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The diversity of living colobines

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Introduction

Taxonomically, the diversity of living colobines is portrayed by the recognition in most classifications of some 30 species (see e.g. Thorington & Groves, 1970; Delson *et al.*, 1982; Napier, 1985). As is discussed below, such arrangements probably underestimate the number of 'good' species in the subfamily.

The living colobines have been grouped into between four and nine genera, and these genera are often arranged in two clusters, one African and one Asian. Napier (1970) argued for an ancient phylogenetic separation of these two clusters, a view supported by Szalay & Delson (1979) in their recognition of two subtribes, Colobina and Semnopithecina (= Presbytina of Delson, 1975*a*) (note also Figure 2.2, this volume). Szalay & Delson acknowledged, however, that the Asian colobines are less clearly united than the African species, and Groves (1989) has argued that *Nasalis* groups with other Asian species largely through sharing a set of retained primitive features. Groves therefore proposed that *Nasalis* (with *Simias*) should be regarded as a sister group to all other colobines, and treated Nasalinae and Colobinae as subfamilies within the family Colobidae.

This chapter examines the generic- and species-level diversity of the living colobines, in the main following the order used by Napier (1985), and retaining the traditional African and Asian clusters. Table 3.1 summarizes the classification that we follow, and Table 3.2 presents information on body weights.

African colobines

Africa's colobus monkeys appear to be a monophyletic group, sharing a vestigial thumb, mid-tarsal shortening, and some other postcranial and dental fea-

Table 3.1. *The species of living colobines*

	Common name
<i>Colobus polykomos</i> (Zimmerman, 1780)	Ursine colobus
<i>Colobus vellerosus</i> I. Geoffroy, 1830	White-thighed colobus
<i>Colobus guereza</i> Rüppell, 1835	Guereza
<i>Colobus satanas</i> Waterhouse, 1838	Black colobus
<i>Colobus angolensis</i> Sclater, 1860	Angolan colobus
<i>Procolobus (Piliocolobus) badius</i> (Kerr, 1792)	Red colobus
<i>Procolobus (Procolobus) verus</i> Van Beneden, 1838	Olive colobus
<i>Pygathrix (Pygathrix) nemaus</i> (Linnaeus, 1771)	Douc
<i>Pygathrix (Rhinopithecus) roxellana</i> (Milne Edwards, 1870)	Sichuan snub-nosed monkey
<i>Pygathrix (Rhinopithecus) bieti</i> (Milne Edwards, 1897)	Yunnan snub-nosed monkey
<i>Pygathrix (Rhinopithecus) brelichi</i> (Thomas, 1903)	Guizhou snub-nosed monkey
<i>Pygathrix (Rhinopithecus) avunculus</i> (Dollmann, 1912)	Tonkin snub-nosed monkey
<i>Nasalis larvatus</i> (Wurmb, 1784)	Proboscis monkey
<i>Simias concolor</i> (Miller, 1903)	Simakobu, pig-tailed monkey
<i>Presbytis melalophos</i> (Raffles, 1821)	Banded leaf-monkey
<i>Presbytis comata</i> (Desmarest, 1822) ^a	Javan leaf-monkey
<i>Presbytis frontata</i> (Müller, 1838)	White-fronted leaf-monkey
<i>Presbytis rubicunda</i> (Müller, 1838)	Red (or maroon) leaf-monkey
<i>Presbytis potenziani</i> (Bonaparte, 1856)	Mentawai leaf-monkey
<i>Presbytis hosei</i> (Thomas, 1889)	Hose's leaf-monkey
<i>Presbytis thomasi</i> (Collett, 1893)	Thomas's leaf-monkey
<i>Trachypithecus vetulus</i> (Erxleben, 1777) ^b	Purple-faced langur
<i>Trachypithecus auratus</i> (E. Geoffroy, 1812)	Lutung
<i>Trachypithecus cristatus</i> (Raffles, 1821)	Silvered langur, or lutung
<i>Trachypithecus johnii</i> (Fischer, 1829)	Nilgiri langur
<i>Trachypithecus obscurus</i> (Reid, 1837)	Dusky langur
<i>Trachypithecus pileatus</i> (Blyth, 1843)	Capped langur
<i>Trachypithecus phayrei</i> (Blyth, 1847)	Phayre's langur
<i>Trachypithecus francoisi</i> (Pousargues, 1898)	Francois's langur
<i>Trachypithecus geei</i> (Gee, 1956)	Golden langur
<i>Semnopithecus entellus</i> (Dufresne, 1797)	Hanuman or grey langur

^aWeitzel & Groves (1985) have explained why the more familiar name for the Javan leaf-monkey, *P. aygula*, is not valid under the rules of nomenclature.

^bIn the behavioural literature, *T. vetulus* is usually referred to as *Presbytis senex*. Napier (1985) has explained why the name *senex* is probably invalid; it was apparently used by Erxleben to describe an albino monkey from an unknown locality.

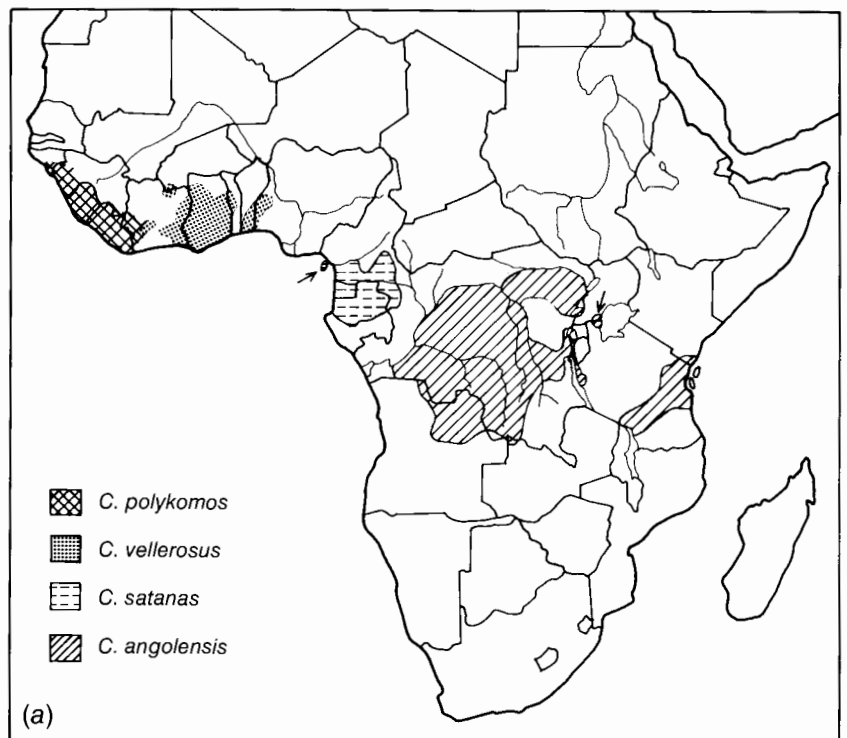
Table 3.2. *Body weights of adult colobine monkeys. Mean weight given in kilograms, with sample size in parentheses, where available*

Species	Female	Male	Source of data
<i>Colobus polykomos</i>	8.3 (10)	9.9 (5)	Oates <i>et al.</i> (1990)
<i>Colobus vellerosus</i>	6.9 (5)	8.5 (3)	JFO
<i>Colobus guereza guereza</i>	9.2 (4)	13.5 (3)	WLJ and JFO
<i>Colobus guereza matschiei</i>	7.9 (7)	10.1 (4)	WLJ
<i>Colobus satanas</i>		10.9 (2)	Eisentraut (1973); M. J. S. Harrison, personal communication
<i>Colobus angolensis</i>	7.4 (6)	9.8 (4)	WLJ; Napier (1985)
<i>Procolobus badius badius</i>	8.2 (16)	8.3 (9)	Oates <i>et al.</i> (1990)
<i>Procolobus badius tephrosceles</i>	7	10.5	Struhsaker & Leland (1979)
<i>Procolobus badius kirkii</i>	5.5 (1)	5.8 (1)	Napier (1985)
<i>Procolobus verus</i>	4.2 (14)	4.7 (20)	Oates <i>et al.</i> (1990)
<i>Nasalis larvatus</i>	10.0 (14)	21.2 (13)	WLJ
<i>Simias concolor</i>	7.1 (1)		Napier (1985)
<i>Pygathrix (Rhinopithecus) bieti</i>	9.0 (1)	13.0 (1)	Jablonski & Pan (1991) ^a
<i>Presbytis melalophos</i>	5.8	5.9	Waterman <i>et al.</i> (1988)
<i>Presbytis rubicunda</i>	5.7 (21)	6.2 (18)	WLJ
<i>Presbytis potenziani</i>	6.4 (4)	6.5 (5)	Tilson & Tenaza (1976)
<i>Presbytis hosei sabanus</i>		6.2 (6)	Davis (1962)
<i>Trachypithecus vetulus</i>	5.9 (3)	8.2 (3)	Napier (1985)
<i>Trachypithecus cristatus</i>	5.7 (25)	6.6 (13)	WLJ
<i>Trachypithecus johnii</i>	10.9 (1)	12.7 (4)	Leigh (1926)
<i>Trachypithecus obscurus</i>	6.6 (22)	7.3 (12)	Napier (1985)
<i>Trachypithecus pileatus</i>	10.0 (3)	12.8 (2)	Oboussier & von Maydell (1959)
<i>Trachypithecus phayrei</i>	6.9 (5)	7.9 (8)	Napier (1985)
<i>Trachypithecus geei</i>	9.5 (1)	10.9 (4)	Oboussier & von Maydell (1959)
<i>Semnopithecus entellus entellus</i>	11.2 (22)	18.3 (3)	Hrdy (1977) (females listed as 'parous')
<i>S. entellus schistacea</i>	15.6 (5)	19.8 (3)	Hrdy (1977) Bishop (unpublished data); Napier (1985)
<i>S. entellus thersites</i>	6.7 (4)	10.6 (8)	Napier (1985)

WLJ, information from specimens in the US National Museum (Washington, DC), the Natural History Museum (London) and the Museum of Comparative Zoology (Harvard), collated by W. L. Jungers (personal communication); JFO, information from museum specimens in the Natural History Museums of London and Paris, collated by J. F. Oates.

^aMale weight stated to be of 'young adult'.

tures (Szalay & Delson, 1979; Strasser & Delson, 1987; Delson, Chapter 2, this volume). As Pocock (1936) and Kuhn (1967) recognized, the colobus monkeys fall into two distinct subgroups, each of which merits generic status. The red and olive colobus, *Procolobus*, are united by a set of anatomical characteristics that distinguish them from members of the black-and-white colobus group, *Colobus*. Female *Procolobus*, unlike *Colobus*, have sexual swellings; male *Procolobus* have separate rather than united ischial callosities and a sagittal crest, and young males have a perineal organ; *Procolobus* have a four-chambered stomach, compared with a three-chambered arrangement in *Colobus*; and *Colobus* have a sub-hyoid sac (absent in *Procolobus*) and a large rather than small larynx (Napier, 1985; Strasser & Delson, 1987). The phylogenetic polarity of these differences is unclear, but Strasser & Delson (1987) have suggested that the discontinuous callosities, perineal organ and four-chambered stomach are derived features of *Procolobus*, while the large larynx, sub-hyoid sac and lack of female swellings are derived features of *Colobus*. Adult male *Colobus* make resonant, low-pitched loud calls that are not heard in *Procolobus* (presumably a correlate of their laryngeal



differences), and *Colobus* mothers allow their infants to be handled by other group members, a behaviour that is very rare in *Procolobus*.

Both *Colobus* and *Procolobus* have a wide distribution in tropical African forests, each occurring from the Atlantic coast of the far west to the Indian Ocean coasts of Kenya and Tanzania.

Genus *Colobus*, black-and-white colobus monkeys

These monkeys have long black or black-and-white pelage. Although all populations of black-and-white colobus monkeys have sometimes been grouped into one species (see e.g. Schwarz, 1929), they are now widely regarded as a diverse group of four or five species. Here we follow Oates & Trocco (1983) in recognizing five forms: *C. satanas*, *C. polykomos*, *C. vellerosus*, *C. guereza* and *C. angolensis*. Figure 3.1 shows the distribution of these species.

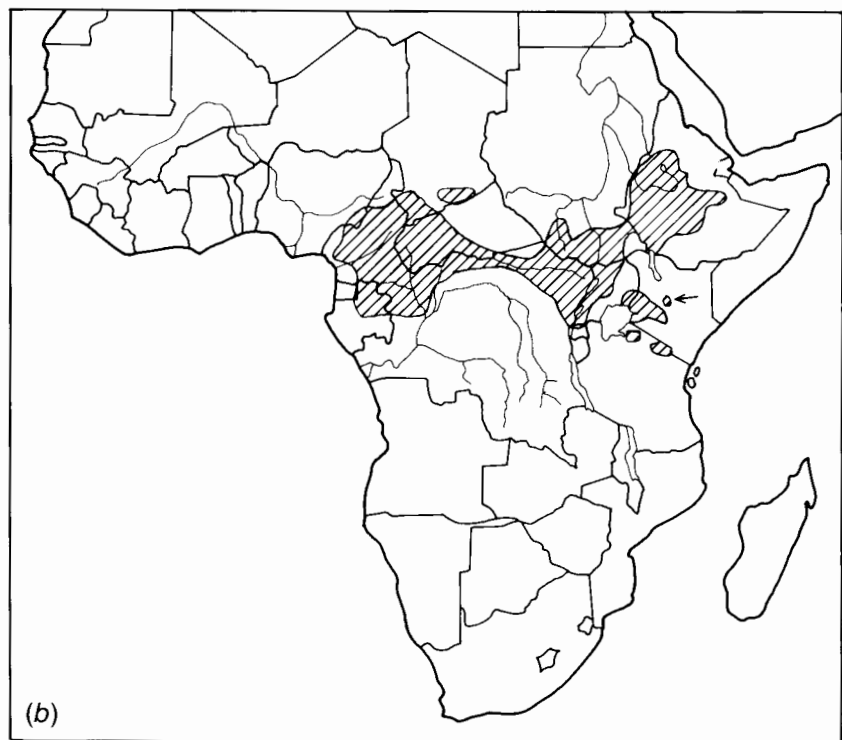


Figure 3.1. Distribution of black-and-white colobus monkeys: (a) *Colobus polykomos*, *C. vellerosus*, *C. satanas* and *C. angolensis*; (b) *C. guereza*. Based on Oates & Trocco (1983), Colyn (1991), Machado (1969), Mitani (1990), Rahm & Christiaensen (1960) and Rodgers (1981). Arrows draw attention to isolated populations.

Each has a different coat pattern: *C. satanas* is all black, *C. guereza* (Figure 3.2) has a characteristic white peridorsal mantle, and the other three have differing combinations of white or grey markings on the tail, thighs, shoulders and/or head (illustrated by Rahm, 1970). A craniometric study by Hull (1979) showed four highly distinct clusters: *polykomos* + *vellerosus*; *angolensis*; *guereza*; and *satanas*. Of these, *guereza* was most distinct, especially in the teeth (e.g. small incisors, longer molars, large female canines), and face (e.g. broader nasal apertures). In the other three clusters, *satanas* had the largest incisors, and *polykomos* (+ *vellerosus*) had larger jaws than *angolensis*. A study of loud call pitch and tempo by Oates & Trocco (1983) found three clusters: *vellerosus* + *guereza*; *polykomos* + *angolensis*; and *satanas*. The low-pitched male loud call of *vellerosus* could not be discriminated from that of *guereza*, and *satanas* had a very distinct high-pitched roar. This evidence led Oates & Trocco (1983) to agree with Dandelot (1971) that the status of *vellerosus* 'is perhaps more nearly specific than subspecific'. The specific status of *C. vellerosus* has been supported in a recent analysis by Groves *et al.* (1993). Relative to other black-and-white colobus, *C. guereza* appears to have the largest number of derived features, while *C. satanas* may be the



Figure 3.2. Group of *Colobus guereza occidentalis* in gallery forest by the River Nile, Murchison Falls National Park, Uganda (photograph by J. Oates).

most primitive member of the group (Grubb, 1978; Oates & Trocco, 1983). *Colobus satanas* is the only form in which the infant is not born with a pure white coat; instead, the neonate is brown (though still noticeably different from the mother's black coat) (M. J. S. Harrison, personal communication).

Unlike the other forms, which have the majority of their populations in moist lowland forest, much of the range of *C. guereza* is in the deciduous forest and savanna woodland zone north of the moist forest, and in the montane forest zone of East Africa, including the Ethiopian highlands. This ecological divergence from other members of the group is discussed in Chapter 4. As Hull (1979) has suggested, the divergence of *C. guereza* from the others in its teeth and jaws is likely to be related to dietary differences. Such adaptive divergence apparently allows *C. guereza* to coexist with other black-and-white colobus species in areas where it enters the moist forest zone; sympatry with *C. angolensis* certainly occurs in eastern Zaire (Thomas, 1991), and distribution records and hunters' reports suggest that until recently it coexisted with *C. satanas* in West Africa (Schwarz, 1929; Rahm, 1970; Oates & Trocco, 1983; Mitani, 1990). *Colobus guereza* may have expanded its range within these moist forest areas in relatively recent times, along with humans. Thomas (1991) reported that, in the Ituri Forest, *guereza* exhibits a strong preference for roadside secondary forest, while *angolensis* occurs mainly in primary forest; in Uganda's Kibale Forest, *guereza* is the only monkey found at higher density in heavily logged than in unlogged or lightly logged forest (Skorupa, 1988).

Genus Procolobus, red and olive colobus monkeys

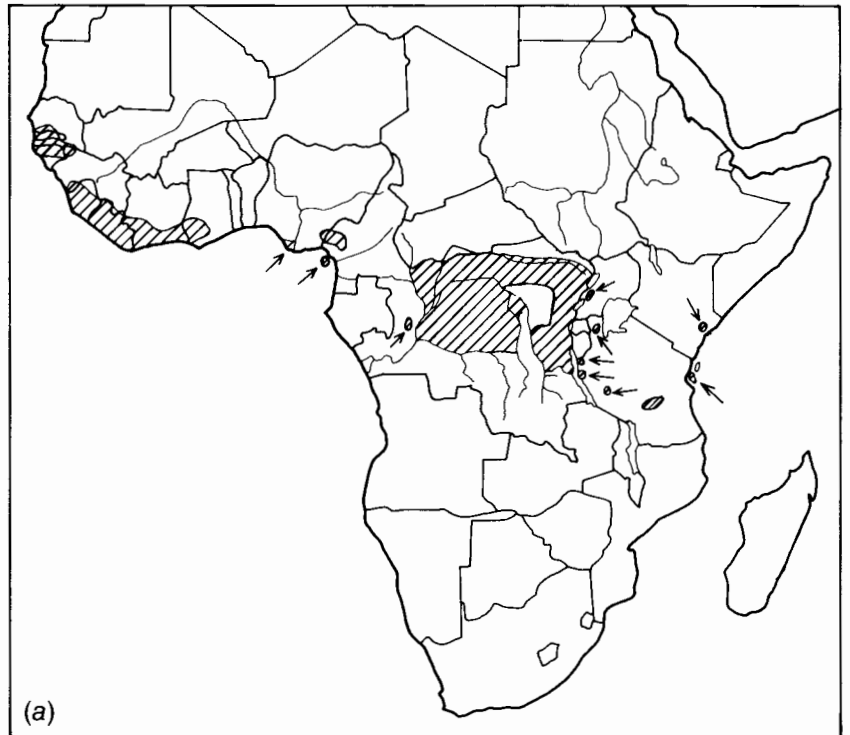
Brandon-Jones (1984), Strasser & Delson (1987) and Groves (1989) have followed Hill & Booth (1957) and Kuhn (1967) in arguing that the red and olive colobus monkeys are more closely related than is either to *Colobus*, and should be united in the genus *Procolobus*, but separated into two subgenera: *P. (Piliocolobus)* for the red colobus and *P. (Procolobus)* for the olive. That arrangement is followed here, but with the recognition that the olive colobus is a very distinctive animal. Several authors (e.g. Verheyen, 1962) have given equal generic or subgeneric status to the red, olive and black-and-white colobus, but such an arrangement ignores the set of shared, derived features uniting the red and olive species.

Groves (1989) has noted that red and olive colobus are also united by the absence of two features present in the black-and-white group: infant-handling by group members other than the mother, and colour contrast between young infants and adults. Although the first point is consistent with field observa-

tions, the latter is not. Struhsaker (1975) reported that newborn red colobus of the *tephrosceles* subspecies are black dorsally, grey ventrally, and totally lacking in red or brown, making them 'very distinct from older monkeys'. Struhsaker also noted differences between neonatal and adult coloration in four other forms of red colobus that he observed. On the other hand, olive colobus infants are not very different in colour from their parents (Oates, personal observation).

Subgenus Piliocolobus, red colobus monkeys

Red (or bay) colobus monkeys occur from Senegambia in West Africa across the continent to Zanzibar (Figure 3.3(a)). However, their distribution within this area is patchy and they are completely absent from a large area of the western equatorial forest (e.g. Gabon and mainland Equatorial Guinea). The nominate form of red colobus, *Procolobus badius badius* from West Africa, is bright reddish-brown on the venter and lower limbs, while the dorsal sur-



face is black. Other populations display varying permutations of black, brown, red and (in some cases) white hair. Red colobus have a complex, graded repertoire of vocalizations (Hill & Booth, 1957; Marler, 1970; Struhsaker, 1975), and wild animals call frequently (as Hill & Booth put it (p. 312), 'the species is notable for its inability to remain silent for any length of time'). The vocal system is very different from that of black-and-white colobus; for instance, there is no distinctive low-frequency adult male loud call. Probably related to this is the relatively small larynx of adult males, which is less than half the length and width of the larynx of *Colobus polykomos* (Hill & Booth, 1957).

A number of widely-followed classifications recognize 14 distinct and allopatric forms of red colobus (see e.g. Rahm, 1970; Dandelot, 1971; Napier, 1985). These are (in the order in which they were named): *badius*, *temminckii*

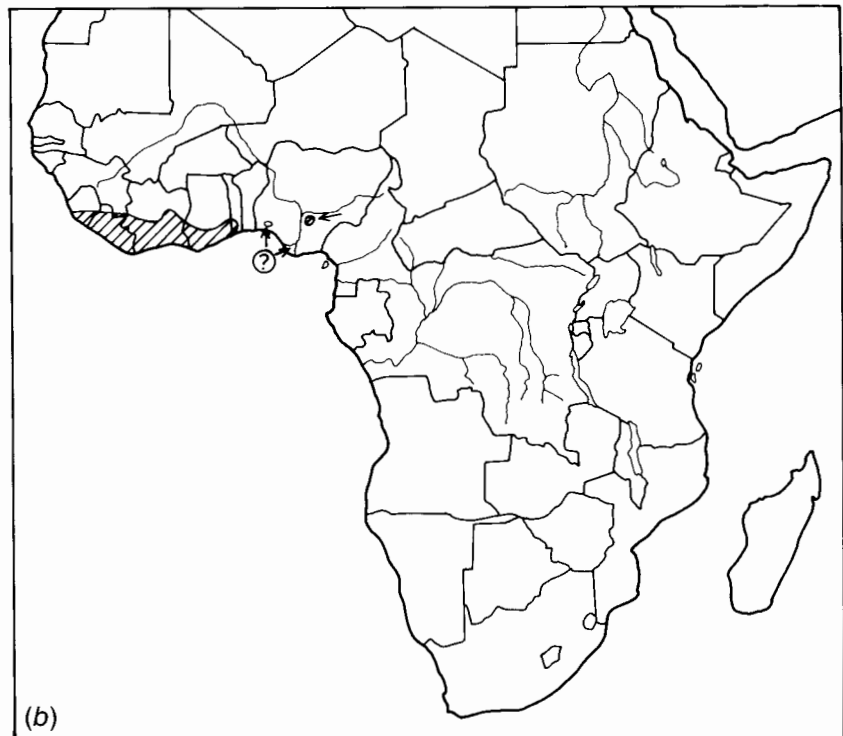


Figure 3.3. Distribution of the genus *Procolobus*. (a) Red colobus monkeys, *P. badius*; (b) olive colobus monkeys, *P. verus*. Based on information from Oates (1981, and unpublished data collated from museum collections), Colyn (1987, 1991), Rahm (1970), Rodgers (1981) and Wolfheim (1983). Isolated populations arrowed.

(Figure 3.4), *pennantii*, *kirkii*, *rufomitratu*s, *tholloni*, *bouvieri*, *foai*, *gordonorum*, *preussi*, *oustaleti*, *tephrosceles*, *elliotti*, and *waldroni*. This arrangement has recently been questioned, however, by Colyn (1991) who has reviewed the zoogeography and taxonomy of monkeys of the Congo Basin. Colyn has recognized a new subspecies from E. Zaire, *parmentieri* (described by Colyn & Verheyen, 1987), and argued that the populations usually labelled *elliotti* actually comprise four distinct subspecies (*langi*, *lulindicus*, *foai* and *semlikiensis*) together with hybrids between them.

Several taxonomists have recognized that the different red colobus forms display more variation (in their pelage, vocalizations, and cranial morphology) than can easily be contained within a single-species concept. However, there is considerable disagreement about how many different red colobus species might therefore be recognized. Rahm (1970) recognized one species, Dandelot (1971) recognized five 'good' species and three 'potential' species, Delson *et al.* (1982) recognized four species and Napier (1985) recognized two. Table 3.3 summarizes these arrangements. An analysis by



Figure 3.4. Red colobus (*Procolobus badius temminckii*) at Abuko, The Gambia (photograph by D. Starin).

Table 3.3. *Classifications of red colobus monkeys*

Rahm (1970)	Dandelot (1971)	Delson <i>et al.</i> (1982)	Napier (1985)	Oates (1986)	Colyn (1991)
<i>Colobus badius</i>	<i>C. badius badius</i>	<i>C. badius badius</i>	<i>C. badius badius</i>	<i>Procolobus badius</i>	
<i>C. b. temminckii</i>	<i>C. b. temminckii</i>	<i>C. b. temminckii</i>	<i>C. b. temminckii</i>	<i>P. b. temminckii</i>	
<i>C. b. waldroni</i>	<i>C. b. waldroni</i>	<i>C. b. waldroni</i>	<i>C. b. waldroni</i>	<i>P. b. waldroni</i>	
<i>C. b. preussi</i>	<i>C. preussi</i>	<i>C. preussi</i>	<i>C. b. preussi</i>	<i>P. pennantii preussi</i>	
<i>C. b. pennantii</i>	<i>C. pennantii pennantii</i>	<i>C. pennantii pennantii</i>	<i>C. b. pennantii</i>	<i>P. p. pennantii</i>	
<i>C. b. bouvieri</i>	<i>C. p. bouvieri</i>	<i>C. p. bouvieri</i>	<i>C. b. bouvieri</i>	<i>P. p. bouvieri</i>	<i>C. badius bouvieri</i>
<i>C. b. oustaleti</i>	<i>C. rufomitratu</i> <i>oustaleti</i>	<i>C. p. oustaleti</i>	<i>C. b. oustaleti</i>	<i>P. rufomitratu oustaleti</i>	<i>C. b. oustaleti</i>
<i>C. b. ellioti</i>	<i>C. ellioti</i>	<i>C. p. ellioti</i>	<i>C. b. ellioti</i>	<i>P. rufomitratu ellioti</i>	<i>C. b. langi, C. b. semi-</i> <i>kiensis, and hybrids</i>
<i>C. b. foai</i>	<i>C. rufomitratu foai</i>	<i>C. p. foai</i>	<i>C. b. foai</i>	<i>P. rufomitratu foai</i>	<i>C. b. foai and C. b.</i> <i>lutindicus</i>
<i>C. b. tholloni</i>	<i>C. tholloni</i>	<i>C. p. tholloni</i>	<i>C. b. tholloni</i>	<i>P. rufomitratu tholloni</i>	<i>C. b. tholloni</i>
<i>C. b. tephrosceles</i>	<i>C. rufomitratu</i> <i>tephrosceles</i>	<i>C. p. tephrosceles</i>	<i>C. b. tephrosceles</i>	<i>P. rufomitratu</i> <i>tephrosceles</i>	<i>C. b. tephrosceles</i>
<i>C. b. gordonorum</i>	<i>C. r. gordonorum</i>	<i>C. p. gordonorum</i>	<i>C. b. gordonorum</i>	<i>P. gordonorum</i>	
<i>C. b. rufomitratu</i>	<i>C. r. rufomitratu</i>	<i>C. rufomitratu</i>	<i>C. b. rufomitratu</i>	<i>P. rufomitratu</i> <i>rufomitratu</i>	
<i>C. b. kirkii</i>	<i>C. kirkii</i>	<i>C. pennantii kirkii</i>	<i>C. kirkii</i>	<i>P. kirkii</i>	<i>C. b. parmentieri</i>

Struhsaker (1981a) of vocalizations showed major differences between West African populations (i.e. *temminckii*, *badius* and *preussi*) and some from central and eastern Africa; Struhsaker did not, however, propose a new taxonomy.

Because there is no broad consensus on the most appropriate classification of the red colobus monkeys, we treat them in this book as a single species, *Procolobus (Piliocolobus) badius*, consisting of different local forms named according to Rahm's (1970) subspecific arrangement. A resolution of phylogenetic relationships within the group must await further research; Colyn's study (1991) is a useful start, but covers only one geographical region and relies largely on traditional craniometric and skin-colour evidence. A broader study should look at vocalizations in populations additional to those examined by Struhsaker (1981a); DNA studies would also be very helpful, perhaps using museum skins and/or faecal extracts.

Subgenus Procolobus, olive colobus monkeys

With a body weight of about 4.5 kg, the olive colobus is the smallest living colobine (see Table 3.2), and at a glance it looks like a small, slender version of the red colobus. More careful examination reveals a number of differences in addition to the size disparity. For instance, the olive colobus coat lacks any distinctive colour pattern – it is light reddish brown above and light grey below – although there is a short but noticeable sagittal crest on the crown of the head; the external ear has a hairy lateral surface; the glans penis bears minute horny papillae (unique among primates); and both the fundus of the stomach and the rectum are sacculated (Hill, 1952). Uniquely among monkeys, young olive colobus infants are carried in their mother's mouth, rather than clinging to her trunk (see Chapter 4). Only one species of olive colobus is recognized, *Procolobus (Procolobus) verus*. This species occurs only in Guinean coastal forests of West Africa (Figure 3.3(b)) and shows no evident subspecific variation, even between populations in Ghana and eastern Nigeria separated by two well-known zoogeographic boundaries, the Dahomey Gap and the Niger River (Menzies, 1970; Oates, 1981). This may be partly a consequence of the monkey's common association with riverine forest, because a tenuous gallery-forest network bridges the Dahomey Gap (Oates, 1988a).

Asian colobines

We have noted above that there is debate as to how recently the Asian colobines have shared a common ancestry. Delson (Figure 2.2, this volume) tent-

actively places their ancestor in the middle Pliocene, but Groves (1989) has suggested that *Nasalis* (with *Simias*) separated from other Asian forms more anciently and that it forms a sister-group to all other living colobines. *Nasalis* apart, Groves notes that the Asian colobines can be distinguished from the African species by a number of shared, derived features, including a shorter face and the presence of a suborbital fossa in the skull.

One well-known classification (Napier & Napier, 1967) has recognized five genera of Asian colobines: *Presbytis*, *Rhinopithecus*, *Pygathrix*, *Nasalis* and *Simias*. Although this classification is widely used, at least in the behavioural literature, it is not accepted by most authorities on Asian colobine systematics. In particular, it is clear that the group of monkeys commonly lumped together as *Presbytis* includes a number of distinct lineages. On the other hand, a generic-level division of the other ('odd-nosed') Asian colobines may not be the best way of expressing their relationships; Groves (1970), for instance, has presented evidence for regarding *Rhinopithecus* as a subgenus of *Pygathrix*, and for uniting *Simias* with *Nasalis*.

A division of *Presbytis* (*sensu lato*) into several genera and/or subgenera has a long history; for instance, Reichenbach (1862) recognized four subgenera of what he called *Semnopithecus*. Hill (1934) and Pocock (1935, 1939) used the coloration of infants, skull morphology, and features of the female external genitalia to separate *Semnopithecus*, *Trachypithecus* and *Kasi* as genera from *Presbytis* (*sensu stricto*). Brandon-Jones (1984) (tentatively followed by Strasser & Delson (1987)) proposed a two-genus arrangement into *Presbytis* and *Semnopithecus* (with the latter including *Trachypithecus* as a subgenus).

Groves' most recent (1989) review of Asian colobine taxonomy used a five-genus arrangement: *Nasalis*, *Pygathrix*, *Presbytis*, *Trachypithecus* and *Semnopithecus*. We feel that in general this arrangement well reflects both existing phylogenetic evidence based on morphology, and patterns of variation in behaviour and ecology. We therefore follow it with one exception; we agree with Medway (1970) and Napier (1985) that the great differences in the external appearance and ecology of *Nasalis* and *Simias* warrant their generic separation. The distribution of the six Asian genera follows a complicated pattern. The odd-nosed genera occupy areas on the northern and eastern boundaries of Asian colobine distribution, with *Pygathrix* occurring in the mountains of southern China and in eastern Indo-China, *Nasalis* in Borneo and *Simias* in the Mentawai Islands. *Presbytis* dominates moist inland forests in South-east Asia, south of the Isthmus of Kra, and *Semnopithecus* occupies the Indian subcontinent (including Sri Lanka). *Trachypithecus* is the most widely distributed genus, occurring from Sri Lanka to Java, with several

species occupying a large area of mainland South-east Asia, including dry forests and mangrove swamps.

Trachypithecus occurs sympatrically with *Presbytis* in many parts of Malaysia and Indonesia, with *Nasalis* in coastal Borneo, and with *Pygathrix* in Indochina. *Simias* is sympatric with *Presbytis* on the Mentawai Islands.

Genus *Pygathrix*, snub-nosed monkeys

We follow Groves (1970) and Napier (1985) in regarding the Chinese snub-nosed monkeys (*Rhinopithecus*) as a subgenus of *Pygathrix*. This genus is notable for its nasal peculiarities; small flaps of skin are present on the upper borders of the nostrils and the nasal bones themselves are reduced or absent. These monkeys are unusual among colobines in having forelimbs almost as long as their hindlimbs, and ischial callosities are separate in both males and females (Napier, 1985).

Jablonski & Peng (1993) have analysed 178 characters in *Pygathrix* and *Rhinopithecus*, and found that all the *Rhinopithecus* species are closer to each other than any of them is to *Pygathrix nemaesus*, which has the largest number of primitive features but also some unique specializations (for instance, in its locomotor apparatus and gut). On this basis, Jablonski & Peng propose the generic separation of *Rhinopithecus* from *Pygathrix*. We regard a subgeneric separation as more sensible, given the clear affinities of these forms.

Subgenus Pygathrix

The douc (or douc monkey), *P. nemaesus*, occurs in the forests of eastern Indo-China (Figure 3.5). Two subspecies of this strikingly coloured colobine are usually recognized, each with a different pattern of grey, white, red and black hair (Figure 3.6). Brandon-Jones (1984) treated the southern form, *nigripes*, as a separate species from the northern *nemaesus*. Doucs have little or no sexual dimorphism in body size (Napier, 1985).

Subgenus Rhinopithecus

These snub-nosed monkeys have extremely reduced nasal bones, and the flaps of skin on the upper borders of the nostrils stand erect, as twin peaks (Napier 1985; Caton, 1991). They occur in northern Vietnam and south-eastern China (including Tibet) (Figure 3.5). There are four allopatric forms, but there has been disagreement on how many species these comprise. Napier & Napier (1967) followed Ellerman & Morrison-Scott (1951) in recogniz-

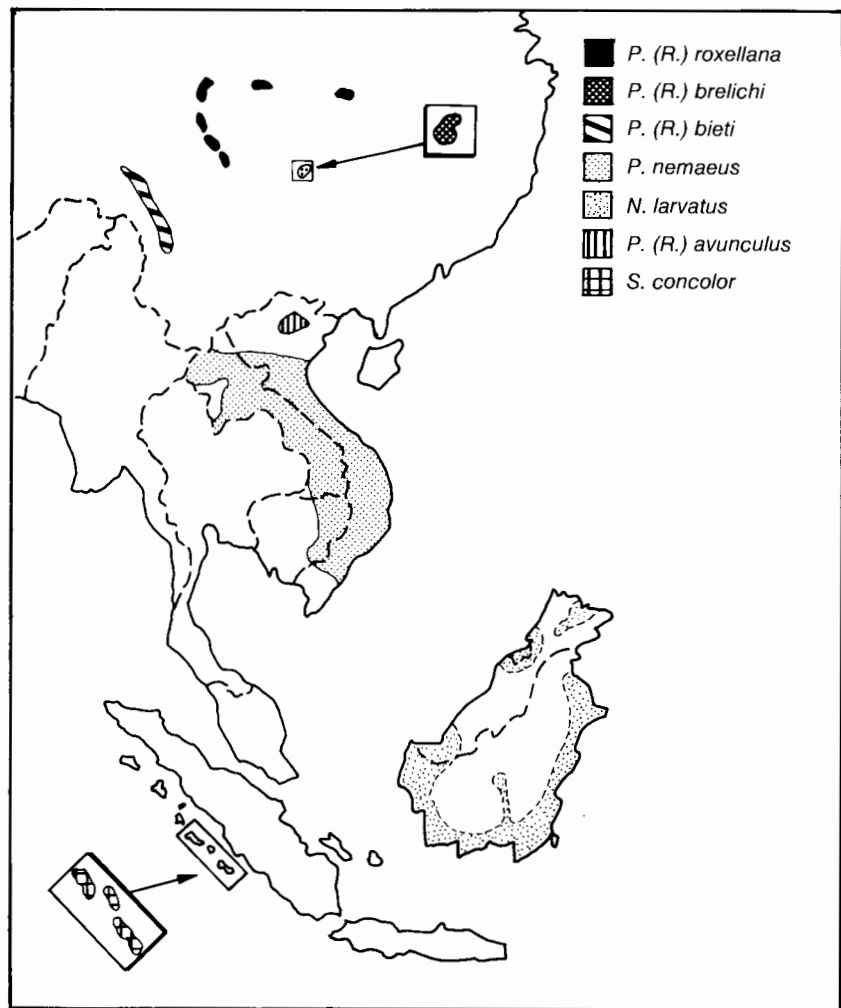


Figure 3.5. Distribution of the genera *Pygathrix* (with subgenus *Rhinopithecus*), *Nasalis* and *Simias*. Based on information from E. Bennett (personal communication), Bodmer *et al.* (1991), Long *et al.* (1994), MacKinnon & MacKinnon (1987) and Wolfheim (1983).

ing two species: *Rhinopithecus roxellanae* containing the three Chinese forms (*bieti*, *brelichi* and *roxellanae*), and *R. avunculus* containing the Vietnamese monkey. Subsequently, Groves (1970) elevated *brelichi* to species status, and has now (1989) accepted *bieti* also as a full species, based on the studies of Chinese zoologists (see e.g. Li *et al.*, 1982). Such a four-species arrangement

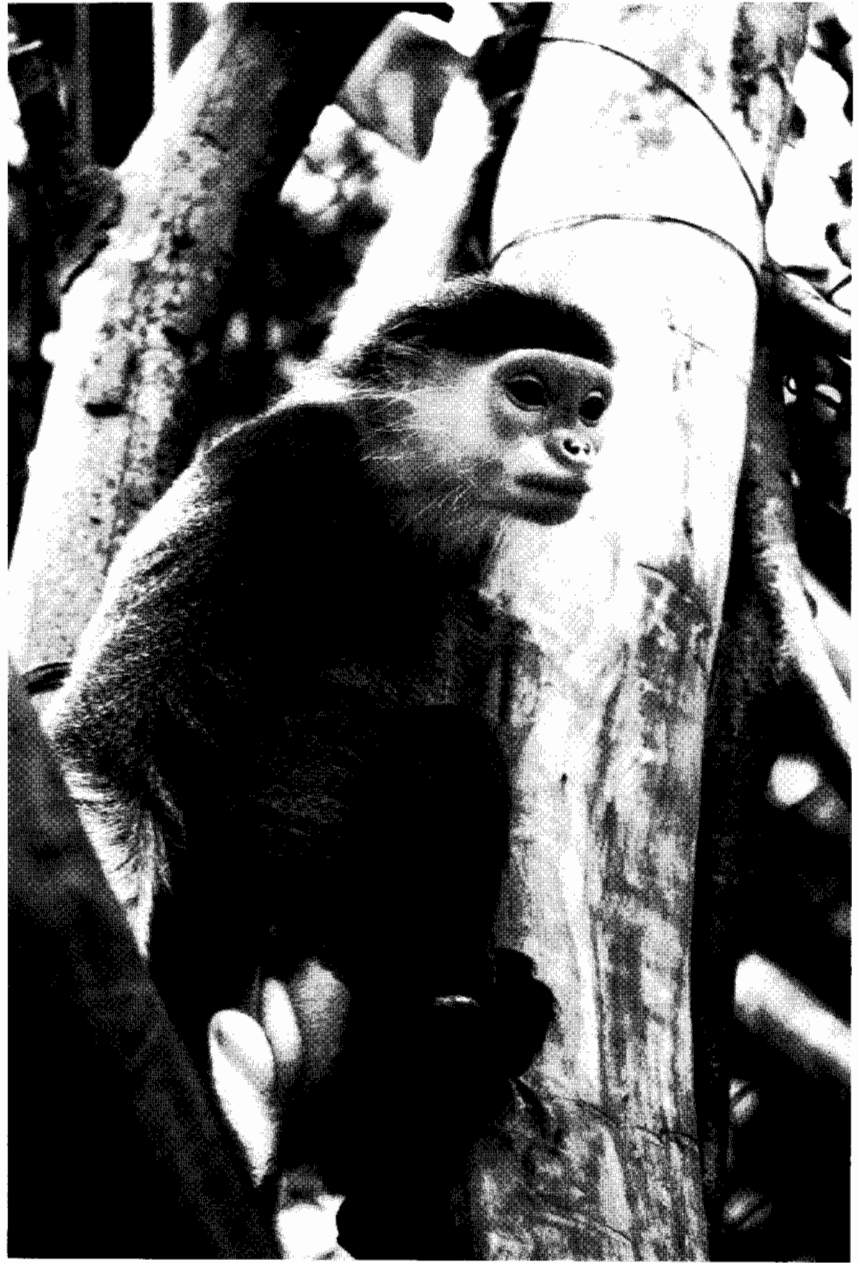


Figure 3.6. The southern form of the douc (*Pygathrix nemaeus nigripes*) (photograph by N. Rowe).

has also been supported by the analysis of Jablonski & Peng (1993), and we therefore accept these four species here: *P. (R.) roxellana*, *P. (R.) bieti*, *P. (R.) brelichi*, and *P. (R.) avunculus*. According to Napier (1985), *roxellana* and not *roxellanae* is the correct name for the Sichuan form, which is often known as the golden monkey. Jablonski & Peng separate *P. (R.) avunculus* as the subgenus *Presbytiscus*, implying a phyletic separation from the other three species, but we do not think such a subdivision is necessary.

P. (R.) roxellana has a greyish-brown back ornamented with long golden strands, and its yellowish-white underparts become golden with age; *P. (R.) bieti* and *P. (R.) brelichi* (Figure 3.7) are darker in colour; *P. (R.) avunculus* is dark brown on the back, and has yellowish-white underparts and an orange throat patch (Napier, 1985). While *P. (R.) avunculus* inhabits lowland forests in northern Vietnam, the other three forms are restricted (at least today) to montane habitats in southern China. Of the three, *P. (R.) bieti* occurs at the highest altitudes (between 3000 and 4300 m), in temperate fir-larch forest subject to harsh winter conditions; this species has 70% of its activity on the ground (Li *et al.*, 1982; Zhao, 1988; Long *et al.*, 1994; Wu, 1993).

Genus Nasalis, proboscis monkey

This genus contains the single species, *N. larvatus*, the proboscis monkey. The species takes its common name from the large, pendulous, fleshy nose of the adult male, a feature unique among primates (Figure 3.8). Proboscis monkeys occur only in Borneo, where they are typically associated with coastal swamp forests, including mangroves, although they also occur in riverine forest far inland (Chivers & Burton, 1988). They are unusual among primates in that they regularly swim. This monkey is also notable for its extreme sexual dimorphism; adult males have an average body weight of 21 kg, twice the size of females (Table 3.2).

Genus Simias, pig-tailed monkey, or simakobu

This is another very unusual colobine. The single species *S. concolor* is found only in the Mentawai Islands, and is the only colobine with a markedly short tail. Both male and female simakobu have short, turned-up noses. In body proportions, simakobu resemble macaques; they have relatively short arms and legs of similar length, and short, bare tails (Napier, 1985). They show little sexual dimorphism in size, and two colour phases occur, not related to sex (Tilson, 1977) (Figure 3.9). Most observed social groups are small (3–8 monkeys), and sometimes monogamous (Tilson, 1977; Watanabe,



Figure 3.7. The Guizhou snub-nosed monkey *Pygathrix (Rhinopithecus) brelichi* in the Wuling Mountains of south-central China (photograph by N. Rowe).



Figure 3.8. Adolescent male proboscis monkeys (*Nasalis larvatus*), part of an all-male group in Tanjung Puting National Park, Kalimantan Tengah, Borneo (photograph by T. Blondal and C. Yeager).



Figure 3.9. Light-phase juvenile simakobu, *Simias concolor* (photograph by R. Tilson).

1981), although Watanabe found two primary forest groups to contain about 20 individuals each. Tenaza (1989) has observed prominent pink sexual swellings in females on S. Pagai Island, a unique feature among Asian colobines. Simakobu may descend to the ground and flee when disturbed by hunters (Tilson, 1977).

Groves (1970) first suggested that simakobu were closely related to proboscis monkeys and classified them as *Nasalis concolor*. Delson (1975a) agreed that the simakobu skull was an excellent structural intermediate between those of *Nasalis* and *Presbytis*, and ranked the proboscis monkey and simakobu as monotypic subgenera of *Nasalis*, given the many differences between the two species. Delson continues to strongly support this argument, which takes a middle course between the simple congeneric association of Groves (1989) and the generic distinction of others. This generic distinction is followed in this volume and favoured by Davies and Oates, because of the ecological distinctiveness of the simakobu.

Genus *Presbytis*, leaf-monkeys

Although these monkeys have often been grouped in the same genus with the langurs (*Semnopithecus* and *Trachypithecus*), they may be distinguished from them by several craniodental features: a short face with weakly developed brow ridges, a convex nasal profile, deep and consistent underbite, relatively broad homomorphic incisors, thick dental enamel and a reduced or absent hypoconulid on the lower third molar (Brandon-Jones, 1984; Napier, 1985; Groves, 1989). Newborn infants are white or whitish and as the coat darkens during development they pass through a stage which displays a dark cruciform pattern on the back and upper head (Pocock, 1928). Compared to *Trachypithecus*, *Presbytis* have relatively longer hindlimbs, leap more (Figure 3.10) and use quadrupedalism less (Fleagle, 1976; Strasser, 1992), and they have relatively smaller stomachs (Chivers, Chapter 7, this volume). Adult *Presbytis* are typically less dimorphic than *Trachypithecus*, with adult males only slightly larger than females (Table 3.2).

The genus *Presbytis* is restricted to rain forests in southern Thailand, the Malay Peninsula, Borneo, Sumatra (including the Mentawai Islands), Java, Bali and the Lomboks (Figure 3.11). We recognize seven species in this region: *P. melalophos*, *P. comata*, *P. frontata*, *P. rubicunda*, *P. potenziani*, *P. hosei*, and *P. thomasi*. Napier (1985) made the same division of this group, modifying Chasen's earlier (1940) arrangement. The seven species are differentiated largely by their coat patterns; skeletally they are difficult to distinguish (Medway, 1970). The distinctive nature of the male loud call was used



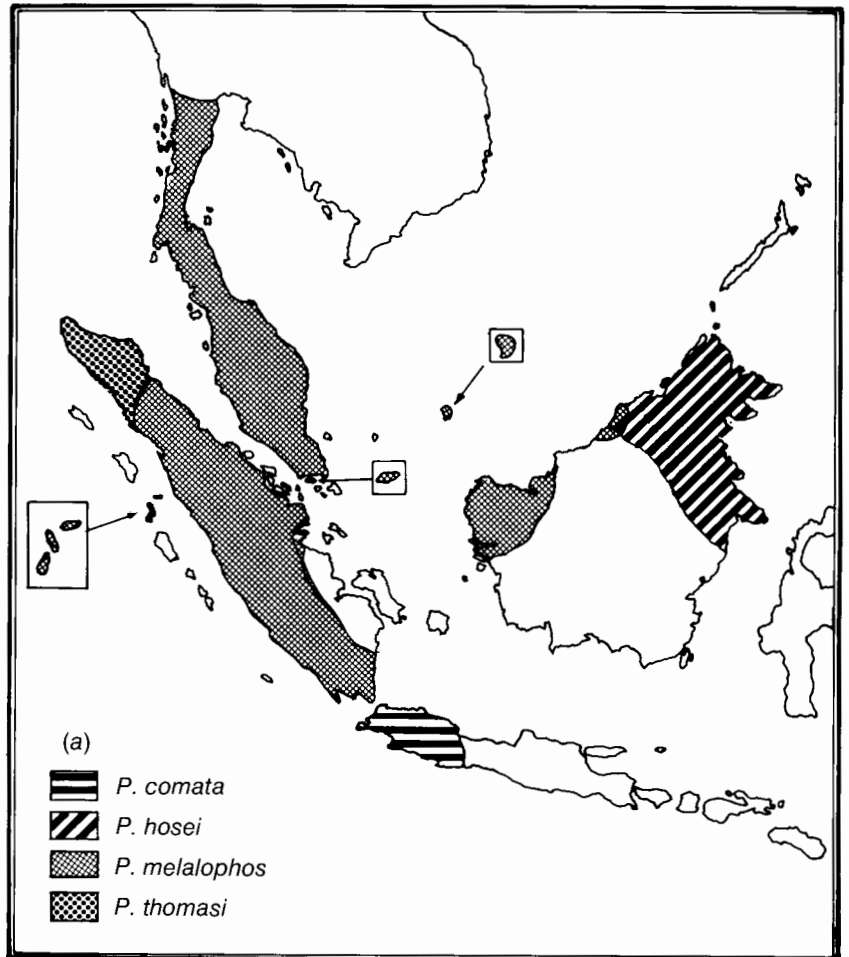
Figure 3.10. Banded leaf-monkey *Presbytis melalophos* leaping, West Malaysia (photograph by J. Fleagle).

by Wilson & Wilson (1975) to justify a separation of *P. melalophos* into three species: *femoralis*, *cruciger* and *melalophos*. However, Bennett & Bennett (1988) have found that differences in the calls of *femoralis* and *melalophos* are not consistent in the wild, and in that light we revert here to regarding *P. melalophos* as one (highly variable) species. We also retain *siamensis* as a subspecies of *melalophos*, although Brandon-Jones (1984) gave it species status.

Brandon-Jones (1977) claimed that *P. potenziani* is the most primitive member of the group, but provided no convincing support for this claim. He implied that he regarded its dark coloration as a significant primitive feature. However, this is by no means an all-black monkey; Brandon-Jones (1984) and Napier (1985) made it clear that the coat carries white and reddish markings. Furthermore, Tilson (1976) observed that *P. potenziani* infants are white at birth, but soon develop the 'cruciger' pattern.

Among the species we recognize, sympatry occurs between *P. hosei* and *P. rubicunda* in north Borneo, and between *P. rubicunda* and *P. frontata* in western and central Borneo.

We refer to the members of this genus as 'leaf-monkeys' because this term has wide usage. The name is not entirely satisfactory, because these monkeys



often include large quantities of seeds in their diet (see Chapter 5), but we think it is more suitable than 'sureli', the name used by Brandon-Jones (1984). *Sureli* is a Javan word and is used for just one, peripheral, member of the genus.

Genus Trachypithecus, langurs

Members of this genus have heteromorphic incisors with an edge-to-edge bite, and the hypoconulid on the lower third molar is unreduced (Weitzel, 1983; Napier, 1985); their newborn young are orange, brown or grey in col-

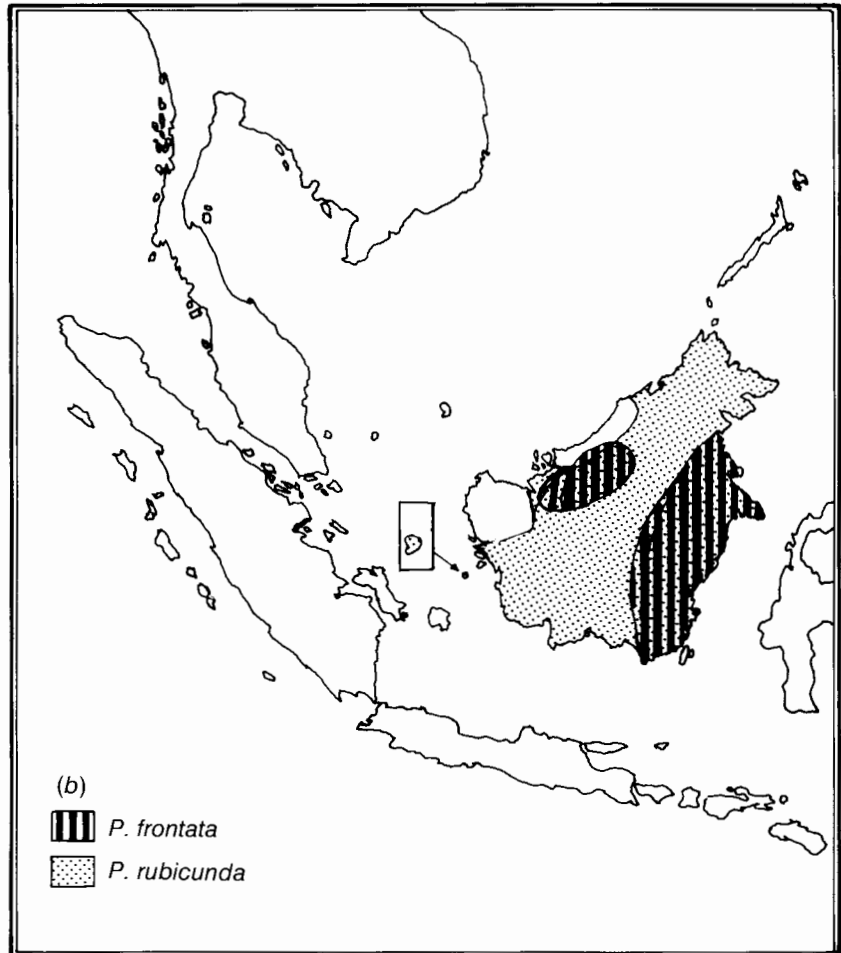


Figure 3.11. Distribution of the genus *Presbytis*. (a) *P. melalophos*, *P. thomasi*, *P. comata* and *P. hosei*; (b) *P. frontata* and *P. rubicunda*. Based on E. Bennett (personal communication), Payne *et al.* (1985) and Wolfheim (1983).

our. Compared with *Presbytis*, they have relatively shorter hindlimbs, engage in more quadrupedal walking and running (Fleagle, 1977), and have relatively larger stomachs in relation to their body size (see Chapter 7). *Trachypithecus* species occur in a wider range of conditions than *Presbytis*; in addition to moist and wet lowland forests, they are found in dry deciduous forests, coastal mangrove swamps, and montane broad-leaved forests. Their range includes Sri Lanka and South India, eastern India and Bangladesh, Burma,

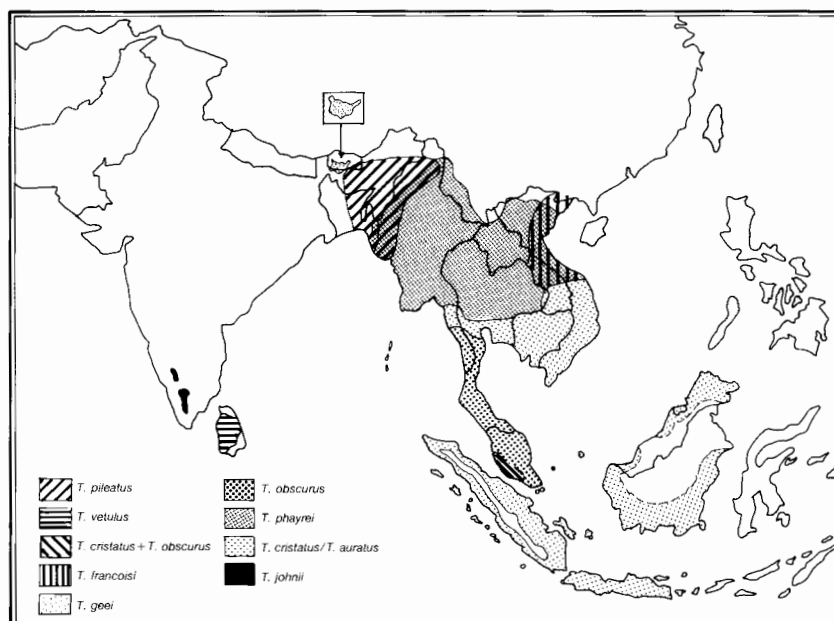


Figure 3.12. Distribution of the genus *Trachypithecus*. Based on E. Bennett (personal communication), Choudhury (1988, 1992), Fooden (1976), Green (1978), MacKinnon & MacKinnon (1987), Medway (1970), Oates (1979), Payne *et al.* (1985), Wilson & Wilson (1977) and Wolfheim (1983).

Indo-China and southern China, the Malayan Peninsula and the Sunda Islands (see Figure 3.12).

There is no entirely appropriate common name for this group of monkeys, but we feel that the widely-used Hindi name 'langur' (originally applied to *Semnopithecus entellus* and referring to the monkey's long tail (Hrady, 1977)) is a suitable term, both because four species of *Trachypithecus* occur in India itself, and because *Semnopithecus* and *Trachypithecus* appear to be sister taxa (an issue discussed below).

We recognize nine species in this group. These species are the eight members of Napier's (1985) *Presbytis cristata* group (i.e. *T. cristatus*, *T. vetulus*, *T. johnii*, *T. obscurus*, *T. pileatus*, *T. phayrei*, *T. francoisi* and *T. geei*) (Figure 3.13) together with *T. auratus*. *T. auratus* was included by Napier and others within *T. cristatus*, but Weitzel & Groves (1985) have shown that this Javan population has distinctive cranial morphology.

Brandon-Jones (1984) questioned the unity of *T. francoisi*, a species from northern Vietnam and an adjacent area of southern China. He regarded the



Figure 3.13. Dusky langur (*Trachypithecus obscurus*) (photograph by J. Caldecott).

subspecies *francoisi*, *leucocephalus* and *delacouri* as full species, apparently on the basis of pelage differences, and recently Ratajszczak (1988) has reported that Chinese zoologists have seen *leucocephalus* and *delacouri* living sympatrically without interbreeding. Brandon-Jones listed another subspecies, *T. francoisi poliocephalus* (from Cat Ba Island in the Gulf of Tonkin), as a subspecies of the South Indian *T. johnii*. We see no cogent reason to accept such a grouping, in the absence of a published analysis; Ratajszczak listed *poliocephalus* as a form of *francoisi*.

Groves (1989) considered *geei* to be a 'well-differentiated offshoot' of *T. pileatus*, although Brandon-Jones (1984) kept it as a species. Brandon-Jones (1984) also placed *phayrei* in *T. obscurus* (but did not justify this), and recognized the form *barbei* as a separate species. Napier (1985) has discussed the position of *barbei* (a species tentatively proposed by E. Blyth in 1847 based on two specimens which are from an uncertain locality), and concluded that its status is in doubt. Gupta, who has studied *T. phayrei* in Tripura, India, considers that the *barbei* specimens belong to *phayrei* (A. K. Gupta, personal communication).

Pocock (1939) separated *T. vetulus* and *T. johnii* (Figure 3.14) from the other *Trachypithecus* and placed them in the genus *Kasi*. The adults of these



Figure 3.14. Nilgiri langur (*Trachypithecus johnii*) at Kakachi, India (photograph by J. Oates).

two species are somewhat larger in body weight than the other species and their newborn infants are not orange but grey (*vetulus* of Sri Lanka) or predominantly reddish-brown (*johnii* of South India). However, parts of the neonatal coat of *johnii* have an orange tinge (J. F. Oates, personal observation), and the skull anatomy and diet of both species are similar to other *Trachypithecus*; we therefore include them here, pending further study.

Apart from a very limited area of sympatry between *T. cristatus* and *T. obscurus* on the west coast of the Malay Peninsula (Marsh & Wilson, 1981), the only sympatry between members of this genus is between *T. phayrei* and other species in the east (*pileatus*) and west (*francoisi*) of its range (see Figure 3.12).

Genus *Semnopithecus*, Hanuman or grey langur

Groves (1989) has noted that, while the Hanuman langur shares many characteristics with *Trachypithecus*, it can also be clearly separated by the blackish-brown coat coloration of young infants and by skull morphology (e.g. heavy horizontal brow ridges with a marked depression posteriorly (Napier, 1985)). In this volume we follow Groves in recognizing *Semnopithecus* as a monotypic genus, containing only the species *S. entellus*. Strasser & Delson (1987),

however, followed Brandon-Jones (1984) in regarding *Semnopithecus* as also including the subgenus *Trachypithecus*, a course which Delson still prefers and one which has the merit of equalizing to some degree the variation seen among colobines; the African genera *Colobus* and *Procolobus* are about as distinct as *Presbytis* and *Trachypithecus*, while the subgenera within *Procolobus* are about as similar as are *Semnopithecus* and *Trachypithecus*. Davies and Oates, on the other hand, are impressed by the considerable ecological divergence between the Hanuman langur and the *Trachypithecus* species. Hanuman langurs do not inhabit closed-canopy tropical forests, they exhibit considerable terrestriality (Figure 3.15), and they have very flexible diets that are rarely as folivorous as those of *Trachypithecus*.

S. entellus is remarkably variable and adaptable, occurring from Sri Lanka north to the Himalayas, from sea level to an altitude of 4000 m (map, Figure, 3.16), and in a great range of habitats from dry tropical scrub jungle to montane coniferous forest (Roonwal & Mohnot, 1977; Wolfheim, 1983). It is commonly associated with human settlements where it has traditionally been tolerated due to its association with the monkey-god Hanuman in Hindu mythology (Hrady, 1977). Many populations are highly terrestrial in their behaviour. Given the wide geographical spread and the range of habitats occupied by Hanuman langurs, it is not surprising that there is a great deal

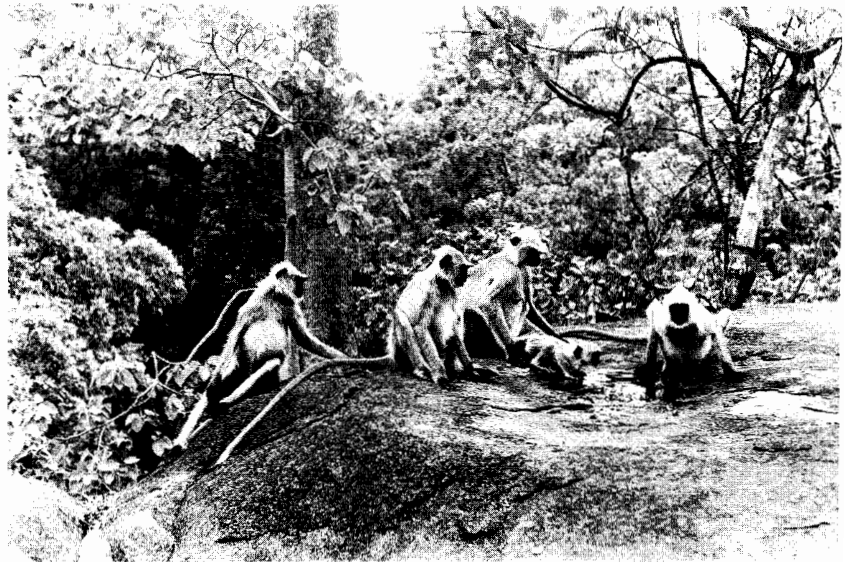


Figure 3.15. Hanuman langurs (*Semnopithecus entellus*) drinking at a boulder pool at Kanha, India (photograph by P. Newton).

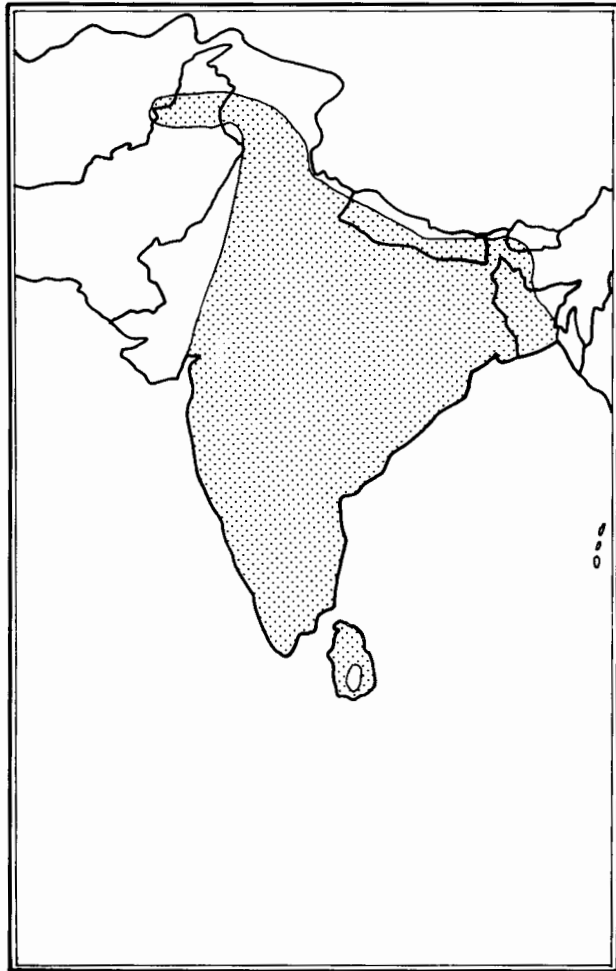


Figure 3.16. Distribution of *Semnopithecus entellus*. Based on Napier (1985), Roonwal (1981) and Wolfheim (1983).

of interpopulational variability in size (adult females from Sri Lanka average 7 kg, those from the Himalayas over 15 kg) and coloration (from predominantly pale grey to dark chocolate brown) (Napier, 1985); this has led to the description of numerous subspecies. Roonwal & Mohnot listed 16 subspecies, while Napier listed 15 in four groups (based largely on pelage colour and pattern). Brandon-Jones (1984) regarded the south-west Indian form *hypo-leucos* as a distinct species. This form lives in relatively moist habitats and

has particularly dark hair; Brandon-Jones appears to believe that this dark coat is a primitive feature, justifying separation at the species level. In the absence of a careful assessment of other characteristic we prefer to follow the traditional arrangement, and recognize only a single species of grey langur.

Following similar logic to that of Brandon-Jones, Groves (1989) argued that *Semnopithecus* is more primitive than *Trachypithecus*, because of the blackish colour of newborn infants. We are not convinced that dark coloration alone is a strong indicator of primitiveness.

Acknowledgements

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