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2 Evolutionary history of the colobine monkeys in paleoenvironmental perspective

ERIC DELSON

Introduction

Colobines are today rarer and less speciose than the cercopithecine subfamily of the Cercopithecidae, but this has not always been the case. At times in the past, for example in the later Miocene and Pliocene of southern Europe or in the Pliocene of eastern Africa, colobines were more numerous (at least in terms of known species) than cercopithecines. The goal of this chapter is to review the past history of Colobinae and explore the evolutionary 'reasons' for their changing diversity and distribution, especially as they may relate to the changing environments in which these animals lived. A number of new fossil samples are in the course of description and interpretation, so that only preliminary results can be reported here. After a brief review of relevant paleoenvironments and current concepts on the origin of the Cercopithecidae and the Colobinae, the fossil record of colobines is surveyed in turn from Eurasia and from Africa.

Review of Neogene paleoclimate

In order to place the fossil colobines in a more explicitly paleoenvironmental perspective, it is useful first to summarize the history of Cenozoic climate evolution. The Paleocene and Eocene epochs of the early Cenozoic, c. 66–34 million years ago (hereafter, Ma = Megennia) were characterized by tropical and subtropical forests across most of the continents (see Berggren & Prothero, 1992). By late in the Eocene, climatic 'deterioration' (drying and cooling) had set in, so that Northern hemisphere habitats favourable to primates were restricted to such areas as southern Europe and the southern United States and Mexico (see Gingerich, 1986). Global temperature fell sharply in the early Oligocene (c. 34–32 Ma), and a few million years (Myr) later, world sea level also dropped precipitously (Haq *et al.*, 1987), permitting greater

interchange of faunas between Africa, Asia and Europe. Both temperature and sea-level rose slowly in the later Oligocene and early Miocene (26–17 Ma), leading to a period of stability in climate, but then both decreased again in the Late Miocene (10.5–5.3 Ma), a time of generally increasing aridity and spread of open-country environments in the Old World (Bernor, 1983; see Figure 2.1).

Around 6 Ma, plate tectonic movements of Africa with respect to Eurasia led to the closure of the Mediterranean Basin in the west (eastern closure had occurred early in the Miocene; see Thomas, 1985) and the desiccation of the seaway. After nearly 1 Myr of alternating local flooding and salt deposition, the Atlantic Ocean broke through in the Gibraltar region, refilling the Mediterranean and initiating an early Pliocene (5.3–3.6 Ma) interval of greater humidity, at least in Europe. By the later Pliocene (2.5 Ma), the combination of earth-orbit-influenced climatic cycles and surface factors such as Antarctic ice-sheet development, Himalayan orogeny and Panamanian isthmus elevation initiated a long interval of increasing climatic fluctuation (Prentice & Denton, 1989).

Through the Pleistocene, temperature cycles increased in amplitude, decreased in period (from 0.5 to 0.1 Myr) and involved worldwide glaciation and related sea-level fluctuation (Van Couvering & Kukla, 1988*a,b,c*). Several dozen major cycles have occurred since the mid-Pliocene and the pattern is expected to continue for some time unless disrupted by the effects of human pollution of the atmosphere.

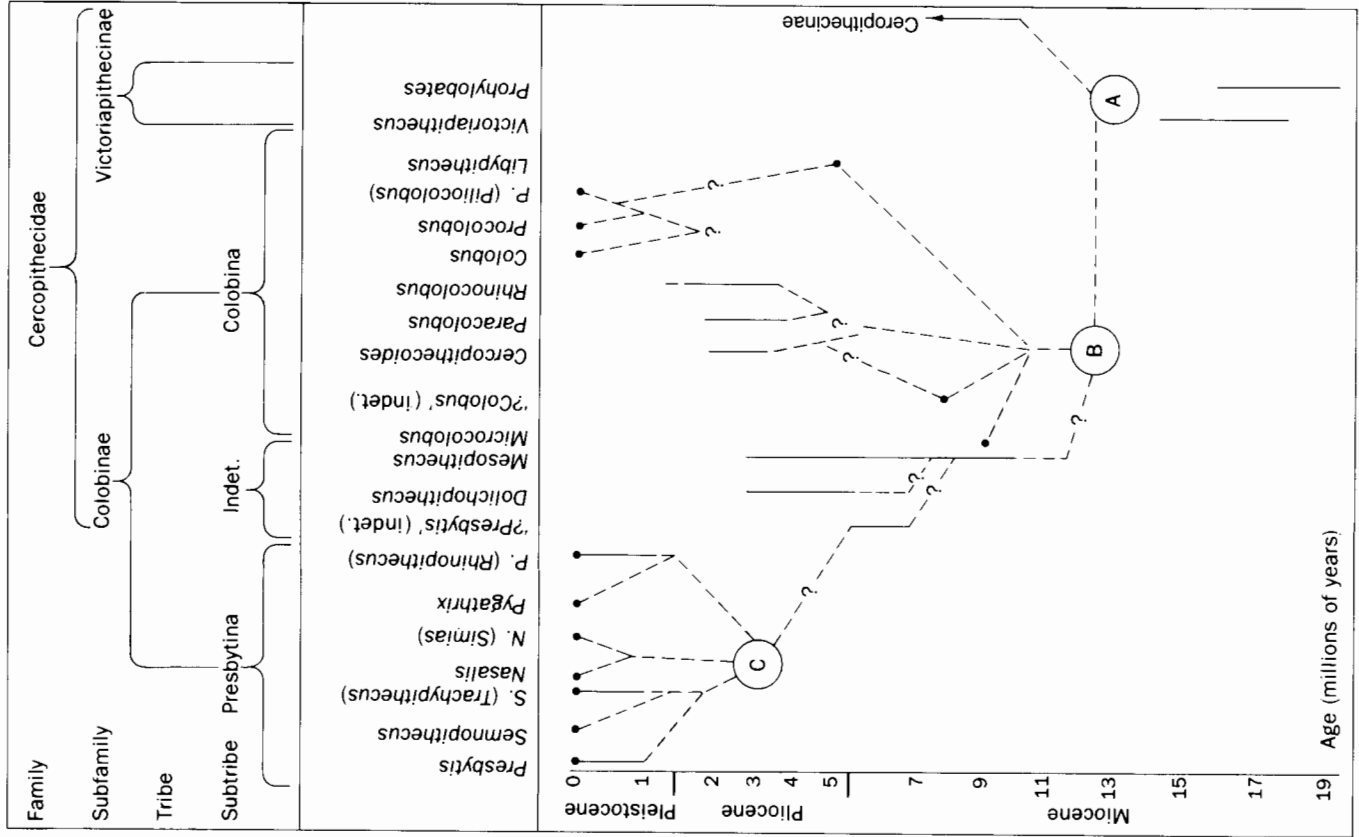
Cercopithecoid origins

The ancestry of the Cercopithecidae is now widely agreed to be traceable to early catarrhines similar to the Fayum propliopithecids (Delson, 1975*a*; Szalay & Delson, 1979; Fleagle, 1988). The oldest known members of the family are two genera of the Early to early Middle Miocene (20–15 Ma), *Prohylobates* and *Victoriapithecus*, usually placed in the subfamily Victoriapithecinae (see Figure 2.2). Based on a limited sample of fossils from Maboko Island, Kenya (see Figure 2.8, below), dated to the end of this interval, Delson (1975*a*) discerned two species of *Victoriapithecus*. Each was linked to a different modern subfamily by minor derived features, and this in turn was said to document the subfamilial divergence.

More recently, as a result of new finds, Benefit (1987, 1993), Benefit & McCrossin (1991, 1993) and Fleagle (1988) have discussed further the morphology of these taxa and their role in cercopithecoid evolution, coming to somewhat differing conclusions, but agreeing that the victoriapithecines are

Age (Ma)	Africa	Europe	Asia
0	Co, Pc, PP		Na, Pg, P, PR, Se, Si, Tr
0.5	Taung (late; Co?) Antalae (Ethiopia; Co?) Other areas		Lang Trang (Vietnam; P?) Xinan (China; PR) Yanjinggou (PR) Gongwangling (PR)
1	Turkana Basin (C?) Olduvai III (Ce)		
1.5	(Rh?, C?) Olduvai II (Ce) (Rh, Pa, Ce, C?) Kromdraai (Ce?)		
2	(Rh, Pa, A) Bolt's Farm (Ce) (Rh, Pa) Sterkfontein (Ce)	Kottovina (Do), Crag (Me) Villafranca (Fornc; Me)	Upper Siwaliks (P?) Shanar, Atsugi (D?) Udunga (D?)
3	(Rh, Pa, A) Makapan (Ce) (Rh, Pa, Ce) Hadar (Rh, A), JM90 (Pa)	Baradot, Wölfershm. (Do, Me) Perpignan (Do, Me) Malusteni, Voinichevo (Do)	
4	Laetoli (Pa?, A?)	Montpellier (Me) Baltavar (Me) Ditiko (Me)	
5	Sahabi (Li) Wadi Natrun (Li)		Yushe Mahui (P?) Hasnot, Dorneli (P?)
6			
7	Lukeino (C?) Marceau (C?)		Kotal Kund (P?)
8			
9	Nakali (Mi?) Ngeringerowa (Mi)	Pikermi, Veles, Bulgaria (Me) R. Zouaves, Grebeniki (Me)	Moleyan (Me) Maragha (Me)
10			
11			
12			
14			
16	Maboko (Mi) Moghara (Py), Loperot (Vi) Zelten (Py), Buluk (Vi?) Napak (Vi?)	Wissberg (Me?)	
18			
20			

Figure 2.1. Chronological table of localities yielding colobine and victoriapithecine fossils. The taxa present at each site are listed in parentheses, according to the following key. Dates on the left refer to the bottom of the respective line in the table, and in general, sites are dated or estimated to date between the age on their line and the next line up, but they may be in error by one line either way, except that for Kotal Kund, ↓ ↑ indicates an uncertainty of 2–3 Ma about time placement of the locality. The top line ('0 Ma') refers to the present. Note the two changes in spacing of time intervals indicated by the symbol 'jff'. Key to taxonomic abbreviations: A, colobine 'species A'; Ce, *Cercopithecoides*; Co, *Colobus*; C?, African colobine species?; Do, *Dolichopithecus*; D?, ?*Dolichopithecus*; Li, *Libypithecus*; Me, *Mesopithecus*; Mi, *Microcolobus*; Na, *Nasalis*; Pa, *Paracolobus*; Pc, *Procolobus*; PP, *P. P. (Ptilocolobus)*; Pr, *Presbytis*; P?, Asian colobine species?; Py, *Prohylobates*; Pg, *Pygathrix*; PR, *Pygathrix (Rhinopithecus)*; Rh, *Rhinocolobus*; Se, *Sennopithecus*; Si, *Simias*; Tr, *Trachypithecus*; Vi, *Victoriapithecus*; ? after any taxon indicates questionable identification. Atsugi is an alternative geographic name for the locality called Nakatsu in the text.



in general conservative by comparison to all later cercopithecoidea. Only one species was recognized in the large dental sample of *Victoriapithecus* from Maboko. Harrison's (1989) review of the Maboko cercopithecoidea postcranial material further substantiated a single species. Thus, Delson's hypothesis appears to be falsified, and it seems likely that the separation between Colobinae and Cercopithecoidea occurred after 15 Ma.

The Maboko sample, along with other smaller samples of Early and Middle Miocene cercopithecoidea, documents the nature of the earliest known Old World monkey adaptations. The typical bilophodont dental pattern was not yet fully developed: a crista obliqua was common on upper molars and the hypocone was relatively isolated; the lower first and second molars sometimes preserved a small midline distal hypoconulid, and the hypolophid mesial to that cusp was incomplete; and the buccal faces of lower cheek teeth flared out even more than in modern cercopithecoidea (compare Benefit, 1993; and Lucas and Teaford, Chapter 6). Postcranially, *Victoriapithecus* was moderately adapted to terrestrial locomotion, supporting the suggestions of Kay (1977b) and others that the differentiation of early Old World monkeys from other catarrhines was at least partially linked to terrestriality.

The environmental background to this differentiation is less clear. Andrews (1981) has suggested that there was a paleoecological 'relay' between hominoids (dominant in the earlier Miocene) and cercopithecoidea (more common in the later Miocene and dominant thereafter). In his opinion, cercopithecoidea became distinct from early catarrhines as a result of adaptation to folivory, although he thought this occurred in an arboreal setting. Colobines further emphasized folivory, as noted below, and Andrews hypothesized that cercopithecoidea might have 'responded' through development of a greater tolerance for secondary compounds in fruit, an idea for which I find little evidence. Temerin & Cant (1983) expanded on this reasoning to suggest that cercopithecoidea concentrated on extracting greater energy from low-quality food sources. They also inferred that early cercopithecoidea might have shifted from

Figure 2.2. Phylogeny and classification of Colobinae. The genera (and subgenera) of colobines recognized here are listed across the top, with higher-level taxa above; victoriapithecoidea are also included. The known time range for each (sub) genus is shown as a solid vertical line, with probable ranges dashed vertically and phyletic relationships indicated by oblique dashed lines. Filled circles represent living taxa and fossils known only from single sites. Lettered circles represent the uncertainty of branching sequence or date for major groups: A, the split between Colobinae and Cercopithecoidea; B, the split between African and Eurasian Colobinae; and C, the divergence among Asian Colobinae. See footnote 1, page 28, as regards generic names of Asian colobines; subgenera are employed in this figure as it was prepared originally for a different book.

arboreal to more terrestrial travel, although they worried that the lack of fossil cercopithecids in forested paleoenvironments might reflect taphonomic bias. Pickford (1987) further suggested that global climatic shifts also affected the relative distribution of primate groups, finding that a major warming seemed to coincide with the more common occurrence of victoriapithecines in the early Middle Miocene (17–14 Ma) and hypothesizing that this warming was the ultimate cause of the spread of more open habitats at this time.

The paleontological evidence for such habitats is controversial. Various authors have argued that the Early Miocene of eastern Africa was typified by moist forest to woodland, and these sites have yielded almost no cercopithecoid fossils (e.g. Andrews *et al.*, 1981 and Pickford, 1983; but perhaps questioned by Bestland & Retallack, 1993). Middle Miocene sites have usually been considered to sample more open habitats, but there has been little agreement about detailed paleoenvironmental parameters at the two most important localities: Maboko Island (with hundreds of *Victoriapithecus* specimens and a large fraction of primates among all mammals) and the slightly younger Fort Ternan site (lacking any cercopithecoid and with five primate species accounting for about 1% of all mammals; see Harrison, 1992). Many approaches have been applied to the analysis of Fort Ternan's paleoenvironment (mammal diversity and functional morphology, gastropod index fossils, paleosol and stable isotope studies), but some workers still contend that the site sampled a Serengeti-like grassland (Retallack, 1992), while others argue for a grassy woodland (Cerling *et al.*, 1992) or as Harrison (1992, p. 517) put it: 'predominantly open to closed woodland/bushland, with scattered grassy glades and more densely vegetated areas consisting of woodland-forest mosaics' which seems to include almost everything! There has been less intense study of Maboko (but see, for example, Nesbit-Evans *et al.*, 1981), and Harrison (1992) infers that it was perhaps more densely wooded, or 'closed', than Fort Ternan, with gallery forests but fewer open glades. Yet Pickford's (1983) interpretation of the presence of gastropods was that Maboko received far less rainfall than Fort Ternan.

In conclusion, the earliest hominoids (26–16 Ma) probably inhabited montane or lowland evergreen forest, with few if any sympatric cercopithecids. Victoriapithecines became more common between 17–14 Ma, although it is unclear if any sites of this age sampled significantly more open woodland than earlier sites. The presumed trend to more open habitats may not be as strongly marked, at least in preserved aspects of the fossil record, than was once thought (see also below). None the less, it does seem likely that Old World monkeys probably took advantage of such microhabitats more frequently than did contemporaneous or sympatric hominoids, and it is possible

that their diversification and biomass increase was delayed until such habitats became more common.

At present, there is no clear evidence of cercopithecids between about 14 and 11 Ma. Szalay & Delson (1979) suggested that the subfamilies had diverged by this time and that the cercopithecine tribes differentiated within or soon after that interval, although the lack of fossils makes this impossible to test. By 11 Ma, colobines appeared not only to have diverged from ancestral cercopithecids but also to have differentiated geographically. In contrast, the oldest known cercopithecine fossils (macaque-like teeth from Algeria) are roughly dated at 8–7 Ma.

Eurasian fossil colobines

Late Miocene

The earliest well-known colobine, *Mesopithecus pentelicus*, was not African but Eurasian. Although mainly recovered over 100 years ago, it is still the best represented, both in number of fossils and range of skeletal parts (Figures 2.3 and 2.4). The largest sample of the species is from Pikermi, near Athens, but small numbers of fossils are known from sites further north in Greek, Bulgarian and Yugoslavian Macedonia, and to the east in Ukraine, Iran and Afghanistan (see Figure 2.5). All of these sites probably date to about 8.5–6 Ma. One upper premolar of a colobine the size of *M. pentelicus* (and referred to that species) was reported by Delson (1973, 1975b) from Wissberg (Germany), a site which appears to be 2–3 Myr older than the others; it is possible, however, that the fauna from this locality was mixed, including elements from two distinct time intervals (see Andrews *et al.*, 1994).

Several authors (e.g. Heintz *et al.*, 1981) have suggested that more than one species may be represented in these sites, but that view was not formalized until de Bonis *et al.* (1990) described *M. delsoni* from the Ravin des Zouaves locality in Greek Macedonia. The diagnostic features of this species were said to involve slight differences in size and proportions of M_3 and the mandibular corpus (only three specimens, all lower jaws, are yet known). Zapfe (1991) considered it to be merely a large *M. pentelicus*, and my recent analysis of *t*-tests on a range of dental variables indicates that, while all the *Mesopithecus* specimens from the Macedonian region are somewhat large, the sample is only significantly different from the Pikermi sample in two or three measures. The species *M. delsoni* is thus considered to be merely a local variant of *M. pentelicus* (see Andrews, *et al.*, 1995). In turn, Zapfe (1991) named a new subspecies *M. p. microdon* for a single mandible from

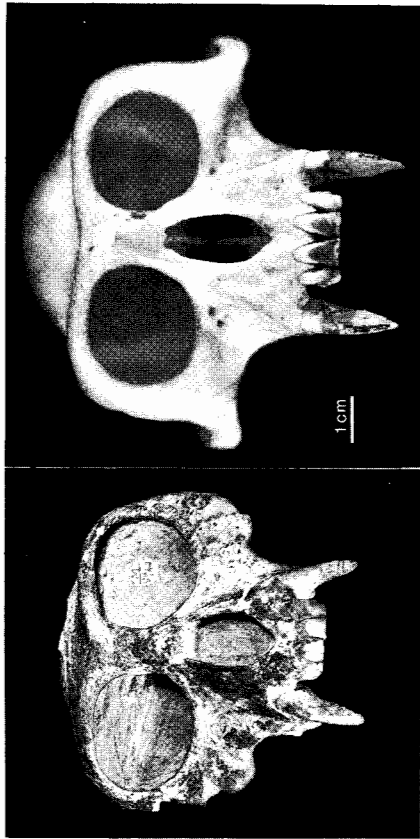


Figure 2.3. Facial view of male *Mesopithecus pentelicus* (left) and *Semnopithecus entellus* (right) at same scale.

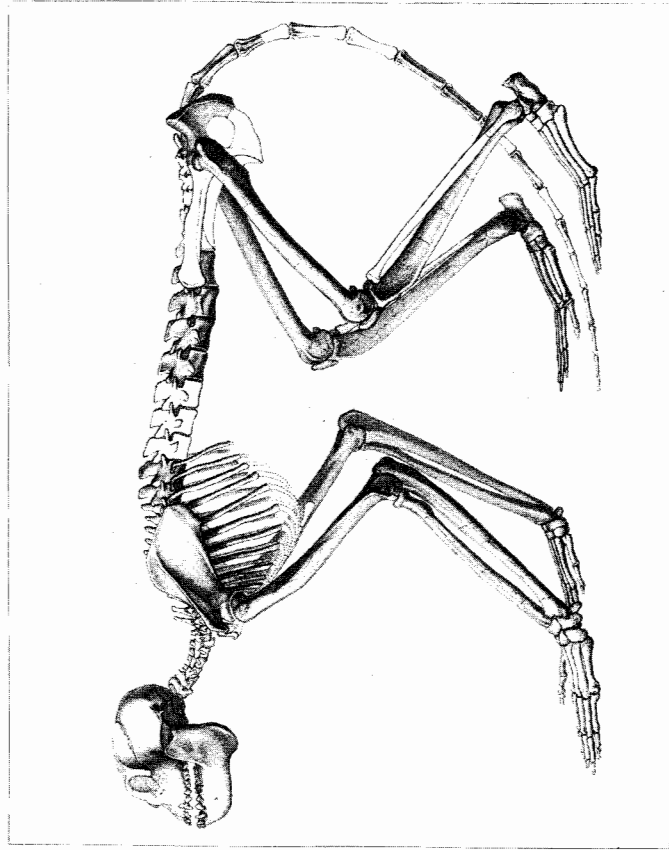


Figure 2.4. Reconstruction of skeleton of *Mesopithecus pentelicus* based on unassociated remains of several individuals; from Gaudry (1862).

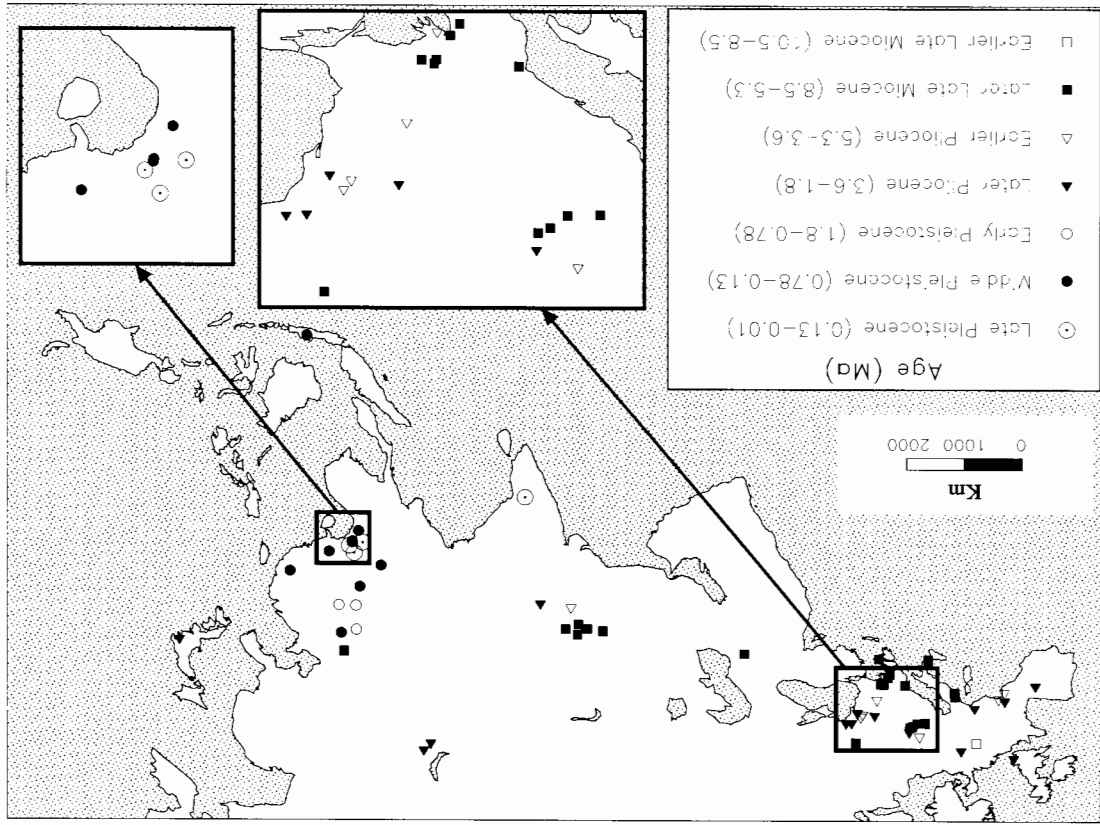


Figure 2.5. Map of Eurasian localities yielding fossil colobines, with symbols indicating site ages. Oceans and major lakes stippled; insets provide enlarged views of central European and south Chinese-Vietnamese regions.

the Chomateri locality near Pikerimi, which may be slightly younger than the main horizon, but its distinctions also appear insufficient to warrant a formal name, at least until a larger sample is known. Several jaws and isolated teeth are known from younger Miocene localities, and where their taxonomic allocation is reasonably secure, they are best allocated to *M. pentelicus*.

The warm and relatively moist environments of the Middle Miocene apparently underwent a trend toward drying in the Late Miocene. Broad surveys (e.g. Delson, 1975b; Bernor, 1983) and some more detailed regional analyses (e.g. von Orgetta, 1979; Demarq *et al.*, 1983; Kovar-Eder, 1987; Bernor *et al.*, 1988) allow the delineation of at least the outlines of climatic evolution. Over much of Europe, mixed woodland characterized the Vallesian (10.5–8.5 Ma). This was generally followed by decreased humidity, more open steppes and restriction of forest to gallery bands in the Turolian (8.5–5.3 Ma). In Greece, for example, paleobotanical work has suggested mixed grassland and coniferous forest in the earlier Turolian, while farther north, a Vallesian mesophytic forest may have changed little into the Turolian. Sites in the eastern Mediterranean often have even more arid faunas and floras late in the Turolian. De Bonis *et al.* (1992) have compared faunal lists and body-size distributions of mammals in these localities and a variety of modern and fossil assemblages using a range of techniques. They conclude that Pikerimi, Samos and the older Macedonian sites with *Mesopithecus* were broadly similar and relatively open, while the younger Macedonian localities near Ditiko may have been more forested. It would therefore seem that *Mesopithecus* species were limited to habitats with mixed forest (at least gallery-type) and grassland, but not adapted to life in more arid steppes.

A different view of the Greek Miocene paleoenvironment, with broader provincial implications, has been put forward by Solounias & Dawson-Saunders (1988). They studied the morphology of the chewing apparatus in ruminant artiodactyls from Pikerimi and the supposedly more arid Samos localities, which are together viewed as a single chronofauna. Somewhat surprisingly, almost all of the extinct bovids were morphologically comparable to modern browsers or intermediate browser-grazers; only one was probably a grazer. Rather than inhabiting an open savanna like those of East Africa, the Samos-Pikerimi species would have lived in a forest-woodland similar to those found today in Sichuan (China), south-east Asia or Kanha (India). By reanalysing the pollen data reported from Pikerimi by von Orgetta (1979), Solounias & Dawson-Saunders (1988, p. 169) suggested that the local environment might have been 'a warm temperate riparian woodland or forest with mixed evergreen and broad-leaf deciduous elements. This woodland was likely to include substantial undergrowth', presumably herbaceous shrubs.

The woodland on plains and low hills might have been broken up by rivers, lakes and bogs, as well as low-lying meadows. Seasonality in temperature or humidity would probably have been low. In this reconstruction, *Mesopithecus* might have lived in more closed habitats than previously thought.

The morphology of *M. pentelicus* has been discussed by several authors since Gaudry's (1862) revision of the Pikerimi fauna, most recently by Szalay & Delson (1979) and Zapfe (1991). The species was comparable in size to *Semnopithecus entellus* (see Figures 2.3 and 2.4) and was at least as terrestrial, as shown especially by studies of the elbow and foot. Strasser & Delson (1987) reported that the proximal cuboid-ectocuneiform facet was absent, as otherwise seen only in African colobines. Delson (1973), however, suggested that *Mesopithecus* was more similar cranially to smaller Asian colobines. The combination of overall postcranial similarity to *Semnopithecus entellus* and the new suggestion of paleoenvironmental similarity of Pikerimi to Kanha forest, which might represent a persisting area of the original habitat of *S. entellus*, reinforces the probable ecological equivalence between *Mesopithecus* and that modern langur.

The record of eastern Asian colobines is much less extensive and is only now becoming reasonably well documented. The oldest Asian colobine east of Afghanistan is represented by only a half-dozen partial jaws from the 'Dhok Pathan' zone of the Pakistan Siwaliks, dated by Barry (1987) between 7–5 Ma. These fossils were originally described as *Cercopithecus* or *Macaca* species in the last century, but Simons (1970) and Delson (1975a) showed that only a single colobine species was involved. This has been termed '?-Presbytis' *sivalensis* to indicate that it is an Asian colobine of uncertain affinities. Only dental morphology is sufficiently preserved to allow comparative study, but colobine teeth are generally quite homogeneous (see Chapter 1), and results to date are inconclusive. There is no clear distinction from (nor linkage with) *Mesopithecus*, *Semnopithecus* or *Presbytis*. As Barry (1987) has summarized, there are a number of faunal differences between the biogeographic 'provinces' on either side of the Baluchi Range (see also Brunet *et al.*, 1984). The Afghan mandible of *M. pentelicus*, found only 300 km to the west, appears to be typical of its species, but not enough gnathic detail is available from the Siwaliks to determine the identity of *sivalensis*.

Pending the recovery of additional fossils or the identification of new morphological characters, a possible source of information might be provided by a still-occluded mandible and lower face, apparently of a small colobine, from the Siwalik locality of Kotal Kund, near the Hasnot site of most ?*P. sivalensis*. If the mandible can be removed from the maxilla and the teeth correspond to those already known, more precise systematic indications

should be forthcoming. Barry (1987) has estimated the age of this specimen as between 10–4 Ma. Barry & Flynn (1990) indicated that climate in the Siwalik region was 'variable' between 12–8 Ma, based on isotopic studies, but with cool episodes between 11–9.5 and 9–8 Ma. It was warmer from 8–6.5 Ma, after which there was marked cooling. It was not clear to Barry & Flynn whether this cooling was related to the local disappearance of primates, but Cerling *et al.* (1993) have documented a strong link between faunal turnover (e.g. hominoids – colobines – no primates) and the development of savannas in the Siwaliks and elsewhere between 7–5 Ma.

Further eastward yet, Miocene colobines (and cercopithecines) were even rarer, as might be expected if they were spreading from a south-west Asian source. Three isolated cercopithecoid teeth have recently been recovered from a horizon of apparently latest Miocene age (Mahui Formation) in the Yushe Basin of Shanxi province, China, south-west of Beijing. Two teeth are cercopithecine upper molars, and a third appears to be a colobine M₃. Comparison is in progress with modern and extinct taxa, but this would seem to afford solid documentation of the arrival in China of both subfamilies at least by 6–5 Ma, if not necessarily contemporaneously. These would be the oldest cercopithecines and among the oldest colobines in Asia, roughly equivalent in age to the Siwalik material, and probably younger than the better-dated Afghan or Iranian *Mesopithecus*.

Pliocene and Pleistocene

Following the refilling of the desiccated Mediterranean Basin in the earliest Pliocene, southern Europe became densely forested, with some floral evidence suggesting a nearly monsoonal climate – warm and wet with strong seasonality. Around 4 Ma, this situation again began to deteriorate, with dry seasons (especially summer) dominating the yearly cycle, for example in south-eastern France (Bessedik *et al.*, 1984). After about 2.5 Ma, further cooling (on a global scale) led to local floristic extinctions and reductions in forest extent in southern Europe. Again, detailed paleoenvironmental reconstructions are not yet available for most of eastern Asia, but ongoing work in China should provide clarification. Glacial conditions of fluctuating temperatures and widespread loess deposition were common across most of northern (and central) Eurasia after about 1 Ma, rendering the region inhospitable for colobines.

The European Pliocene was characterized by two further colobine species, sometimes found together and/or in association with a macaque similar or

identical to *Macaca sylvanus*. *Mesopithecus monspessulanus* occurs in Early to Middle Pliocene localities from France into Romania and Ukraine and north to Hungary, Germany and England (and perhaps in the latest Miocene of Northern Greece). Mainly known from mandibles and isolated teeth as well as a few fragmentary limb bones, this species is marginally distinguishable from *M. pentelicus* morphologically, but appears to have been more of a forest dweller. The English specimen, an isolated tooth from the Red Crag of East Anglia, is apparently the youngest record of a European colobine, if it is indeed associated with the other Red Crag taxa. Most of the latter are estimated to date about 2.3 Ma, but Hooker (1989) indicated that some specimens may be reworked from older deposits.

Far more interesting is the large-bodied *Dolichopithecus ruscinensis*, from the latest Miocene to mid-Pliocene. This species is also mainly known from a single sample, that from the 4 Myr-old type Ruscinian at Perpignan, southern France, but other Pliocene specimens come from Spain, Germany, Romania, Ukraine (see Maschenko, 1991, who recognized a second species on what seem to be insufficient grounds) and most recently from Greece (Koufos *et al.*, 1991). An ulna from Pestszentlőrinc, Hungary, which is indistinguishable from Perpignan specimens was thought to date to the Late Miocene, but has now been shown to be earlier Pliocene in age (L. Kordos, personal communication). This relating removes a key bit of 'evidence' supporting the hypothesis of the origin of *Dolichopithecus* in apparently forested environments in the Late Miocene of Hungary and Austria. If *Dolichopithecus* is derived from *Mesopithecus* (see below), it is still possible that a peripheral population of the latter underwent reproductive isolation and adapted to life on the forest floor, spreading widely across southern Europe when its prime habitat expanded early in the Pliocene, but no paleontological support for this view remains.

The morphology of *D. ruscinensis* was first discussed by Depéret (1890) and reviewed most recently by Szalay & Delson (1979). Several partial female crania permit a restoration of the skull of this *Rhinopithecus*-sized species (Figure 2.6). The face was relatively long for a colobine, and the interorbital pillar correspondingly narrow, perhaps analogous to *Nasalis larvatus*. Strasser & Delson (1987) noted that, as in the mid-foot of most Asian colobines, the cuboid preserved a small proximal contact facet for the ectocuneiform. Most striking, however, was the degree of terrestrial adaptation as evidenced by aspects of the elbow joint and the short phalanges, features commonly seen in cursorial living cercopithecines. In light of its forested habitat, it is likely that *Dolichopithecus* foraged both terrestrially

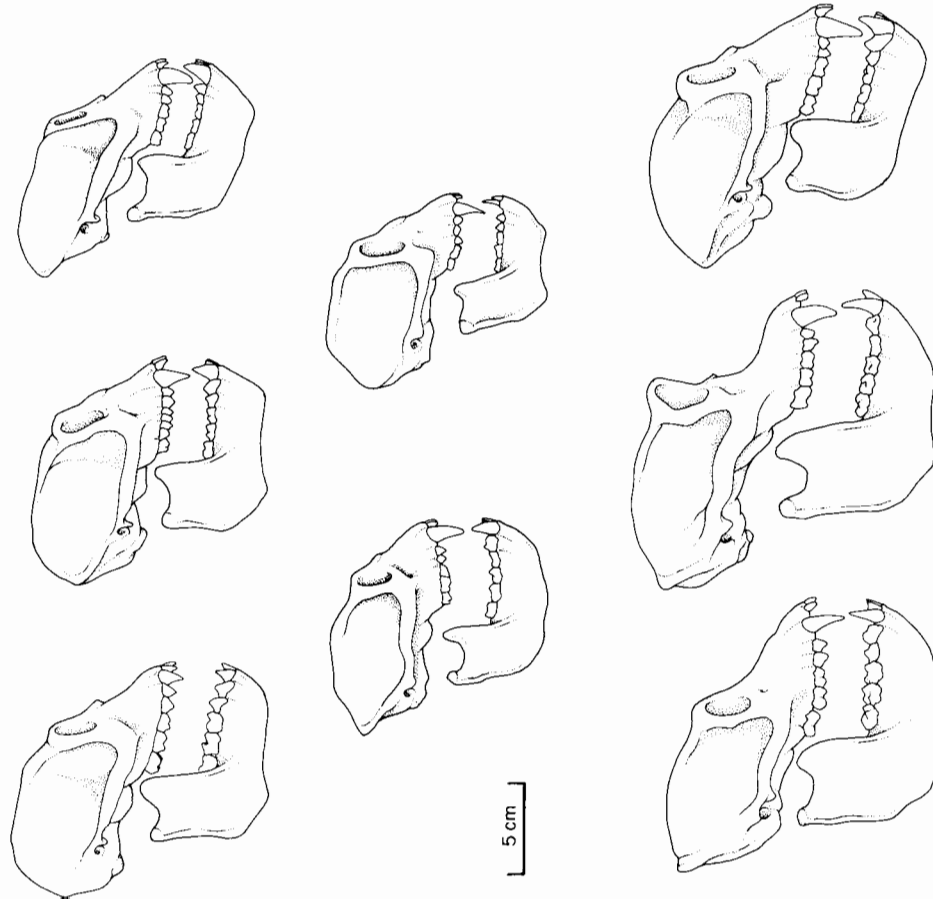


Figure 2.6. Reconstructed crania (male except as noted) in right lateral view of extinct (and selected extant - middle row) colobines: top row *Dolichopithecus rusciniensis* (female), *Mesopithecus pentelicus*, *Libypithecus markgrafi*; middle row *Colobus polykomos* (F), *Nasalis larvatus* (F); bottom row *Paracolobus chemeroni* (F), *Rhinocolobus turkanaensis* (F), *Cercopithecoides williamsi* (F). All to same scale; skulls marked (F) redrawn after Fleagle (1988), with permission; others from Szalay & Delson (1979).

and perhaps in the lower arboreal strata; analogies may be suggested with the larger colobines from south-east Asian and, although they have a different diet, the African mandrills, *Papio (Mandrillus)* species.

Previously, Delson (1973, 1975a,b, 1977; Szalay & Delson, 1979) had suggested that because *Mesopithecus pentelicus* was in all known features relatively 'primitive' by comparison to *D. rusciniensis*, and since it appeared that the two genera were each other's closest relatives, there might have been an actual ancestor-descendant relationship between them (as even earlier indicated by Gaudry, in Depéret, 1890). Strasser's discovery that *Mesopithecus* was more derived than *Dolichopithecus* in having a shorter tarsus suggested closer links between *Mesopithecus* and African colobines (Strasser & Delson, 1987). Another possibility is that the two European species, each represented by a single pedal element, fall within the variation range of some modern Asian colobines (see Strasser, 1988) and are indeed closely related.

With the spread of more open conditions in the Middle Pliocene, c. 2.5 Ma, *Dolichopithecus* apparently died out, about the same time as *Mesopithecus*. Macaques, which had been rarer components of the southern European mammal faunas of the earlier Pliocene, became more common, and the larger terrestrial cercopithecine *Paradolichopithecus* also spread between Spain and Central Asia, perhaps ecologically replacing *Dolichopithecus* in some ways before becoming extinct by the Early Pleistocene.

No definite extinct colobines are known from the Indo-Pakistan region after the Miocene, although a problematic population is represented by a mandibular corpus with P₄-M₃ and a fragment with M₃ (see Delson, 1980) from the 'Upper Siwaliks' of India. Barry (1987) has dated these in the range of 3.2-1.7 Ma (Late Pliocene). Originally termed *Semnopithecus palaeindicus* by Lydekker (1884), they were transferred to *Macaca* by Delson (1975a), but have recently been suggested to be colobine (Jablonski & Pan, 1988). Pending further study, they are accepted here as cercopithecine (as Jablonski, personal communication, has agreed for at least one of the two). Other than some latest Pleistocene specimens of *Semnopithecus entellus* (see e.g. Badam, 1979), no other colobine fossils are known in south Asia.

One of the most surprising finds of recent years was the occurrence of a rather large colobine in the later Pliocene (c. 3-2.5 Ma) of north-eastern Asia. Borissoglebskaya (1981) described as *Presbytis eohanuman* two mandibles, a distal humerus and most of an ulna lacking the distal quarter and part of the olecranon process, from the locality of Shamar, Mongolia. These fossils are quite close in detail to corresponding elements of *Dolichopithecus rusciniensis*, and it is perhaps best to refer the species to that genus (as suggested

by Delson, 1988), accepting the important zoogeographical implications of such a move. In this case, there appears to be sufficient morphology preserved to document the close similarity between the two species, which is (as noted above) not yet true for the Miocene Siwalik monkey. More recently, Kalmykov & Maschenko (1992) reported some maxillary dentition of the same species from slightly farther north, at Udunga (near Lake Baikal) in Siberian Russia. They named the new genus *Parapresbytis* for this species, based on features which appear to relate to large body size and incisor development (and wear?) but are not significantly distinct from *Dolichopithecus*.

Even more intriguing is the report by Hasegawa (1993, in a semi-technical journal) of the recovery of a well-preserved partial face of a large colobine in Japan (see Figure 2.7). This fossil, from the Nakatsu locality near Yokohama, could belong to the same species based on tooth size and morphology, and the face is not dissimilar to that expected for a male *Dolichopithecus*. The site is dated to about 2.5 Ma, based on marine invertebrates, and also yielded proboscidean, deer and hippopotamus, as well as marine taxa such as whale, walrus, squid and turtle. Presumably it represents a coastal deposit with some forest indicated by the deer and proboscidean. It would thus appear that some eastern population of *D. rusciniensis* extended north-eastward into

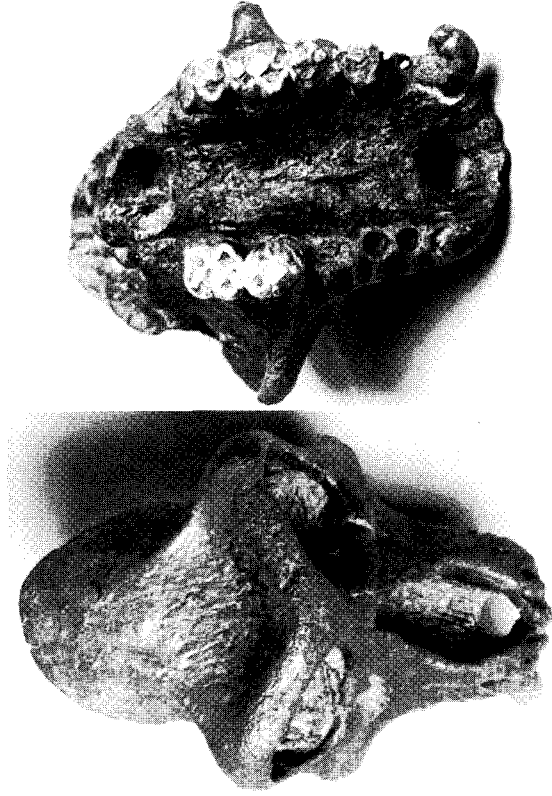


Figure 2.7. Superior (left) and palatal views of new large fossil colobine from Nakatsu, Japan, tentatively referred to *?Dolichopithecus cohanuman*. Courtesy of Dr Y. Hasegawa.

central and then north-eastern Asia during the Pliocene. It is conceivable that movement was in the opposite direction, but that appears unlikely, given the early occurrences of *Dolichopithecus* in the west and the lack of other colobines in the eastern Asian Pliocene, where sites are not uncommon.

A variety of colobines are known in the Pleistocene of China as well. *Pygathrix (Rhinopithecus)* was first reported from the early Middle Pleistocene fissure fillings of Yanjinggou (Yenchingkou, Wan County), in Sichuan province. Matthew & Granger (1923) named the sub-adult skull and partial jaws *Rhinopithecus tingianus*, Colbert & Hooijer (1953) identified the population as a subspecies of *R. roxellana*, while Groves (1970) allocated them to *Pygathrix (R.) brelichi*. An adult cranium, crushed laterally but quite complete (Figure 2.8), has recently been recovered from apparently Middle Pleistocene sediments in Henan province, well north of the current range of any 'golden monkey' (Gu & Hu, 1991). This cranium is comparable in size and facial length to both the Sichuan fossils and the living *P. (R.) roxellana* and has been referred to *R. r. tingianus*.

Jablonski and colleagues (Jablonski & Gu, 1988, 1991; Jablonski & Pan, 1988; Gu & Jablonski, 1989) have suggested that a crushed mandible (Figure 2.8) and other jaws from the Gongwangling locality at Lantian may also be colobine. Lantian is the source of a partial cranium of *Homo erectus*, and the fauna was described in some detail by Hu & Qi (1978). Recent paleomagnetic studies demonstrate a Matuyama age (> 0.78 Ma) for these fossils, perhaps close to 1.2 Ma (An & Ho, 1989). Hu & Qi named the taxon *Megamacaca lantianensis* for the Gongwangling cercopithecoid fossils, with the mandible as holotype. The name apparently referred to the great depth of the corpus, as the teeth are not distinctly larger than those of *Macaca anderssoni* (= *M. robusta*) from Zhoukoudian and other sites; part of this depth may be due to crushing and plastic deformation. Jablonski & Gu (1991) referred this species to *P. (Rhinopithecus)*, reducing *Megamacaca* to a synonym. Its northern location, similar to that of the Henan cranium noted above, was at the time probably covered by warm and moist forest, as documented by both faunal and floral remains. However, An & Ho (1989) noted that the fossiliferous horizon at Gongwangling was a thick silty loess with carbonate concretions, which indicated a dry and cold glacial climate; they suggested that local tectonic uplift might have isolated the region from the northern faunal province, and this does seem to be a satisfactory resolution of the conflicting climatic indications.

Fragmentary remains probably referable to *P. (Rhinopithecus)* are known from a variety of southern Chinese cave sites, such as Lingyian cave, in Lijiang county, Guanxi province; most are probably of later Pleistocene age.



As indicated by Pan & Jablonski (1987), no fossil remains of smaller colobines (*Presbytis* or *Trachypithecus*¹) have yet been reported from China.

The reverse situation holds for south-east Asia, where fossils have been reported for the two common living genera, but not the 'odd-nosed' colobines, *Nasalis* and *Simias*¹. Hooijer (1962) described specimens allocated to several species of both *Presbytis* and *Trachypithecus* from Middle Pleistocene caves in Java, and Holocene (late Late Pleistocene) sites in both Java (only the latter genus) and Sumatra. Niah Cave on Borneo has also yielded both genera, in deposits ranging between 40 000 and 5000 years ago. Kahlke (1973) has mentioned *Trachypithecus* fossils from several Middle Pleistocene caves farther north, in Vietnam, and recent work there may lead to publication of further details (Ciochon *et al.*, 1990). In terms of paleoenvironments, Indonesia is the best known, but the details are still unclear for all of south-east Asia.

De Vos and colleagues have recently reviewed the collections of mammalian fossils made by Dubois in the early 1890s, concluding that new correlations are required among the various faunal units at Trimi, Sangiran and

¹ Although I prefer to rank *Trachypithecus* and *Simias* as subgenera of *Semnopithecus* and *Nasalis*, respectively, in the interests of consistency throughout this volume, I have agreed to rank them here as full genera; see discussion in Chapter 3, page 57.



Figure 2.8. Left lateral views of Chinese *Pygathrix* (*Rhinopithecus*): left, *P. (R.) roxelana* ?*tingianus* cranium from Henan Province; right, mandibles of modern *P. (R.) brelichi* above *P. (R.) lantianensis* from Gongwangling (last two courtesy of N. G. Jablonski).

elsewhere. De Vos (1989) summarized some of this work and argued that the main Trilim collection was indeed from a single broad Middle Pleistocene horizon. From these fossils, de Vos suggested that: (1) the low number of species indicates an isolation of the island from the mainland (more species might be expected if later forms were mixed in, as had been suggested by others); and (2) the presence of several bovids might imply an open woodland landscape, and in turn a colder climate. Pope (1988), however, noted the absence in Indochina and Indonesia of any indisputable open-country mammals such as camelids, giraffids or equids. He suggested that the number of specimens upon which de Vos and colleagues based their interpretation of open woodland habitats in Indonesia was too small for definite determination of paleoenvironment, and argued that the region was basically forested throughout the Pleistocene.

African fossil colobines

Miocene

As opposed to the record of apparent slow diversification of colobines in Eurasia to a modern peak, the pattern in Africa was one of increase into the Pliocene and then reduction (at least at the genus level) to the present. This is presumably tied to regional climatic change and perhaps the rise of competition from cercopithecines, among other factors. Unfortunately, the Late Miocene is not well known in Africa, even in the eastern zone. Hill (1988; Hill *et al.*, 1985, 1991) has discussed the Baringo Basin sequence in central Kenya, which extends discontinuously from Middle Miocene through Middle Pleistocene. A flora from early in this sequence (about 12 Ma) indicates forested conditions, based on distribution of identified taxa and the common occurrence of entire margins and acuminate tips. By about 10 Ma, equids and other grassland mammals (such as an increasing variety of bovids) appear in the record. Hill *et al.* (1985) suggested that the modern African open-country fauna was well developed by the end of the Miocene (5–6 Ma). Northern Africa was perhaps less densely forested than the east, with development of the Sahara as a zoogeographic barrier during the Late Miocene (see Delson, 1975b; Bernor, 1985; but compare Geraads, 1982, 1987).

Cerling (1992) has examined this problem from an entirely different approach. Most plants utilize one of two photosynthetic pathways, known as C₃ or C₄, which can be distinguished by differences in the relative amounts they contain of the carbon isotope ¹³C. Most trees, shrubs and cool-season grasses are C₃ plants, with a value of δ¹³C between -2.3 and -2.9‰; grasses

and dwarf shrubs of open country or savanna (warm season) are C₄ plants, with δ¹³C of about -0.2‰. Soil carbonates of modern or fossil soils have values which reflect the dominant plant types: C₃ leading to -1.1 ± 0.1‰ and C₄ averaging +0.2‰. Intermediate values reflect a mixture of the two photosynthetic pathway types. Values at two Middle Miocene East African sites were in the pure C₃ range, confirming the essentially forested (closed-canopy) nature of these environments. At the Ngeringerowa locality in the Baringo sequence (as yet not dated directly, but c. 10–9 Ma), a δ¹³C value of around -0.8‰ indicated the presence of C₄ plants in moderate frequency. Other results are discussed in sequence below.

The oldest definitely colobine fossil from Africa (Figure 2.9) is a mandible with nearly complete dentition (but damaged corpus and no rami) from Ngeringerowa. Benefit & Pickford (1986) named this specimen *Microcolobus tugensis* and showed that it combines clearly colobine teeth with several distinctive features of the mandible: the lack of an inferior transverse torus of the symphysis, the lack of a median mental foramen, a fairly even inferior border of the corpus below the molars and a long and steep planum alveolare. Moreover, the mandible and teeth are smaller than those known in any other colobine, only slightly larger than those of *Miopithecus talapoin*. One isolated lower molar of similar size is slightly younger, and a premolar somewhat older, but no other colobines from East Africa are definitely pre-Pliocene.

In the Maghreb, the locality of Menacer (previously named Marceau) has yielded several dozen cercopithecoid teeth, of which about seven are colobine. Originally, Arambourg (1959) allocated all the monkeys to a species of macaque, but Delson (1973 *et seq.*) showed that the type of Arambourg's species and a variety of isolated molars belonged to a medium-sized colobine, which he termed '*Colobus flandrini* (Arambourg), using the modern generic name as a 'form-genus' to indicate African colobines of uncertain affinity. The teeth seem most similar in proportion to those of *Cercopithecoidea* (see below).

Pliocene and Pleistocene

About eight taxa of colobines are known in the African Pliocene and Pleistocene, and the co-occurrence of up to five of these in the same region indicates that a diverse radiation of colobines occurred at this time (Figure 2.6). The global cooling discussed above for Eurasia also affected African climate over the past 5 Myr, although there was greater buffering in the more equatorial regions. Major floral and faunal changes have been described in the late Pliocene (c. 2.5–2.0 Ma), especially in eastern Africa, which appear to reflect

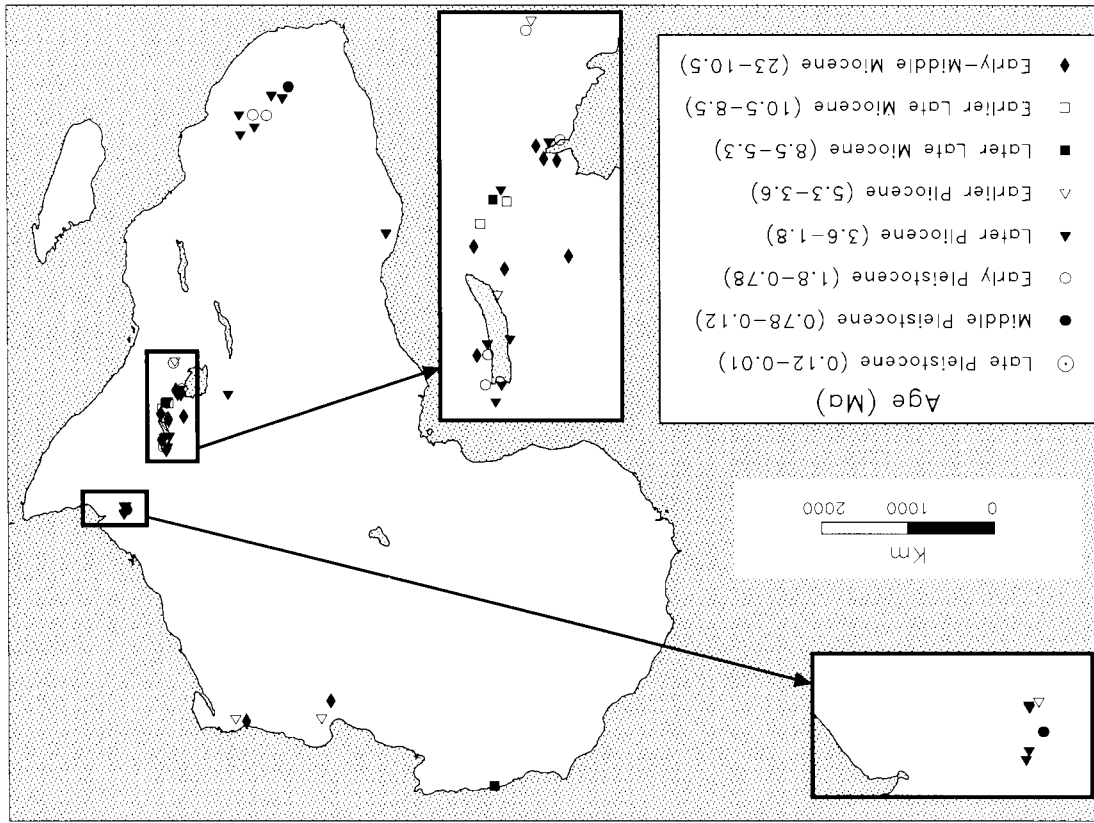
this cooling and a related increase in relative aridity (see Bonnefille, 1984; Coppens, 1989; and many papers in Coppens, 1985). The work of Bonnefille and collaborators (among others) on palynology has allowed careful reconstruction of paleoenvironments at a number of East African sites yielding Plio-Pleistocene hominids (and colobines).

Paleoenvironmental reconstructions

At Laetoli, Tanzania, deposits aged 3.75–3.45 Ma seem to document a mainly open savanna environment, dominated by a variety of grasses indicating a slightly warmer and drier climate than today's (Bonnefille & Riollet, 1987). About 10–15% of the pollen represents tree species, mainly of the Afromontane flora of the East African mountains, of an altitude similar to that of the region today (1500–1800 m). Most (75%) of the plant species are found locally today, indicating that Pliocene floras were essentially modern in composition and diversity. Most individual reports (in Leakey & Harris, 1987) on elements of the Laetoli mammalian fauna, as well as the summary by Harris (1985), agreed with the essentially savanna nature of the assemblage, but Andrews (1989) has reanalysed the data and concluded that the high species diversity suggests a more wooded paleoenvironment than any present in the Laetoli/Serengeti region today. He has further suggested that some faunal mixing might be involved, given the 0.3-Myr span of the deposits, but the high number of primate, giraffe and rodent species still indicates the presence of woodland, perhaps with shifting ecotonal margins. This is not entirely at odds with the work of Bonnefille & Riollet (1987), as they recognized significant tree pollen but thought it represented a restricted ecozone. Cerling (1992) reported $\delta^{13}\text{C}$ values between -0.4 and -0.8% for paleosol carbonates from the Laetoli Beds, which again suggests a flora of mixed C_3 and C_4 type, i.e. grassy woodland with regional variation in canopy closure.

The Hadar deposits (Ethiopia; see Aronson & Taieb, 1986; Tiercelin, 1986) sample lakeside situations dating between 3.35 and 3.0 Ma. Faunas are generally dominated by forest-dwelling mammals in the lower (SH) and upper (KH) horizons but suggest more open environments in the middle (DD) member dated 3.2–3.1 Ma. Bonnefille *et al.* (1987) described a discontinuous series of pollen samples which mainly indicate montane forest and evergreen bushland in the SH and KH members. These floras suggest seasonal climates and environments similar to those found today above 1600 m (about 1000 m higher than the current elevation), with annual rainfall above 800 mm. In the

Figure 2.9. Map of African localities yielding fossil colobines and victoriapithecines, with symbols indicating site ages. Oceans and major lakes stippled; insets provide enlarged views of Awash Valley (Ethiopia) and central Rift Valley (Ethiopia–Kenya–Uganda–Zaire) regions.



DD member, more arid pollen spectra were recovered, indicating extensive savanna with scattered acacia trees and a much lower rainfall.

The Lake Turkana Basin includes a number of fossiliferous regions, of which the most important are the Lower Omo Valley deposits (southern Ethiopia), Koobi Fora (= East Turkana, ex-East Rudolf) and West Turkana (Nachukui Formation), both in northern Kenya. Geology, paleogeography and geochronology were reviewed recently by Harris *et al.* (1988), Brown & Feibel (1989, 1991) and Feibel *et al.* (1989), while paleoenvironments were explicitly evaluated by Feibel *et al.* (1991). Pollen records are poor for these long sequences (mainly dating between 4 and 1 Ma), but Bonnefille & Vincens (1985) summarized their most recent findings. The Omo deposits, mainly riverine and deltaic sediments, record mostly woodland and wooded grasslands of broadly Sudano-Zambezi character. The region may have been relatively moister around 3 Ma and after 1.7 Ma, relatively drier between 2.6–2.1 Ma. Contrary to Bonnefille & Vincens (1985), the more recent dates on this sequence (Feibel *et al.*, 1989) show that the relatively cold and dry interval recorded at Gadeb, in the Ethiopian highlands, between 2.5 and 2.35 Ma coincided with, rather than predated, the Omo drying. From Koobi Fora, lakeshore, riverine and floodplain deposits between 2 and 1.4 Ma yielded far more pollen spectra, representing both local Sudano-Zambezi wooded grassland floras and regional Afromontane forest floras. Before 1.9 Ma, the pollen rain was almost entirely of Graminae (grasses), indicating a relatively more open and perhaps drier environment than found after 1.9 Ma, when the area was characterized as a sub-desertic landscape even somewhat drier than that found locally today. Cerling *et al.* (1988) analysed the isotopic composition of Koobi Fora carbonates, finding that a mixed C₃/C₄ plant assemblage ($\delta^{13}\text{C} = -1.0$ to -0.5%) probably dominated before 1.8 Ma, with a change to mostly C₄ plants ($\delta^{13}\text{C}$ of -0.6 – -0.0% , wooded or dwarf-shrub grassland) after. They further found that major climatic instabilities may have occurred around 3.4–3.1 and 1.8 Ma on the basis of oxygen isotope values. Williamson (1985) had suggested the spread of rainforest into eastern Africa about 3.4–3.3 Ma on the basis of snail distributions at East Turkana, but Bonnefille *et al.* (1987) accepted only the increased evidence of humidity, as their data for Hadar suggested seasonality at that time. No palynological work has yet been reported for West Turkana.

Many authors have employed interpretations of mammalian fossil assemblages to offer paleoenvironmental reconstructions, but Vrba (1980, 1985, 1989) has concentrated on relative percentages of various bovid tribes by reference to their modern adaptations. Shipman & Harris (1989) modified and extended this work to survey all three Turkana Basin sequences. For the

Lower Omo Valley sequence, they found no fossil assemblages equivalent to modern open/arid zones, but instead found mainly closed environments with differing degrees of moisture. The oldest layers studied, between 3 and 2.8 Ma, were moderately wet, followed by drier deposits between 2.8 and 2.3 Ma, then slightly more moist between 2.3 and 2.0 Ma, and younger levels significantly wetter (2.0–1.4 Ma); the resulting climatic pattern agrees well with that reported by Bonnefille & Vincens (see above). Among the most interesting results (not indicated by the authors) is that, except for the driest interval of 2.5–2.4 Ma, most of the levels between 2.8 and 2.0 Ma have no modern counterparts. Almost all of the localities studied from Koobi Fora (and the few of West Turkana) were indicative of a closed and moist habitat, which is rather at odds with the pollen work cited above.

Feibel *et al.* (1991) reviewed these and other lines of evidence in a detailed investigation of local paleoenvironments around Lake Turkana, especially in the Koobi Fora (East Turkana) region. In the older horizons at Koobi Fora, differing results are suggested by the several types of data analysed (flora, mammals, geochemistry), perhaps implying local variation and the presence of both woodland and grassland patches around the lake. Later horizons may indicate several decreases in Omo River outflow (caused by deltaic silting) and temperature increase, leading to more savanna-like conditions.

From the lacustrine deposits of Olduvai Gorge (northern Tanzania), Bonnefille & Vincens (1985) reported a wooded grassland between 1.8 and 1.75 Ma, followed by a very dry interval around 1.75–1.7 Ma and the spread of moist woodlands ('closed/wet' habitats) around 1.6 Ma. Shipman & Harris (1989) discerned the dry interval and considered some of the early levels fairly wet, but they found little evidence for the later forested period, despite having fossils from the same site as the pollen. Cerling (1992) discussed the Olduvai paleoenvironment in terms of $\delta^{13}\text{C}$ values, which showed great variation (-0.8 to -0.1% , probably grassy woodland with mixed canopy closure) in the 1.75–1.7 Ma interval, then a change to more open conditions (-0.5 – -0.0%). Evidence for high C₄ proportions was clearly marked at 1.2 Ma and 0.6 Ma, as well as during the last 200 thousand years.

The East African results reveal that comparisons between even relatively nearby regions are fraught with difficulty. Analyses of the paleoenvironments for the South African cave sites that have yielded both hominids and cercopithecids are even more problematic. Cadman & Rayner (1989) provided one of the few palynological studies, in which they examined a sequence of samples from the Makapansgat site, probably spanning part of the 3.1–2.9-Ma interval. Low in the section there was an increase of arboreal elements, mainly bushveld trees with varying if generally moisture-loving habitats. A

period of open grasslands followed, in turn replaced by dry bushveld, and then a dramatic increase in wet forest elements in the first layers that yielded mammalian fossils. As Cadman & Rayner reported, studies of the mammals have generally implied a relatively moist but open environment in this interval.

In the Sterkfontein (or Blaaubank) Valley to the south, several collapsed caves have also yielded important fossil collections. Vrba (1980, 1985, 1989) has analysed these in terms of relative frequencies of bovid groups, finding a general trend toward more open and dry habitats in a broadly bushveld regime. Thus the Sterkfontein Member 4 site unit, dated roughly at 2.7–2.4 Ma, was thought relatively more closed than the younger Swartkrans Member 1 and Kromdraai A units (estimated to date at 1.9–1.5 Ma). The Kromdraai B unit was thought to be intermediate in age on the basis of the less derived australopith and relatively wet on the basis of the bovids and presence of a monkey (see below). Delson (1984, 1989) questioned the age distinction from the younger group and the monkey-based climatic inference, but the presence of the bovids might thus imply local variation in habitat within that time range. Shipman & Harris (1989) found little difference among the Sterkfontein and Swartkrans subunits they analysed, placing all as open-arid habitats, but Vrba (1989) noted that their analysis was effectively less fine-grained than hers, which included more taxa and compared site units within the admittedly narrow range of habitats in the valley, seeking local differences rather than regional or subcontinental comparisons. Overall, their results appear compatible.

Colobine radiation

With that detailed framework available, it is now possible to examine fossil colobine species and their distributions and look for patterns of habitat utilization. One of the largest of these species was *Rhinocolobus turkanaensis*, known from long-faced male and female crania (see Figure 2.6), numerous jaws, and rare postcranial elements which suggest a rather arboreal habitus (Leakey, 1982) and body size perhaps comparable to that of modern larger species of *Pygathrix* (*Rhinopithecus*). The best representation is in the Omo sequence (M. G. Leakey, 1987), with several good specimens (including partial postcranial elements associated with a mandible fragment) known from Koobi Fora (Leakey, 1982). Unpublished specimens from Hadar (SH and DD members), including four jaws and a partial humerus, appear referable to this species, in the 3.35–3.0 Ma range.

Paracolobus chemeroni (and the quite similar *P. mutiwa*) were shorter-

faced than *Rhinocolobus*, but seem to have had larger teeth and perhaps skulls (see Figure 2.6). Until better comparisons of limb bones and of tooth-to-skull size are available, it is unclear which genus had a larger body size, but they were probably in the same range. A nearly complete skeleton (Figure 2.10) of *P. chemeroni* from the type locality in the Chemeron Formation (probably close to 3.2 Ma – see Delson & Dean, 1993) indicates a mainly arboreal adaptation in the hindlimb and superficially more cursorial-appearing forelimb (Birchette, 1982). *P. mutiwa* is represented all around the Turkana Basin by fragmentary jaws and isolated teeth between 3.5 and 1.9 Ma (M. G. Leakey, 1982, 1987) and by a new partial face and skeleton from West Turkana (c. 2.5 Ma; Harris *et al.*, 1988). A smaller and unnamed species is represented only by dentognathic material at Laetoli (Leakey & Delson, 1987). Laetoli is famous for its mammalian footprints preserved in volcanic ash, and several cercopithecid trails are known (M. D. Leakey, 1987). Skelton (1990) has suggested that one print with a short thumb impression (according to Leakey & Hay, 1979) might represent a colobine, presumably *Paracolobus* sp., which would thus have been at least occasionally terrestrial. However, I

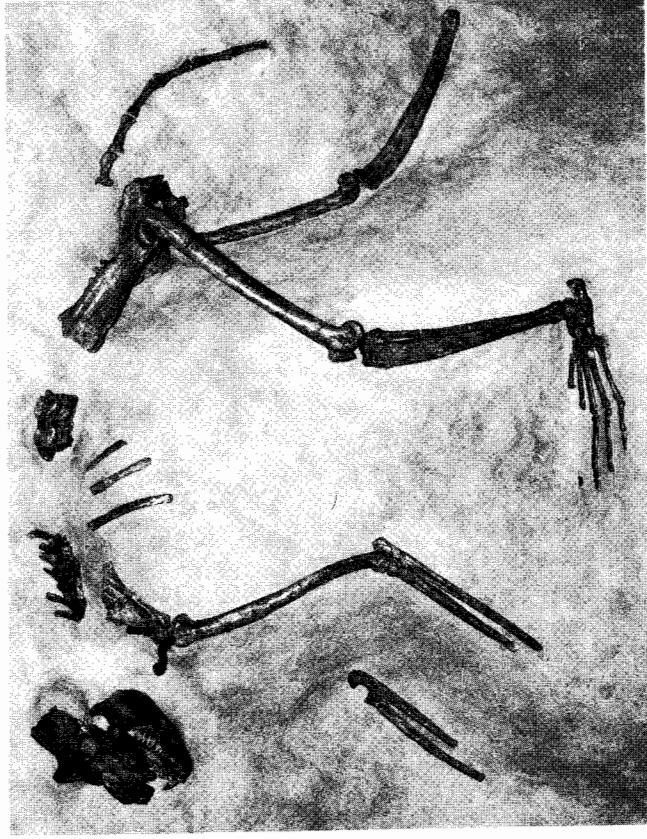


Figure 2.10. Mounted reconstruction of partial skeleton of *Paracolobus chemeroni* from Loc. JM 90, Chemeron Formation, Kenya. Designed (with casts) for Hall of Mammals and Their Extinct Relatives in the American Museum of Natural History.

question the distinctiveness of this trail by comparison with the others, with supposedly longer thumbs.

The third large extinct African colobine, *Cercopithecoides*, is the most common and widespread. In South Africa, *C. williamsi* is represented by numerous craniodental elements (see Figure 2.6) at Makapansgat (c. 3–2.9 Ma), Sterkfontein Member 4 (c. 2.7–2.4 Ma) and Bolts Farm (estimated 2.2–2.0 Ma); a single mandible is also known from the Leba fissure filling in Angola (Delson, 1984). Jaws and a partial associated skeleton apparently of the same species are known from Koobi Fora in the 2.0–1.9 Ma range (Leakey, 1982). They indicate an extreme terrestrial adaptation (Birchette, 1981), supported by the high tooth wear indicative of a diet including gritty food items found at or below the ground surface. No postcranial elements from South Africa have been identified for this species, but given the lack of associations with teeth, they may have been misidentified as baboons. The species was probably comparable in body size to a large *Nasalis larvatus* or smaller *P. (Rhinopithecus)*.

A slightly larger 'variant' of *C. williamsi* has been recovered from the later Sterkfontein Valley sites (2.0–1.5 Ma) of Kromdraai (A and B and nearby Cooper's A) and Swartkrans (provenance and/or identification ambiguous) (Delson, 1984, 1989). The still larger *C. kimeui* (perhaps approaching *Rhinocolobus* in body size) is less frequent but also has heavy dental wear (Leakey, 1982). It is represented by jaws and teeth from Koobi Fora over a long but discontinuous range: c. 3.4–3.3 Ma and 2.0–1.7 Ma, and at Olduvai Gorge by a partial skull from c. 1.65–1.3 Ma and an isolated tooth potentially younger than 1 Ma.

The habitat preferences of these three genera are less clear than might be expected. The Laetoli and earlier Hadar and Omo intervals suggest a wooded and well-watered landscape verging on denser forest, where *Rhinocolobus* and *Paracolobus* occur predictably, given the arboreal adaptations of these taxa, but rarely sympatrically. The presence of *Rhinocolobus* in the more open Hadar DD Member is unexpected, but given the low number of specimens it is not possible to tell if the changing climate led to local disappearance; the species is not recognized from the later KH member which saw a return to woodland habitat. The lack of *Paracolobus* at any Hadar level is surprising, given its locomotor adaptations, perhaps in some ways comparable to (if not as cursorial as) *Semnopithecus entellus*. Both taxa do occur sympatrically in the relatively open habitats of the middle Turkana horizons, with no apparent reduction in frequency at Omo through the cool and dry phase of 2.5–2.1 Ma. Based upon an adaptation to terrestrial locomotion and gritty diet, *Cercopithecoides* would be expected to occur in more open habitats,

such as at Koobi Fora after 2 Ma, in what is characterized by some as open to sub-desertic savanna. Although there may be a trend toward drier conditions through time, all indications point to the southern African Pliocene sites as also representing broadly open and poorly watered habitats. *C. kimeui* may have had a wider habitat tolerance, as it is known from relatively wetter conditions in the early Omo horizons and the later Olduvai levels; I might predict a less cursorial locomotor adaptation on this basis, but no postcrania are yet reported. The general scarcity of primates at Omo in post-2-Ma time renders distribution here less meaningful, although the presence of *Rhinocolobus* in the later forested span is reasonable.

Delson (1973, 1975a; Szalay & Delson, 1979) suggested that *Cercopithecoides* and *Paracolobus* were close relatives, based on preliminary analyses of craniofacial shape, but M. G. Leakey (1982, 1987) has rejected this view. In 1987, she suggested that *Paracolobus* and *Rhinocolobus* shared more recent ancestry and were closely linked to the living colobines, while the more terrestrially adapted *Cercopithecoides* might be specially related to the (semi-) terrestrial European colobines. I would agree with the former hypothesis, and in fact my earliest views combined these two taxa before *Rhinocolobus* was formally named. On the other hand, I would reject the second suggestion without better evidence, as I would Leakey's (1982) conjecture that *Rhinocolobus* might be phylogenetically linked to other 'long-faced' colobines like *Nasalis* or *Libypithecus*.

Both facial elongation and postcranial adaptations to terrestriality have occurred several times within the Cercopithecidae and are not themselves sufficiently unique derived features on which to link taxa. Instead, I would suggest that *Cercopithecoides* is definitely an African colobine, perhaps part of a Pliocene radiation which preceded the differentiation of the modern genera, and thus a possible sister-taxon to *Paracolobus* and *Rhinocolobus* (see Figure 2.2). Interpretation of 'species A' (below) and the Marceau colobine is required before these alternatives can be tested carefully.

Two other extinct forms are smaller than the preceding but larger than most extant African colobines. *Libypithecus markgrafi* is known from a single partial cranium at the North African site of Wadi Natrun (Egypt; see Figure 2.6). It is most comparable to male *Procolobus badius* (Szalay & Delson, 1979), in terms of size and especially sagittal crest development, which is rare in smaller cercopithecids. A colobine of similar dental size was reported at nearby Sahabi, Libya (Meikle, 1987), where apparently colobine postcranial elements are neither strongly terrestrial nor as arboreally adapted as those of living African colobines. Both sites are probably earliest Pliocene in age, c. 5 Ma, and sampled the interface between woodland and savanna.

Another taxon, as yet unnamed and known informally as 'species A', is represented by a partial cranium and robust associated skeleton from the Hadar region, which seems to suggest a (semi-) terrestrial habitus. This site (Leadu) is not well-dated, but closely similar jaws and a humerus fragment were identified from the main Hadar SH Member (3.35–3.1 Ma). None of these fossils have yet been fully published (see Delson, 1984). Some workers have suggested that this probably new species might best be placed in the genus *Libypithecus*, but although a natural endocast is preserved at Leadu, the dorsal surface of the neurocranium is lacking and it is impossible to tell whether a sagittal crest was present. Specimens of comparable size have been tentatively referred to this taxon, although identification is obviously uncertain on size alone, from Laetoli, Omo (c. 3.0–2.5 Ma), and Koobi Fora (c. 2.0–1.8 Ma) (see M. G. Leakey, 1987; Leakey & Delson, 1987). Most of the site units mentioned (except for Koobi Fora and perhaps Laetoli) are relatively tree- or bush-covered and well-watered.

Finally, smaller teeth, comparable to those of living colobines, have been reported from Turkana (c. 1.8–1.0 Ma) and the Kanam East region (Kenya, perhaps 3.5–3.0 Ma; Szalay & Delson, 1979; M. G. Leakey, 1987; Harris & Harrison, 1991). These intervals would all appear to represent at least partially forested habitats.

From the Taung region (northern Cape Province, South Africa), an apparently later Pleistocene collection of about 50 isolated cercopithecoid teeth includes a half-dozen which are identifiably colobine, comparable in size to those of the living taxa. It is not yet possible to allocate them to species or even genus, but from a distributional point of view, their presence in a relatively arid area in association with *Cercopithecus* cf. *aethiops* and *Papio hamadryas* cf. *ursinus* implies the past presence of moister habitats, at least gallery forest, and a significant range extension.

Summary and conclusions

The colobines presumably differentiated from cercopithecines in Africa but exited to Eurasia early in the Late Miocene, perhaps via a wooded savanna 'corridor'. Colobines did not reach eastern Asia until the end of the Miocene. The European genera represent the most terrestrial radiation, if indeed they are closely related to each other. *Dolichopithecus* demonstrates that a terrestrial or cursorial locomotor adaptation does not imply open country habitats, as most fossils can be linked to woodland or subtropical forest; Andrews (personal communication) has noted that because subtropical and temperate forests have generally simple canopies, a large primate would probably be

forced to travel on the ground due to the lack of suitable arboreal pathways between feeding areas. A member of this genus may have reached north-eastern Asia in the later Pliocene, when possible relatives are known in Mongolia, Siberia and Japan. The oldest representative of a modern genus is *Pygathrix (Rhinopithecus) lantianensis* from central China, perhaps just over 1 Myr old.

African Miocene colobines are rather distinctive but poorly known; *Microcolobus* was probably the smallest colobine ever. The Pliocene witnessed a major differentiation of large colobines, with the arboreal *Rhinocolobus*, a terrestrial *Cercopithecoidea*s and perhaps intermediate *Paracolobus*, *Libypithecus* and 'species A'. They inhabited a range of environments, including grasslands and woodlands, although no true moist forest habitats are yet known in the African Plio-Pleistocene record. Fossils possibly referable to modern genera may occur in the Pleistocene.

As opposed to the cercopithecines (see Szalay & Delson, 1979), most extinct colobine taxa cannot be linked to living forms. They are thus archetypally catarrhine: whereas platyrrhine generic lineages extend back into the Middle or even Early Miocene, no catarrhine genus can be traced back beyond 12 Ma (*Pongo* to *Sivapithecus*). Extant cercopithecines and humans, on the other hand, can be linked to later Miocene or Early Pliocene taxa (*Macaca*; *Papio* and *Theropithecus* to *Parapapio*; *Homo* to *Australopithecus*). Colobines apparently underwent 'adaptive radiations' in Europe and Africa, producing a variety of distinctive species that died out, to be replaced by collateral relatives that survive today.

Colobines were never dominant members of the primate fauna except in Europe; in Africa, *Theropithecus* and *Parapapio* were always more common, as was *Macaca* in eastern Asia. The last genus supplanted colobines during the Pleistocene in Europe, probably during early episodes of glacial climatic regime, and in Africa the large colobines of the Pliocene also disappeared by the Early Pleistocene. It is unlikely that early human hunting or habitat interference was related to this disappearance, such effects becoming important only later in the Pleistocene. Only in eastern Asia did colobine variety increase, and there is as yet no clear evidence of the antiquity of that radiation, nor its phyletic fine-structure.

On the other hand, it might be possible to determine whether the African colobines truly represent a monophyletic radiation. The living taxa (see Chapters 1 and 3) are linked by their reduced thumb and mid-tarsal shortening. If animals as different in locomotor adaptation as *Cercopithecoidea*s and *Rhinocolobus* were found to share these features, it would be a strong confirmation of the monophyly hypothesis. Moreover, it was noted above that terrestriality

and facial elongation had apparently evolved independently several times among cercopithecids, including colobines. Although this pair of features occurs together commonly in cercopithecines (*Papio*, some *Theropithecus* and *Macaca*, and *Paradolichopithecus*), they are typically disjunct in colobines: only *Dolichopithecus* presents both, with the highly terrestrial *Cercopithecoides* being relatively short-faced and the more arboreal *Rhinocolobus* and *Nasalis* more 'snouty'. The relatively terrestrial extinct colobines are distinctive in comparison to their modern relatives, and thus they appear to be more common in the fossil record than was probably the case. This apparent frequency is further exaggerated by the prevalence of relatively open habitats sampled, although the Eurasian *Dolichopithecus* implies that forested regions might have been inhabited by more terrestrial colobines (or cercopithecines) as well.

In light of recent discussions (Happel, 1988; Davies, 1991) of the likely diet of ancestral cercopithecids and especially colobines, it is reasonable to suggest that some dietary specializations away from an eclectic cercopithecoid pattern characterized the earliest members of the subfamily. Dental and presumably digestive modifications probably followed soon after, so that by 11–10 Ma, the earliest colobines in Africa and Europe were recognizably colobine in those systems. Thumb reduction appears most likely to have been homologous among colobines; if so, it had also begun by the same time, as *Mesopithecus* is characterized by a thumb relatively shorter than in any cercopithecine, but longer than in living colobines. At present it is not possible to determine the time of origin of such other diagnostically colobine traits as aunting behavior and contrasting natal coats.

Recent paleoenvironmental reappraisals summarized here (Andrews, 1989; Solounias & Dawson-Saunders, 1988; Cerling, 1992) have demonstrated that two of the most widely-cited examples of Late Miocene and Pliocene open-country faunas may be more accurately characterized as woodland assemblages. The Pikermi (and Samos) 'savannas' of Late Miocene southeastern Europe were shown to be probably mixed riparian woodlands on the basis of both palynology and functional morphology of fossil bovids (but compare de Bonis *et al.*, 1992). The mid-Pliocene Laetoli assemblage from Tanzania has indicators of species diversity typical of discontinuous seasonal forested environments, and its paleosol carbonates yield $\delta^{13}\text{C}$ values indicative of mainly C_3 plants, i.e. woodland. It appears from these studies that open, nearly treeless plains are quite a recent feature of the landscape in Europe as well as Africa (although not farther east, where C_4 grasslands are known in Pakistan back to 6 Ma – Quade *et al.*, 1989; Cerling *et al.*, 1993). Some of the increase in open environments is presumably due to human activity,

especially burning. As a typical catarrhine, *Homo* replaces many contemporaneous primates one way or another.

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