certain subspecies. The main quantitative study has been made by Colyn (1990) on central African populations. A canonical analysis of 14 variables for *langi*, *parmentieri* and *tholloni* separated the sexes completely along Axes 1 and 2, which accounted for over 80 percent of the variability. Dispersion of points for females was similar to that of males but displaced along axis 2. Within each sex, *langi* and *parmentieri* were completely separated (they are also separated geographically by the upper Congo River in the neighbourhood of Kisangani); on the plot, *tholloni* overlapped the dispersions of both the other taxa.

Keeping the sexes separate, a second study using 10 variables treated a wider range of forms (*bouvieri*, *foai*, *langi*, *lulindicus*, *oustaleti*, *parmentieri*, *tholloni*). Axis 1 completely separated *langi* from *foai*, *oustaleti* and *parmentieri* while *lulindicus* and *tholloni* were intermediate, but along Axis 2, *tholloni* was almost completely separated from all the others. Males of *bouvieri* were not available, but females were strongly displaced from female *tholloni*, lying within the range of *oustaleti* and *parmentieri*.

A third study addressed eight variables in males of *foai*, *langi*, *lulindicus*, *oustaleti*, *parmentieri*, *semlikiensis*, *tephrosceles* and *tholloni*. Again, *langi* was completely separated from others, in this case *foai*, *oustaleti*, *parmentieri*, *semlikiensis* and *tephrosceles*, while *lulindicus* and *tholloni* occupied the intermediate position; *tholloni* was partly separated from all others along Axis 2 but this time with more overlap.

Based on the second and third studies, phenograms of morphological distance between the forms gave consistent results suggesting the following relationships: ((*tholloni*)(*lulindicus*, *langi*))((*oustaleti*, *foai*)(*parmentieri*)(*tephrosceles*, *semlikiensis*))). Colyn attached phylogenetic and historical biogeographical significance to these results, particularly in linking taxa from a presumed fluvial refuge (*tholloni*, *lulindicus*, *langi*). But associating *oustaleti* with *foai* and *parmentieri* with *tephrosceles* and *semlikiensis* as sister-taxa seems topologically improbable.

GEOGRAPHIC VARIATION - VOCALISATIONS

Struhsaker (1981) suggested a phylogeny based on vocal similarities, giving rise to a dendrogram of the following form: ((*temminckii*, *badius*) (*preussi*)) ((*tholloni*, *tephrosceles*, *rufomitratu*) (*gordonorum*, *kirkii*)). The vocalisations of *oustaleti* and *elliotti* are now found to be very similar to those of *tephrosceles* (Struhsaker in preparation). [4]

GEOGRAPHIC VARIATION - GROUPS OF TAXA

External morphology, particularly of the pelage, has been the principal feature used to determine relationships among red colobus so far. Struhsaker (1981, appendix) has warned that the apparent lability of coat colour makes it of limited use in determining phylogenetic affinities at the specific and subspecific levels. Colyn's (1991, 1993) multivariate analysis of pelage characters in eastern Congo-Kinshasa is valuable because it provides a more objective assessment of variation within and between taxa and takes into account the very problems highlighted by Struhsaker (1981). Colyn's method could be extended to cover taxa from other parts of Africa.

If a cladistic analysis of pelage traits is to be attempted, it must be done with caution, because the variability of their character states within a population will make their polarity 'fuzzy'. Nevertheless, some aspects of polarity among character states can be identified. According to the hypothesis of metachromism (Hershkovitz 1968), agouti-speckling of relatively dull pelage is a primitive character-state while spread of melanistic or erythristic pigmentation especially when leading to tricolour (red, black and white) or bicolour (red and black; or red and white) pelage are derived states, as is depigmentation of the upperparts or of the face. Whorls of hair on the crown is a primitive character possessed by the outgroup taxon *Procolobus verus*. Black hands and feet and limitation of erythristic tones to the crown are probably primitive states, from their distribution among red colobus taxa, and presence of a well-defined crest a derived character.

Vocalisations are important because they provide a wholly independent source of data to compare with pelage. Also, it appears that groups of subspecies based only on vocalisations are larger than groups based on external appearance, suggesting perhaps that vocalisations have evolved more slowly than pelage features. Their main drawback is that they have not been recorded for many taxa.

Phylogenetic proximity is implied by similarities between subspecies of red colobus. The subspecies are loosely described as 'related' or 'relatives' but precise phylogenetic relationships have not often been postulated. Those that are thought to be related have been placed in a 'division' or 'group' (Table 1). While 'group' is not a technical word, a group of taxa is intended to be monophyletic. The group may really be paraphyletic or even polyphyletic and if this were to be demonstrated, its status and content would have to be revised. Prefer to use the term 'division' as 'group' is often a supraspecific category.

If we could describe the evolution of red colobus subspecies in terms of a series of vicariance events, each subspecies may be regarded as the sister of either another subspecies or a lineage including several subspecies. If subspecies differentiated recently, then geographically adjacent taxa could well be sister-taxa. If several taxa are

in contact, not every pair can represent sister-taxa. One has to identify which are likely to be more closely allied. This may not be obvious if they have differentiated strongly. It is quite probable that some geographically adjacent taxa will be phylogenetically distant from each other and this is clear with *kirkii* and *rufomitratu*s, or *parmentieri* and *langi*. Struhsaker (1981) discussed such cases among red colobus.

But by describing the diversification of subspecies in terms of vicariance events it is implied that two sister-taxa are generated at each event. This premise is not supported by empirical evidence. It is perfectly possible that some subspecies are the ancestors of others, or that one subspecies has given rise to several others (Grubb 1999) - that is, subspecies can be paraphyletic and their relationships are expressed by chains as well as branches. A further assumption has been that each subspecies is monophyletic and that gene exchange between such taxa has been secondary. There is no reason however why some subspecies should not have a polyphyletic origin. The *langi-elliotti* zone of intergradation may illustrate an early stage in such a development.

These contingencies would confound attempts to place taxa in natural groups or to carry out a cladistic analysis. Therefore, we cannot necessarily expect a conventional cladogram to represent the evolution and diversification of red colobus monkeys.

The different forms of red colobus show more diversity than is usually found in a single species but unlike black-and white colobus or mona monkeys, for instance, major subdivisions are not obvious. In his systematic study of Central African red colobus, Colyn (1991) kept the subspecies in a single species. Other authors divided the red colobus into groups of subspecies and/or species (Table 1) and they include Schwarz (1928), Dandelot (1974), Napier (1985), Groves and Dandelot (in Napier 1985), Grubb (1990), Kingdon (1997) and Groves (2001). [1] Struhsaker (1981) recognised groups among certain taxa, based on vocalisations. A consensus view of red colobus systematics was provided by primatologists at the workshop of the IUCN/SSC Primate Specialist Group held at Orlando, Florida, in February 2000. In their opinion, present evidence allowed three species to be delineated relatively easily (*Procolobus badius*, *P. gordonorum*, and *P. kirkii*). The Tana River red colobus was probably a fourth species, *P. rufomitratu*s, though it has close relationships to forms farther west. The workshop recognized two further assemblages of red colobus forms, each of which contains several good subspecies and probably a number of species, but which were all included provisionally within *P. pennantii*. The western or *pennantii* section includes *P. p. pennantii*, *P. p. bouvieri*, *P. p. preussi*, and *P. p. epieni*. Each of these forms merits at least subspecies status. Within the central or *tholloni* section, *P. p. oustaleti* and *P. p. parmentieri* merit at least subspecies status, and *P. p. tholloni* and *P. p. tephrosceles* are particularly discrete, but the workshop could not agree on individual species status for any one of them. It was thought that a further four forms (*P. p. foai*, *P. p. elliotti*, *P. p. lulindicus* and *P. p. langi*) of the forests of the eastern Congo Basin cannot readily be assigned to different subspecies, although all authorities list *foai* as a valid taxon. It was considered that relationships in this group require further study. [5]

While there is some correspondence between the divisions in Table 1, with smaller categories of one author nested within the larger categories of another, there are still considerable differences between the classifications of different authors. The grouping of subspecies remains much more uncertain than taxonomy at the subspecies level. This is because we may have enough data to delineate subspecies, but we do not have sufficient data to evaluate their relationships.

AN ATTEMPT TO GROUP TAXA

The following account debates the evidence for relationships between taxa. Publications by Schwarz (1928), Dandelot (1974), Napier (1985), Grubb (1990), Kingdon (1997) and Groves (2001) [1] are cited by the authors' names only.

1) There is general agreement that *temminckii*, *badius* and *waldroni* are related, supported by studies of vocalisations of *temminckii* and *badius* (Struhsaker 1981), although Dandelot treated *waldroni* as a distinct species on the grounds that the shape of the nose was different from that of the otherwise similar *badius*. Apart from the black upperparts and the white perineal hairs, the pelage of *waldroni* and *badius* is wholly mahogany brown, without contrasting light underparts, a character not present in any other red colobus.

2) The form *preussi* resembles *temminckii*, *badius* and *waldroni* in the all-blackish colour of the mantle extending onto the crown, red cheeks and sides of neck and red (not black) hands and feet. According to Groves

the skull is similar, though larger. Vocalisations are distinct but indicate affinity with *temminckii* and *badius* (Struhsaker 1981). Dandelot, Kingdon and Groves have treated it as a species on grounds that have not been explicitly stated.

1, 2) *Temminckii*, *badius*, *waldroni* and *preussi* (*badius* group): Schwarz, Napier and Grubb placed *preussi* in the *badius* group which from geography, a number of shared derived characters of the pelage and vocalisations could be a monophyletic group.

3) *Epieni* and *pennantii* are similar to each other and agree with the *badius* group (including *preussi*) in the blackish dorsal colour extending onto the crown, but cheeks and neck are not red and hands and feet are black; *epieni* retains primitive character states (crown whorls and agouti-speckled dorsum); *pennantii* is apparently more derivative (loss of crown whorls and agouti speckling) but its variability is not well known; *pennantii* is placed in the *badius* group by Schwarz but in its own group with *bouvieri* by Dandelot, Napier, Grubb, Kingdon and Groves.

4) The form *bouvieri* was synonymised with *pennantii* by de Pousargues (1896), placed in the *tholloni* group by Schwarz but grouped with *pennantii* by other authors. Pelage differs from that of *tholloni* by the distribution of dark tones on the back and lack of tufts at the base of the tail.

1, 2, 3, 4) *Badius* group, plus *epieni*, *pennantii* and *bouvieri* (provisionally treated as the '*pennantii* group'): Discovery of *epieni* increases known diversity in West African taxa. Possibly the *badius* and *pennantii* groups are parts of a single lineage [monophyletic]. Primitive and derived character states can be apportioned to the various taxa (see box), but if used to construct a phylogeny would involve several parallelisms out of only a few characters. Furthermore, variability in some of these taxa is not well known, so character-states may not be accurately described. Nevertheless, the trend is for more derived character states to occur farther to the west.

It may also seem that *bouvieri* is intermediate between *pennantii* and *tholloni* both geographically and in pelage (Colyn 1991). However, for females at least, skulls of *bouvieri* are widely separated from those of *tholloni* in a canonical analysis (Colyn 1991). Doubts that *preussi*, *epieni*, *pennantii* and *bouvieri* link *waldroni*, *badius* and *temminckii* with *tholloni* arise because vocally *preussi* is associated with *temminckii* and *badius*, while *tholloni* is grouped with taxa occurring farther to the east (Struhsaker 1981); there may be a major division between a Western African lineage and a Central and East African lineage, at variance with the provisional conclusions of the Primate Specialist Workshop, discussed above. More information is needed to support Struhsaker's (1981) hypothesis, which predicts that the vocalisations of *bouvieri*, *epieni* and *pennantii* will be shown to be related to those of *preussi* and not to *tholloni*. Studies of skulls of *preussi*, *epieni*, *pennantii* and *bouvieri*, all of which are very rare in museums, are also needed.

5) *Tholloni* is placed with *bouvieri* (Schwarz) or in its own group (Dandelot, Napier, Grubb, Kingdon, Groves). Pelage differs from that of *bouvieri* by the distribution of dark tones on the back and tufts at the base of the tail; vocally it is linked with East African taxa (Struhsaker 1981). The long prognathous skull is distinct, contrasting particularly with that of *preussi*; *tholloni* differs from *bouvieri*, *oustaleti* and the *foai* group (for definition, see below) in canonical analysis of skull measurements (Colyn 1991). The forms *bouvieri* and *tholloni* are adjacent and seem quite similar but if their resemblances are convergent, one should look for a sister-group relationship in other adjacent taxa, the *rufomitratu*s group or the *foai* group. Based on a phenogram, Colyn (1991) associated *tholloni* with the rather different *langi* and *lulindicus* (*foai* group) but it is uncertain whether this indicates phylogenetic relationships. Unlike the *foai* group but like *epieni*, *pennantii*, *bouvieri* and *oustaleti*, there is no red colour on the face of *tholloni* and this might suggest that it derives from an erythristic *oustaleti*-like ancestor.

6) *Oustaleti* has been placed with the *foai* group, *tephrosceles* and *rufomitratu*s (Schwarz, Dandelot, Napier) or in a group excluding the last two (Groves) or with those last two alone (Grubb). It is distinct from adjacent taxa *bouvieri*, *tholloni*, *parmentieri*, *langi* and *elliotti*, all of which are separated by rivers (except between the Ituri and Semliki), and subjectively is most similar in pelage to *tephrosceles* and *rufomitratu*s.

Inferred primitive and derivative states (in that order) of pelage characters in western African red colobus

1. Whorls on crown present (*epieni*) or absent (*bouvieri*, *pennantii*, *preussi*, *waldroni*, *badius*, *temminckii*).
2. Pelage agouti-banded (*epieni*, *preussi*) or not agouti-banded (*bouvieri*, *pennantii*, *waldroni*, *badius*, *temminckii*).
3. Crown all reddish (*bouvieri*) or reddish anteriorly only, rest black, blackish pigment continuing forward onto head (*waldroni*, *temminckii*), or all black (*epieni*, *pennantii*, *preussi*, *badius*).
4. Nape blackish (*bouvieri*, *epieni*, *pennantii*, *preussi*, *waldroni*, *badius*) or with a russet patch (*temminckii*).
5. Blackish tract restricted to midline of back (*bouvieri*) or extends over most of upperparts of body (*epieni*, *pennantii*, *preussi*, *waldroni*, *badius*, *temminckii*).
6. Blackish dorsal tract continues uninterrupted onto tail (*bouvieri*, some *epieni*, *pennantii*), or stops at base of tail (some *epieni*, *preussi*, *temminckii*, some *badius*), or tail all black (*waldroni*, some *badius*).
7. Hands and feet black (*bouvieri*, *epieni*, *pennantii*), or red (*preussi*, *waldroni*, *badius*, *temminckii*).
8. Red colour does not extend onto neck (*epieni*, *pennantii*) or extends forward at least along sides of neck (*bouvieri*, *preussi*, *temminckii*, *badius*, *waldroni*).
9. Red colour does not extend onto cheeks (*bouvieri*, *epieni*, *pennantii*), or does extend onto cheeks (*preussi*, *waldroni*, *badius*, *temminckii*).
10. Red colour does not intrude onto midline of underside of neck, inner sides of limbs and ventral surface of body, leaving these areas whitish or buff, so that pelage is tricoloured (*bouvieri*, *epieni*, *pennantii*, *preussi*, *temminckii*), or extends onto these areas, so that pelage almost entirely bicoloured (*waldroni*, *badius*).
11. Outside of forearm russet (*bouvieri*, *pennantii*, *preussi*, *waldroni*, *badius*, *temminckii*) or invaded by white inner-arm colour (*epieni*).

Suggested cladogram: (*bouvieri*)((*epieni*, *pennantii*)((*preussi*)((*temminckii*)(*badius*, *waldroni*))))

7) *Tephrosceles* has been placed with *rufomitratu*s, *oustaleti* and the *foai* group (Schwarz, Dandelot, Napier), with *rufomitratu*s and *oustaleti* only (Grubb), with *oustaleti* and the *foai* group only (Kingdon), or treated as a full species (Groves). The dull coloration with reddish crown and pale limbs is not unlike some *oustaleti*. It retains prominent crown-whorls but does not have agouti speckling. Variants with blacker dorsum, redder crown, whiter underparts and reddish colour on lumbar region are not strongly differentiated from 'typical' specimens yet resemble *gordonorum* and account for the affinity said to exist between the two taxa (Dandelot, Groves). Struhsaker and Leland (1980) contrasted *tephrosceles* with *gordonorum*; in the field, the two taxa are very distinct. *Gordonorum* differs even from the variant *tephrosceles* in its black limbs, much sharper contrast between black upperparts and whitish underparts on cheeks, neck, arms, flanks and base of tail; much more strongly differentiated reddish tract on lumbar region, when present; stronger iridescence of pale hair shafts on underparts and legs; lack of crown whorls; lack of nasion groove; and vocalisations. There are three possibilities. (1) Variant *tephrosceles* and *gordonorum* are similar only through convergence. (2) They are similar only because of secondary gene flow between more typical *tephrosceles* and *gordonorum* in the past. (3) They are phylogenetically proximate - for instance, *tephrosceles* might be regarded as the sister taxon of *gordonorum* (plus *kirkii*); cladistic relationships in the relevant clade might be expressed as: ((*tephrosceles*)(*gordonorum*, *kirkii*))(*rufomitratu*s). Andrews et al. (1975) supported a similar view, in which *rufomitratu*s and *gordonorum-kirkii* 'are related not to each other but to the geographically nearest *tephrosceles* population.' More field studies and analysis of mitochondrial DNA in relevant museum specimens are needed to evaluate these three hypotheses in relation to the alternative suggestion that the *gordonorum-kirkii* group is derived from the *foai* group (see below). The latter proposal is compatible with hypotheses (1) and (2) above, and hypotheses (1), (2) and (3) are

all compatible with the suggestion that there were two waves of north-eastward dispersal by red colobus monkeys in East Africa (Groves et al. 1974 and see under discussion of *rufomitratu*s) [1].

Compared with *rufomitratu*s, *kirkii* is very distant from *tephrosceles*. The notional cladogram - ((*tephrosceles*)(*gordonorum*, *kirkii*))(*rufomitratu*s) - suggests rapid evolution in a *tephrosceles-gordonorum-kirkii* lineage and evolutionary stagnation in *rufomitratu*s and this may not correctly represent their history. Are there any further clues to their affinities? [1]

The specimens of *tephrosceles* that most resemble *gordonorum* emanate from the Biharamulu region, by the south-west corner of Lake Victoria, far from the Udzungwa Mountains. The monkeys in these forests (*Cercopithecus neglectus*, *C. mitis doggetti*, *C. ascanius schmidti*, *Procolobus badius tephrosceles*, *Colobus angolensis ruwenzorii*) belong to a different fauna from those in Udzungwa (*Lophocebus* sp., *Cercocebus sanjei*, *Cercopithecus mitis moloneyi*, *Procolobus badius gordonorum*, *Colobus angolensis palliatus*). The two faunas are associated with 'northern' and 'southern' routes of dispersal by Kingdon (1971) and with Central and Eastern Faunal Zones by Grubb (2001). The representatives of *Cercopithecus mitis* and *Colobus angolensis* in these faunas are not particularly closely allied (not regarded as sister-taxa). Other representatives of the two faunas, again subspecies of *Cercopithecus mitis* (*C. m. stuhlmanni* and *C. m. albogularis*), form a hybrid zone in a small area near Lake Manyara, far away from any presumed gene flow between *gordonorum* and *tephrosceles*.

The zoogeographical picture does not strongly support any particular phylogenetic hypothesis but would be compatible with independent origins of the *tephrosceles-rufomitratu*s and *gordonorum-kirkii* lineages.

8) *Rufomitratu*s is associated with the *foai* group, *oustaleti* and *tephrosceles* (Schwarz, Dandelot, Napier), with the latter two only (Grubb), or treated as a distinct species (Kingdon, Groves). It resembles *tephrosceles* very closely in colour pattern and vocalisations while the skulls are not dissimilar. It is likely to be derived from a *tephrosceles*-like ancestor and the two might be regarded as sister-taxa. *Procolobus badius rufomitratu*s and the [Tana River] mangabey *Cercocebus galeritus* are endemic to the Tana River valley, a relatively isolated and faunistically depauperate locality for forest primates. How they reached this site is a matter of debate. A direct eastward dispersal (from *P. b. tephrosceles*-like and *C. agilis*-like ancestors) has no parallel in the distribution of any other forest mammals (Andrews et al. 1975) and so is most improbable. Mangabeys are also present on the Udzungwa Mountains (*C. sanjei*), so their dispersal could have been from the Congo Basin through the Southern Arc Mountains to Kenya. But among the red colobus presently occurring along this route, *gordonorum* and/or *kirkii*, with their specialised pelage, cannot be ancestors of *rufomitratu*s; if *rufomitratu*s reached Kenya by the same route as the mangabeys, it would have had to have made an independent and presumably earlier north-eastward dispersal than the *gordonorum-kirkii* lineage (Groves et al, 1974; Grubb, 1990; Kingdon 1971).

6, 7, 8) *Oustaleti*, *tephrosceles* and *rufomitratu*s (*rufomitratu*s group): The taxon *oustaleti* includes the most conservative pelage patterns among red colobus and occupies a central geographical position in Africa; *oustaleti*, *tephrosceles* and *rufomitratu*s (*rufomitratu*s group) represent a lineage that extends into East Africa, retains conservative coloration yet shows progressively more derived characters from west to east.

9) *Ellioti* (including *semlikiensis*, *langi*, *lulindicus*, *foai* and *parmentieri* (*foai* group) are placed with *oustaleti* by Schwarz, Dandelot, Napier, Kingdon and Groves (Dandelot treated *elliotti* sensu stricto as a separate species) but regarded as a separate group by Grubb. Dorsal pelage is red and black in various patterns, strongly contrasting with that of *oustaleti*, from which they are separated by all except the easternmost reaches of the Ituri-Aruwimi River, but skulls have not been differentiated by canonical analysis (Colyn 1991). Studies of vocalisations have not been published but vocally *elliotti* is said to be similar to *tephrosceles*, *rufomitratu*s and *tholloni* (Struhsaker, unpublished). [4]

In Zaire south of the Aruwimi-Ituri Rivers, east of the Lualaba (upper reaches of the Congo River) and west of the Rift Valley highlands, there are four stable morphotypes (*langi*, *semlikiensis*, *lulindicus* and *foai*) according to Colyn (1991). He resurrected the names *langi* and *lulindicus* from synonymy and described *semlikiensis* as a new subspecies, though there are grounds for treating this last name as a synonym (discussed later). Variation in geographical intermediates is considerable and at least in part they are also phenotypic intermediates, the result of gene flow between *langi* and *semlikiensis* and between *semlikiensis* and *oustaleti*. The prior name based on *langi-semlikiensis* intermediates is *elliotti*, which has seniority over both *langi* and *semlikiensis*, but was discarded by Colyn (1991) because it was attributed to a 'hybrid' population. There are also

phenotypic intermediates between *lulindicus* and *foai*, and other intermediates link *semlikiensis* with *lulindicus* and with *foai*.

From east of the Semliki River, between it and the Ruwenzori highlands, the race *semlikiensis* is known from three localities (four museum specimens), and intermediates from another locality (one specimen). From 12 localities west of the Semliki and south of the Aruwimi-Ituri, 20 specimens have been recorded, together with another 23 specimens of intermediates (though some of those cited by Colyn or studied in BM [6] are very similar to 'pure' *semlikiensis*). In other words, *semlikiensis* is a variant within a variable population. On the other hand, the taxon *langi* is known in pure form farther to the west, in the cul-de-sac between the Lualaba and Aruwimi Rivers.

Using 22 variables and 107 character-states of pelage, Colyn (1991, 1993) demonstrated that *langi*, *semlikiensis*, *lulindicus* and *foai* (89 skins) are separated from each other in that sequence along Axis 1 of his multivariate analysis. A subset of 18 intermediates was also examined, out of a total of 171 available skins. Most were from localities close to the range of *semlikiensis* and were separated from that form along Axis 2, that is, with a tendency towards the dispersion of *oustaleti* specimens on the plot. Indeed, the intermediates that approached *oustaleti* most closely on the plot were also closest geographically, coming from the area between the Ituri and Semliki Rivers where they meet up with *oustaleti*. The intermediate skins possess agouti-speckled annulation of the pelage, a character typical of *oustaleti*. Evidently there is a zone of (secondary?) intergradation between *semlikiensis* and a very different and pale-coloured form of *oustaleti* ('powelli').

Others of the selected specimens bridged the gap along Axis 1 between *semlikiensis* and *langi*. Specimens resembling *langi* but not used in Colyn's (1990, 1993) analysis were recorded from close to the distribution of *semlikiensis* and to the type locality of *elliotti*. The *langi* morphotype seems to have a wider range than the *semlikiensis* morphotype, reaching from the vicinity of Kisangani to Lake Kivu. Geographical intermediates between *langi* and *semlikiensis* are not always phenotypically intermediate but include wholly reddish specimens such as the holotype of *elliotti*, possibly the consequence of genetic recombination. Evidently there is a broad and complex zone of intergradation between *langi* and *semlikiensis*. The uneven distribution of collected specimens (their concentration near the range of *semlikiensis*) and the small samples of intermediates compared by Colyn with 'pure' stock suggest that more information is needed to fully describe the zone of intergradation.

Specimens of *lulindicus* approaching so-called '*elliotti*' (*langi/semlikiensis* intermediates) or regarded as *lulindicus/elliotti* intermediates are located between other intermediates and typical *lulindicus* both geographically and on Colyn's (1991, 1993) plot of pelage characters. Intermediates between *foai* and '*elliotti*' are recorded just north of typical *foai*, in the neighbourhood of Mt Kahuzi. Several intermediates between *lulindicus* and *foai* have an appropriately intermediate geographical location and three of them ('*kabambarae*') also approach *lulindicus* on Axis B in Colyn's plot. Reasons for treating *lulindicus* as a subspecies separate from *foai* are given above.

Colyn (1991, 1993) also made a canonical analysis of skull measurements, indicating a complete separation of pure *langi* and pure *semlikiensis* plus *oustaleti* along Axis 1. Twenty-eight selected intermediates extended over a broader range in the bivariate plot of Axes 1 and 2, incorporating the dispersion for *semlikiensis* plus *oustaleti*, approaching *langi*, or located within the range of *langi*. In contrast to the pelage scores, *semlikiensis* and *oustaleti* were not differentiated in this study. If Colyn's (1991, 1993) phenogram is interpreted as a cladogram, the *foai* group would be polyphyletic. However, similarities of pelage within the *foai* group suggest that *langi* is the sister taxon of *semlikiensis*; *langi* is like *semlikiensis* but with reddish pigment invading the whole forequarters. In turn, *langi* plus *semlikiensis* could be the sister taxon of the trio *lulindicus*, *foai* and *parmentieri*, where the reddish colour has developed in different areas, invading the hand, arms, flanks, lumbar region, legs and feet.

Groves (2001) interpreted the data in a different way from Colyn. Intergradation was thought to reflect variation between three subspecies, *elliotti* (including *langi*), *semlikiensis* and *foai* (including *lulindicus*).

The status of the name *elliotti* needs to be clarified. Colyn (1991) regarded it as part of a 'hybrid' population and did not use it as a name for a taxon, though it has priority over *langi* or *semlikiensis*. Groves (2001) treated it as a senior synonym of *langi*. The name *elliotti* can not be ignored - it can be categorised neither as a *nomen dubium*, nor as a *nomen oblitum*. Hybrid specimens as such (e.g. a mule, a first-generation hybrid) are excluded from the provisions of the Code of Zoological Nomenclature (ICZN 1999, Article 1.3.3) and a species-group name established for an animal later found to be a hybrid must not be used for either of the

parental taxa (Article 23.8), but a distinction is made for a taxon of *hybrid origin* (not a first-generation hybrid). The availability of such a name is not affected if it is applied to a taxon (Article 17.2). One of the topotypes of *elliotti* is blackish above and much more like *semlikiensis* than the holotype, while the type locality of *elliotti* is closer to that of *semlikiensis* than that of *langi*. Therefore, it is thought more appropriate to treat *elliotti* as the senior synonym of *semlikiensis* than the senior synonym of *langi* and hence reduce *semlikiensis* to synonymy, as indicated above.

Geographically, *elliotti* (including *semlikiensis*) is adjacent to *oustaleti* ('*powelli*'). It is also geographically close to *tephrosceles* which it resembles in its lack of agouti speckling, dark hands and feet, and dark upperparts. It differs in its blacker pelage, regular presence of red on cheeks and arms, legs differently coloured and not contrasting with the back, and somewhat reduced crown whorls. Possibly *elliotti/semlikiensis* and *tephrosceles* are 'related' and are phylogenetically as well as geographically proximate, though the resemblance is rather general. Possibly the *foai* group is the sister taxon of *tephrosceles* plus *rufomitratu*s. If so, a category including both the *foai* group and *oustaleti* but excluding *tephrosceles* and/or *rufomitratu*s (Groves, Kingdon, IUCN/SSC Specialist Group) would be paraphyletic.

More derived pelage with much more red coloration and other specialisations are more geographically distant from *tephrosceles*; the most derived pelages (in *foai*, *lulindicus* and *parmentieri*) are in the most distant populations.

The race *parmentieri* is more similar to *foai* than other taxa in spite of being widely separated geographically (Colyn and Verheyen 1987). Its precursor is likely to have crossed the upper reaches of the Lualaba and percolated northward between the Lualaba and Lomami towards their confluence. A suggestively similar pattern of distribution is shown by *Cercopithecus mitis heymansi*, *C. wolfi elegans* and intermediates between *C. ascanius katangae* and *C. a. whitesidei*, which range from outside the Lualaba-Lomami interfluvium northward towards or into the same cul-de-sac (Colyn 1988). Though the outsides of the limbs are red, not black, the red-black-white tricolour pattern of *foai* and *parmentieri* is suggestive of the tricolour pattern in *gordonorum* and *kirkii*. The sharply defined white tone on the insides of the limbs and its intrusion onto their outer surfaces, together with depigmentation on the face are similarities between *parmentieri* and the *kirkii* group. The resemblance is rather general and data to support the hypothesis that they are related are lacking but it makes geographical sense. If a proto-*gordonorum/kirkii* had a distribution extending from the Congo Basin south of Lake Tanganyika to the Southern Arc mountains and coastal forests of Tanzania, this would mean an independent origin from the other East African taxa, *tephrosceles* and *rufomitratu*s, and would account for the differences between the two groups.

10) *Gordonorum* and *kirkii* (*kirkii* group): Similarities between *gordonorum* and some *tephrosceles* are discussed above. The form *kirkii* resembles *gordonorum* in striking tricolour pattern including black outsides of limbs, depigmented areas on face, and vocalisations, as well as orange lumbar region (shown by variants of *gordonorum*); there is less sexual dimorphism in *gordonorum* and *kirkii* than in *tephrosceles* (Struhsaker 1981, Struhsaker and Leland 1980). Struhsaker and Leland (1980) noted the resemblances between *gordonorum* and *kirkii*; furthermore, the *gordonorum* infant closely resembles the adult *kirkii*; *gordonorum* and *kirkii* are probably sister taxa. The latter differs strongly from all other red colobus in its white crest and is particularly different from the geographically nearest form (*rufomitratu*s) in pelage, vocalisations and skull architecture, suggesting they are only remotely related.

PHYLOGENETIC CONCLUSIONS:

Red colobus monkeys have here been partitioned into the *badius* group, with *waldroni* and *temminckii*; the *pennantii* group, with *bouvieri*, *preussi* and *epieni*; the *tholloni* group; the *rufomitratu*s group, with *oustaleti* and *tephrosceles*; the *foai* group with *elliotti/semlikiensis*, *langi*, *lulindicus* and *parmentieri*; and the *kirkii* group, with *gordonorum*. The taxon *oustaleti* (*rufomitratu*s group) includes the most conservative pelage patterns and occupies a central geographical position in Africa; the *rufomitratu*s group extends into East Africa showing progressively more derived characters from west to east. The *foai* group shows derived character states (dominance of black and red colours in pelage, loss of agouti speckling and reduction or loss of crown whorls) especially in its most peripheral forms *parmentieri* and *foai*. In the past it may have been connected with a proto-*gordonorum-kirkii* whose distribution extended into Tanzania. Alternatively, there may once have been gene

flow between *gordonorum* and *tephrosceles*. Affinities of *tholloni* have not been securely identified except that it has vocalisations like those of *tephrosceles* and *rufomitratu*s. A further lineage of red colobus extends into West Africa, with retention of conservative characters in geographically intermediate taxa (crown whorls in *epieni*; agouti speckling in *epieni* and *preussi*; black hands and feet in *epieni*, *pennantii* and *bouvieri*). Geographic dispersion of subspecies-groups tends to approach a morphoclinal or phylogeographic pattern, with primitive and successively more derived states of several characters distributed across the taxa constituting each group. The trend is for more derived characters to occur in more peripherally located taxa. This applies for instance to *badius* in relation to *epieni*, *rufomitratu*s in relation to *oustaleti*, *foai* or *parmentieri* in relation to *elliotti*, or *kirkii* in relation to *gordonorum*. The most peripheral taxa are very distinct from each other, for instance, *badius*, *tholloni*, *foai*, *rufomitratu*s and *kirkii*. Incorporating a provisional assessment of cladistic relationships within each subspecies-group, and combining the *badius* and *pennantii* groups, the suggested history behind this pattern is one of dispersal from central Africa:

- 1) (*bouvieri*) ((*epieni*)(*pennantii*) (*preussi* ((*temminckii*)(*badius*, *waldroni*))))); extend westward from Congo to Senegal;
- 2) *tholloni*; in the Cuvette Central
- 3) *oustaleti* (*tephrosceles*, *rufomitratu*s); extend from Congo to Uganda, looping south through Tanzania and then north to Kenya
- 4) (*elliotti*, *langi*)(*lulindicus*, *foai*, *parmentieri*); extend south from the Aruwimi River to Zambia and also doubling back towards the Equator;
- 5) *gordonorum*, *kirkii*; from Central Tanzania to Zanzibar.

In addressing the phylogeny of subspecies-groups, several questions remain outstanding. Can we be sure that the groups are not polyphyletic? How is the *pennantii-badius* group related if at all, to the *tholloni* group? How is the *kirkii* group related to other groups? Are the *pennantii* and *foai* groups paraphyletic and how are they related to the *rufomitratu*s group? If the *foai* and *kirkii* groups are related, then their phylogeny could take this form (or a similar one): (*elliotti*, *langi*)(*lulindicus*, *foai*, *parmentieri*)(*gordonorum*, *kirkii*)

A cladistic model could treat the *rufomitratu*s group as paraphyletic, with the *foai* group paraphyletic in relation to the *kirkii* group: (*badius* group)((*tholloni*)(*oustaleti*)(*foai* plus *kirkii* groups)(*tephrosceles*, *rufomitratu*s))). An alternative, with the *foai* group now monophyletic is as follows: (*badius* group)((*tholloni*)(*oustaleti*)(*foai* group)(*kirkii* group, *tephrosceles*)(*rufomitratu*s))).

Obviously, more permutations are possible and one must remember the caveats about interpreting the red colobus in terms of any cladogram at all. Only further multivariate analysis of pelage traits and skull dimensions and mitochondrial DNA or allozyme analysis, as well as more studies of vocalisations, may test these hypotheses and contribute to fine-tuning of relationships within lineages.

SPECIES STATUS

If there is a division among red colobus between West African taxa and those of Central and East Africa, as suggested by the data on vocalisations (Struhsaker 1981), the two major lineages could be classed as species. Their names would be *Procolobus badius* (including *pennantii*) and *P. rufomitratu*s. If more species were to be recognised, in view of the strong differences between many taxa, the subspecies-groups discussed above could be treated as species, though many workers might demur at recognising paraphyletic taxa and would require problems of parphyly to be clarified. If the most distinctive taxa are picked out as species, the remaining taxon could be relegated to paraphyletic status - a residual 'paraphyletic rump'. Evidence for separation into western and eastern lineages is also apparent in *Cercopithecus mona* and *C. cephus* species-groups, and among species of *Cercocebus*.

The maxim or premise that species are the smallest diagnosable assemblages of interbreeding organisms and that there are no subspecies constitutes the 'Phylogenetic Species Concept'. Though sympathetic to this

premise, Groves (2001) categorised only nine out of 17 taxa of red colobus as species and recognised the others as subspecies (Table 1); groups with non-overlapping character states were species, those with overlapping conditions were subspecies (Groves 2001), imperfectly diagnosable entities. However, all red colobus taxa are apparently diagnosable. Therefore a 'pure' phylogenetic species-concept should rank them all as separate species. This would convey no more information than placing them all in a single species, so there would still be a call for an intermediate 'group' category, whether we call it 'species' or not. Other authors have not explicitly stated what criteria they have adopted in determining species status among red colobus.

The 'diagnosable' criterion probably presents as many problems as the 'reproductive isolation' criterion alleged to be the hallmark of the Biological Species Concept. More criteria are actually in use for defining species but together they cannot ensure that each taxon in a monophyletic group of allopatric populations can definitively be identified as a species or a subspecies. We may come closer to agreement but must grasp the nettle that a final answer can not be reached.

HISTORICAL BIOGEOGRAPHY

Red colobus monkeys are partitioned geographically into subspecies much like other mammalian species-groups in the rainforest of Africa, so that it is possible to allocate them to the same shared Centres of Endemism (Grubb 1990, 2001). Correspondence is particular close where a taxon of red colobus has a distribution that includes or is included by only single taxa from other species-groups (Table 2). Most subspecies of red colobus can be assigned to named Centres of Endemism. A few exist where there are sympatric but not endemic primates (*P. b. temminckii*, *P. b. kirkii* and *P. b. bouvieri*). There are no red colobus in the important Rio Muni, Ogôoué and Kasai Centres. Mammalian endemism in the Albertine highlands and neighbouring forest is complex and includes the primates *Cercopithecus mitis schoutedeni*, *C. m. doggetti*, *C. m. kandti*, *C. hamlyni kahuziensis*, *Colobus angolensis ruwenzorii* and *Gorilla gorilla beringei*. The red colobus taxa of the same region, *P. b. tephrosceles* and *P. b. foai*, do not have distributions coinciding precisely with any of these other endemics.

Fourteen subspecies and the whole *foai* group of red colobus are separated from each other by seas, large rivers, or gaps in distribution (in some cases including inhospitable habitat). Constraints on gene flow would seem to be in force at present. Intermediates between *oustaleti* and *elliotti* show that some river boundaries do not now wholly prevent gene flow. Nevertheless, it seems possible that river barriers may have contributed to the differentiation and diversity of red colobus taxa. Adverse climatic episodes could also have contributed by restricting populations to refuges (Struhsaker 1981). In doing so they could have enhanced the effects of river barriers by the forest contracting away from headwaters where it would have been easier to cross and exchange genes. The correspondence between centres of endemism and refuges has not often been critically considered. Grubb (2001) has suggested that major refuges may have enclosed what are now several centres of endemism. Suggested refuges with associated red colobus include the Guinea refuge (*badius*, *waldroni*), a minor refuge in the Niger Delta (*epieni*), a Cameroon-Gabon refuge (*preussi*, *pennantii*), an Albertine refuge or refuges (*elliotti*, *foai*, *tephrosceles*), and East African refuges (*rufomitratu*, *gordonorum*, *kirkii*). These correspond closely with the refuges mapped by Struhsaker (1981). Work by Colyn (e.g. Colyn 1991) emphasises that there was also a major riverine refuge that existed in the Cuvette Central, central Zaire, in the late Pleistocene. Listed geographically in clockwise sequence, *bouvieri*, *oustaleti*, *langi*, *lulindicus*, *parmentieri* and *tholloni* differentiated in this refuge from other taxa stranded in peripheral refuges already cited. Since the Congo and its major tributaries have been faunal boundaries and retain this role, affinities can have been closer between central and peripheral taxa than within the major riverine refuge itself. For instance, *langi* and *lulindicus* are closer to *elliotti* and *foai* than to *oustaleti*, *bouvieri* or *tholloni*.

The only taxon not accommodated by this hypothetical scheme of refuges is *temminckii* but there are other endemic taxa within its range such as the Guinea baboon (*Papio papio*) and the crowned duiker (*Sylvicapra grimmia coronata*) which may have shared a similar history of differentiation.

There are different philosophies of how the process of cladogenesis might have operated in Quaternary Africa. According to one implicit interpretation, mammals differentiated into numerous subspecies and allopatric species *in situ*. Another approach suggests that differentiation accompanied dispersal over the continent. The first hypothesis is unlikely (Grubb 1999) because it seems to address events following one major dispersal event, yet environmental change was episodic during the later Quaternary of Africa, with a period of 100,000 yrs., so phases of geographical isolation and dispersal could have alternated. According to the second hypothesis, at least

some adverse episodes recurrently contributed to the isolation and differentiation of allotaxa. The same taxa could have become geographically isolated on more than one occasion. Conversely, during at least exceptionally favourable climatic episodes, red colobus would have been able to disperse and increase their range. This periodic model suggests that cycles of dispersal and differentiation occurred repeatedly, leading to increasing diversity in these monkeys. Some taxa are younger than others. Patterns of geographic variation in red colobus, however tentatively interpreted, do indeed suggest a process of successional dispersal and differentiation away from Central Africa.

Table 2. Taxa with similar ranges to red colobus taxa (in the sense that their ranges more or less correspond or one is included within the range of the other).

(no Centre designated) *Procolobus badius temminckii*

Liberian Centre: *P. b. badius* (*Cercocebus atys atys*, *Cercopithecus diana diana*, *C. campbellii campbellii*, *C. petaurista buettikoferi*, *Colobus polykomos*)

Gold Coast Centre: *P. b. waldroni* (*Cercocebus atys lunulatus*, *Cercopithecus diana roloway*, *C. campbellii lowei*, *C. petaurista petaurista*, *Colobus vellerosus*)

Niger River Centre: *P. b. epieni* (*Cercopithecus erythrogaster pococki*)

West-Cameroon Centre: *P. b. preussi* (*Mandrillus leucophaeus leucophaeus*, *Cercopithecus preussi preussi*, *C. nictitans ludio*, *C. pogonias ssp.*, *C. erythrogaster camerunensis*)

Bioko Centre: *P. b. pennantii* (*Mandrillus leucophaeus poensis*, *Cercopithecus preussi insularis*, *C. nictitans martini*, *C. pogonias pogonias*, *C. erythrogaster erythrogaster*, *Colobus satanas satanas*)

(no Centre designated) *P. b. bouvieri*

Ubangi-Uele Centre: *P. b. oustaleti* (*Cercocebus agilis*, *Colobus guereza occidentalis* and *C. angolensis cottoni* have similar distributions)

Kivu Centre: *P. b. ellioti*, *P. b. langi*, *P. b. lulindicus* (*Colobus angolensis cordieri*), *P. b. foai*

Lomami-Lualaba Centre: *P. b. parmentieri* (*Cercopithecus mitis heymansi*)

Salongo Centre: *P. b. tholloni* (*Cercocebus chrysogaster*, *Cercopithecus dryas*, *C. ascanius whitesidei*; in addition, *Lophocebus aterrimus aterrimus*, *Allenopithecus nigroviridis*, *Cercopithecus wolffi wolffi*, *Colobus angolensis angolensis* and *Pan paniscus* have similar distributions but also occur with other subspecies of red colobus)

(no Centre designated) *P. b. tephrosceles*

Eastern Centres: *P. b. rufomitatus* (*Cercocebus galeritus*), *P. b. gordonorum* (*Cercocebus sanjei*, *Colobus angolensis palliatus*), *P. b. kirkii*

DATA ON SKULL AND BODY MEASUREMENTS

Skull lengths and breadths in mm for different samples of red colobus monkeys *Procolobus badius* (sources: Colyn, 1990; Natural History Museum London; Verheyen, 1962).

Subspecies (and region)	Greatest skull length (prosthion-inion)	Greatest skull width (bizygomatic)
<i>P. b. temminckii</i> males	99.8 (99 - 101), n = 2	77, n = 1
<i>P. b. temminckii</i> females	93.4 (88 - 103), n = 5	68.5 (66 - 71), n = 5
<i>P. b. badius</i> males	105.0 (100 - 106), n = 5	78.3 (74 - 82), n = 4
<i>P. b. badius</i> females	98.0 (93 - 105), n = 10	72.7 (70 - 75), n = 9
<i>P. b. waldroni</i> males	101.0 (92 - 109), n = 8	79.5 (72 - 86), n = 8
<i>P. b. waldroni</i> females	95.3 (92 - 101), n = 15	71.2 (67 - 73), n = 15
<i>P. b. epieni</i> male	106, n = 1	78, n = 1
<i>P. b. pennantii</i> (male)	117.0, n = 1	91.0, n = 1
<i>P. b. pennantii</i> (female)	105.5, n = 1	71.5, n = 1
<i>P. b. preussi</i> males	111.5 (103 - 114), n = 2	84.5 (84 - 85), n = 2
<i>P. b. preussi</i> females	101.5 (104 - 109), n = 2	78.0 (75 - 81), n = 2
<i>P. b. bouvieri</i> female	108, n = 1	78, n = 1
<i>P. b. oustaleti</i> (Akenge) males	112.2 (108 - 118), n = 17	87.8 (84 - 93), n = 18
<i>P. b. oustaleti</i> (Akenge) females	104.5 (98 - 109), n = 17	76.2 (72 - 83), n = 16
<i>P. b. oustaleti</i> (Zokwa) males	108.3 (105 - 112), n = 7	86.9 (84 - 90), n = 6
<i>P. b. oustaleti</i> (Zokwa) females	103.3 (100 - 106), n = 3	75.5 (73 - 78), n = 2
<i>P. b. oustaleti</i> (Faradje) males	114.4 (110 - 121), n = 12	90.3 (87 - 93), n = 11
<i>P. b. oustaleti</i> (Faradje) females	104.2 (99 - 108), n = 13	76.8 (72 - 80), n = 12
<i>P. b. oustaleti</i> (Oubangui) males	111.8 (107 - 115), n = 7	86.2 (82 - 89), n = 7
<i>P. b. oustaleti</i> (Oubangui) females	101.5 (99 - 105), n = 4	77.6 (74 - 81), n = 4
<i>P. b. langi</i> males	103.1 (98 - 109), n = 31	78.3 (74 - 86), n = 31
<i>P. b. langi</i> females	98.9 (94 - 104), n = 32	69.8 (66 - 72), n = 32
<i>P. b. lulindicus</i> males	107.8 (98 - 113), n = 24	81.5 (74 - 86), n = 22
<i>P. b. lulindicus</i> females	100.4 (94 - 107), n = 13	70.8 (68 - 76), n = 13
<i>P. b. foai</i> males	113.0 (107 - 120), n = 18	86.0 (82 - 93), n = 18
<i>P. b. tholloni</i> males	113.6 (108 - 119), n = 16	84.4 (78 - 90), n = 16
<i>P. b. tholloni</i> females	104.4 (97 - 111), n = 26	72.9 (67 - 78), n = 26
<i>P. b. parmentieri</i> males	112.0 (105 - 118), n = 31	86.0 (79 - 91), n = 29
<i>P. b. parmentieri</i> females	104.7 (101 - 109), n = 32	75.4 (69 - 80), n = 32
<i>P. b. ellioti</i> (hybrid zone) males	108.3 (99 - 116), n = 32	84.4 (71 - 91), n = 28
<i>P. b. ellioti</i> (hybrid zone) females	100.2 (90 - 107), n = 27	73.2 (67 - 79), n = 27
<i>P. b. ellioti</i> (cf. <i>semlikiensis</i>) males	110.3 (108 - 114), n = 9	84.9 (81 - 92), n = 9
<i>P. b. tephrosceles</i> males Semliki	108.7 (105 - 112), n = 9	84.6 (80 - 88), n = 9
<i>P. b. tephrosceles</i> males Uganda	110.8 (105 - 115), n = 12	84.0 (79 - 88), n = 11
<i>P. b. tephrosceles</i> male Nyamanzi R.	116, n = 1	88, n = 1
<i>P. b. tephrosceles</i> male Mbizi Forest, Ufipa	119, n = 1	94, n = 1
<i>P. b. tephrosceles</i> females Uganda	99.3 (95 - 102), n = 4	73.5 (71 - 77), n = 4
<i>P. b. tephrosceles</i> female Ruiga Bay	96, n = 1	70, n = 1
<i>P. b. rufomitratu</i> s male	101, n = 1	80, n = 1
<i>P. b. rufomitratu</i> s females	92.0 (91 - 94), n = 5	68.0 (66 - 70), n = 5
<i>P. b. kirkii</i> males	98.2 (92.5 - 103.5), n = 7	74.8 (73.0 - 77.0), n = 7
<i>P. b. kirkii</i> females	91.2 (87.0 - 94.0), n = 10	67.9 (62.5 - 70.5), n = 7

Body Measurements (sources: Allen, 1925, Natural History Museum, London):

Procolobus badius temminckii

Female

HB 522 mm

T 730 mm

HF 166 mm

E 35 mm

P. b. badius

Males, n = 3

HB 611 (584-627) mm

T 676 (635-706) mm

HF 159 (152-173) mm

E 29 (25-33) mm

Females, n = 6

HB 562 (500-635) mm

T 715 (630-800) mm

HF 175 (165-185) mm

E 31 (27-34) mm

P. b. waldroni

Males, n = 8

HB 499 (435-570) mm

T 603 (500-686) mm

HF 1162 (150-174) mm

E 29 (20-38) mm

Females, n = 8

HB 496 (415-565) mm

T 555 (515-750) mm

HF 164 (146-175) mm

E 30 (27-34) mm

P. p. tholloni

Females, n = 2

HB 580, 600 mm

T 690, 412 (broken?) mm

HF 170, 150 mm

E 35

P. b. oustaleti (cf. *powelli*)

Males, n = 17

HB 540 (455-590) mm

T 726 (650-800) mm

HF 186 (170-198) mm

E 39 (35-42) mm

Females, n = 12

HB 524 (480-565) mm

T 713 (645-790)

HF 182 (170-202) mm

E 37 (35-40) mm

P. b. oustaleti (cf. *brunneus*)

Males, n = 2

HB 555 (550-560) mm

T 700 (630-770) mm

HF 178 (160-195) mm

E 30 (25-35) mm

Females, n = 5

HB 490 (450-520) mm

T 580 (430-650) mm
HF 163 (154-172) mm
E 32 (29-35) mm

P. b. oustaleti (cf. *brunneus*)

Males, n = 10
HB 582 (525-610) mm
T 714 (633-785) mm
HF 191 (180-200) mm
E 40 (38-42) mm
Females, n = 5
HB 559 (510-585) mm
T 709 (650-750) mm
HF 189 (183-203) mm
E 39 (35-42) mm

P. b. tephrosceles, Uganda

Males, n = 5
HB 615 (584-648) mm
T 691 (660-724) mm
HF 182 (171-191) mm
E 35 (32-41)
Female
HB 584 mm
T 686 mm
T 171 mm
E 29 mm

P. b. tephrosceles, Ruiga Bay

Female
HB 485 mm
T 620 mm
HF 168 mm
E 27 mm

P. b. langi

Male
HB 500 mm
T 665 mm
HF 170 mm
Female
HB 485 mm
T 650 mm
HF 170 mm

P. b. ellioti (cf. *semlikiensis*)

Males, n = 5
HB 512 (480-540) mm
T 640 (540-750) mm
HF 168 (160-189) mm
E 31 (29-33) mm
Females, n = 3
HB 520 (500-540) mm
T 643 (600-680) mm
HF 170 (165-175) mm
E 30 (29-30) mm

P. b. ellioti, holotype (measured from dry skin)

Male

HB 760

T 650 mm

HF 150 mm

E 30 mm

P. b. foai, holotype of *graueri* (measured from dry skin)

Male

HB 690 mm

T 670 mm

HF 170 mm

E 27 mm

P. b. kirkii

Male

HB 450 mm

T 595 mm

HF 144 mm

E 33 mm

Females, n = 3

HB 473 (455-500) mm

T 670 (640-715) mm

HF 161 (157-165) mm

E 32 (31-34) mm

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Footnotes (Provided by Thomas M. Butynski, John F. Oates, Thomas T. Struhsaker, and Yvonne A. de Jong)

[1] As indicated in Table 1, Kingdon (1997) elevated *Piliocolobus* from a subgenus to full genus, in which he recognised eight subspecies. He reserved the genus *Procolobus* for a single species, *Procolobus verus*, the olive colobus. Groves (2001) followed this generic arrangement, recognising nine species in *Piliocolobus*. Grubb *et al.* (2003, 2013), Struhsaker (2010), and Ting (2008a,b) all retained the subgenus *Piliocolobus*.

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[2] Since 1997, the former ‘Zaire’ has been known as the ‘Democratic Republic of Congo’.

[3] There is an introduced population on Pemba Island, Tanzania:

Butynski, T. M. and De Jong, Y. A. 2011. Zanzibar red colobus on Pemba Island, Tanzania: population status 38 years post-introduction. In: *Global Re-introduction Perspectives: 2011*. P. S. Soorae, ed. IUCN/SSC Re-introduction Specialist Group, Abu Dhabi, UAE. Pp. 168–174.

[4] Published in Struhsaker (2010).

[5] The Orlando consensus was published in Grubb *et al.* (2003).

[6] Natural History Museum, London.

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