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Middle Miocene Dispersals of Apes

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Key Words

Migration • Africa • Turkey • Paşalar • Palaeo-ecology • Phylogeny • Hominoidea • Hominidae • Fossil

Abstract

The earliest record of fossil apes outside Africa is in the latest early Miocene of Turkey and eastern Europe. There were at least 2, and perhaps 4, species of ape, which were found associated with subtropical mixed environments of forest and more open woodland. Postcranial morphology is similar to that of early Miocene primates and indicates mainly generalized arboreal quadrupedal behaviours similar to those of less specialized New World monkeys such as *Cebus*. Robust jaws and thick enamelled teeth indicate a hard fruit diet. The 2 best known species of fossil ape are known from the site of Paşalar in Turkey. They have almost identical molar and jaw morphology. Molar morphology is also similar to that of specimens from Germany and Slovakia, but there are significant differences in the anterior teeth of the 2 Paşalar species. The more common species, *Griphopithecus alpani*, shares mainly primitive characters with early and middle Miocene apes in Africa, and it is most similar phenetically to *Equatorius africanus* from Maboko Island and Kipsaramon. The second species is assigned to a new species of *Kenyapithecus*, an African genus from Fort Ternan in Kenya, on the basis of a number of shared derived characters of the anterior dentition, and it is considered likely that there is a phylogenetic link between them. The African sites all date from the middle Miocene, similar in age to the Turkish and European ones, and the earliest emigration of apes from Africa coincides with the closure of the Tethys Sea preceding the Langhian transgression. Environments indicated for the African sites are mixtures of seasonal woodlands with some forest vegetation. The postcrania of both African taxa again indicate generalized arboreal adaptation but lacking specialized arboreal function. This middle Miocene radiation of both African and non-African apes was preceded by a radiation of arboreal catarrhine primates in the early Miocene, among which were the earliest apes. The ear-

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liest Miocene apes in the genus *Proconsul* and *Rangwapithecus* were arboreal, and because of their association with the fruits of evergreen rain forest plants at Mfwangano Island, it would appear that they were forest adapted, i.e. were living in multi-storied evergreen forest. The same or similar species of the same genera from Rusinga Island, together with other genera such as *Nyanzapithecus* and the small ape *Limnopithecus*, were associated with plants and animals indicating seasonal woodland environments, probably with gallery forest forming corridors alongside rivers. While the stem ancestors of the Hominoidea were almost certainly forest adapted, the evidence of environments associated with apes in the later part of the early Miocene and the middle Miocene of East Africa indicates more seasonal woodlands, similar to those reconstructed for the middle Miocene of Paşalar in Turkey. This environmental shift was probably a requisite for the successful emigration of apes out of Africa and made possible later movement between the continents for much of the middle Miocene, including possible re-entry of at least one ape lineage back into Africa.

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Introduction

Early evidence of ape evolution is restricted to Africa, and the earliest evidence for apes outside Africa comes from Europe at around 15–17 million years (Ma) ago. The generally held assumption is that their occurrence there is the result of dispersal from Africa. The aim of this paper is to examine the phylogenetic evidence for this event and to investigate its ecological background. A second aim is to consider the possibility of the return of apes to Africa in both the middle and late Miocene [Begun, 2000, 2001].

Evidence from Europe in the Middle Miocene

Central to the discussion of the dispersal of apes out of Africa are two European sites, Engelswies in Germany and Paşalar in Turkey. Engelswies has a single hominid molar found by Heinz Tobien in the 1970s but not described until 2001 [Heizmann and Begun, 2001]. The fossils occur in freshwater limestones of the upper Molasse sequence in Germany, preceding the Langhian transgression dated to between 16.5 and 14.9 Ma. There is a good small mammal record from the site, attributable to MN5 mammal stage, and a fragmentary large mammal fauna from a different depositional level, the latter including the single hominid tooth. This is a fragment of M3 worn nearly flat, but it is apparent that the tooth had thick enamel and a low dentine relief, for dentine exposure on the occlusal surface is limited despite the heavy wear. It is similar in this respect to an upper molar from Děvinská Nová Ves in Slovakia [Glässner, 1931; Holec and Emry, 2003], which is now attributed to *Griphopithecus darwini* [Martin and Andrews, 1993; Kelley, 2002]. There is little morphological detail on the Engelswies molar, but its similarity to *G. darwini* led Heizmann and Begun [2001] to attribute it to an indeterminate species of *Griphopithecus*, a conclusion that is generally accepted.

There are also 2 lower molars from Děvinská Nová Ves that are extremely similar to the lower molars from Paşalar in Turkey. Early excavation at the Paşalar site

(again by Heinz Tobien) produced a collection of 86 isolated hominid teeth, which were originally assigned to 2 existing species, *Sivapithecus darwini* (now *G. darwini*) and *Ramapithecus wickeri* (now *Kenyapithecus wickeri*) [Andrews and Tobien, 1977]. Further excavations commenced in 1983 and have continued to the present day, resulting in the recovery of a large number of specimens [Alpagut et al., 1990; Martin and Andrews, 1993; Gençtürk et al., in press; Kelley et al., in press]. One species is more common ($n = 1,668$ specimens, MNI = 80 individuals) and is now assigned to *Griphopithecus alpani* [Martin and Andrews, 1993], the type specimen of which comes from the approximately contemporaneous site of Çandır in central Turkey [Tekkaya, 1974], and the second species ($n = 64$ specimens, MNI = 8 individuals) is assigned to a new species of *Kenyapithecus* [Kelley et al., in press].

The age of the fossiliferous deposits at Paşalar is based on faunal correlations and is attributed to mammal stage MN5/6. Over half the species identified at Engelswies are also found at Paşalar, although the Paşalar fauna is more than double the size of the Engelswies fauna (59 species compared with 27). Some of the Paşalar and Çandır faunal elements correlate with MN5 or even MN4b [Sen, 1990] and some with MN6 [Fortelius and Bernor, 1990], and the age of all three sites is suggested by Begun et al. [2003] to be about 16–16.5 Ma: a summary of correlations for each major taxonomic group is given in Bernor and Tobien [1990].

The morphology of *G. alpani* has many similarities with a group of African middle Miocene apes [Andrews and Tobien, 1977; Kelley and Alpagut, 1999; Ward et al., 1999; Kelley, 2002]. The central incisors have a median pillar on the lingual side; the upper lateral incisors are asymmetrically conical and small, while the lower lateral incisors are asymmetrical and larger than the centrals; the lower canines are relatively low crowned and robust with a double distal ridge producing characteristic wear patterns on the apex and distal ridges, leaving an island of enamel exposed in the middle of the distal surface; the upper canines are also low crowned and are mesiodistally symmetrical; the lower third premolars lack continuous cingula but have a pronounced mesial beak which is almost certainly cingular in origin; the upper third premolars are asymmetrical, with the buccal cusp much larger than the lingual one; the upper molars have low, rounded cusps, a low dentine relief and thick enamel, with M^2 being the largest tooth; the lower molars retain at least a partial buccal cingulum, which is sometimes pronounced and continuous. Many of these characters are shared with *Equatorius africanus* from Africa, but as will be discussed below they are mostly considered to be primitive retentions from early Miocene apes such as *Proconsul*. As such they provide an indication of geographic continuity between apes in Turkey and East Africa, but they do not indicate a cladistic relationship between them (but see further below).

The morphology of the species from Paşalar attributed to *Kenyapithecus* is distinct (fig. 1) [Andrews and Tobien, 1977; Alpagut et al., 1990; Kelley, 2002; Kelley et al., in press]. The central incisors lack the median pillar but instead are broader and have prominent mesial and distal marginal ridges converging at the base of the crown in a V shape depression; the upper lateral incisors are relatively small and more symmetrical than in *G. alpani*; the lower incisors also have distinct marginal ridges meeting cervically in a sharp V; the male upper canines bear a buccal cingulum; the P_3 has a continuous lingual cingulum; the upper and lower canines have relatively more slender and higher crowns, and the upper premolars have distinct and unbroken transverse crests. In contrast to these differences in the anterior den-

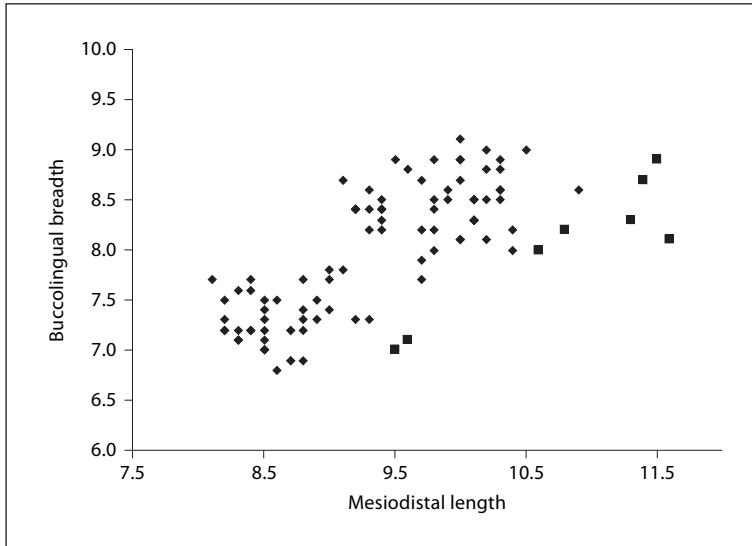


Fig. 1. Size and shape variation in the two hominid species from Paşalar. Length/breadth measurements (mm) are shown for the I¹ sample, with the specimens of *Kenyapithecus* sp. shown as squares. Both species have similar ranges of variation, but the *Kenyapithecus* incisors are generally wider mesiodistally and at the upper end of the range of the sample of *G. alpani*.

tition, no definitive differences have yet been identified in molar morphology between any of the ape species from Paşalar, Děvinská Nová Ves and Engelswies, and, apart from the lower molar cingula, there is little difference from other Eurasian ape species such as *Sivapithecus* and *Ankarapithecus*, or from middle Miocene apes from Africa. No differences were found in molar microwear within the Paşalar sample [King et al., 1999], and there is also little difference in maxillary morphology, in so far as it is known: the 2 Paşalar species share robust and moderately deep maxillary alveolar processes, with a degree of robusticity that is similar to that of *K. wickeri*. In addition to being elevated, the floor of the maxillary sinus in the *Kenyapithecus* species is restricted in area and relatively flat, lacking the compartmentalization evident to varying degrees in many other taxa. The zygomatic process originates high above the alveolar margin. No mandible has yet been identified for the *Kenyapithecus* species from Paşalar, but several mandibles attributed to *G. alpani* have robust mandibular bodies and massively robust mandibular symphyses.

Palaeo-Ecology of the European Sites

Ecological reconstruction of the site at Engelswies is based on several lines of evidence all indicating subtropical evergreen forest, although it should be noted that this evidence comes from different stratigraphic levels. The deposits consist of a sequence of freshwater limestones [Kempf and Matter, 1999], with small mammals at one level, large mammals from another level several metres below and plant remains from yet another level. The plant remains are particularly interesting, for they pro-

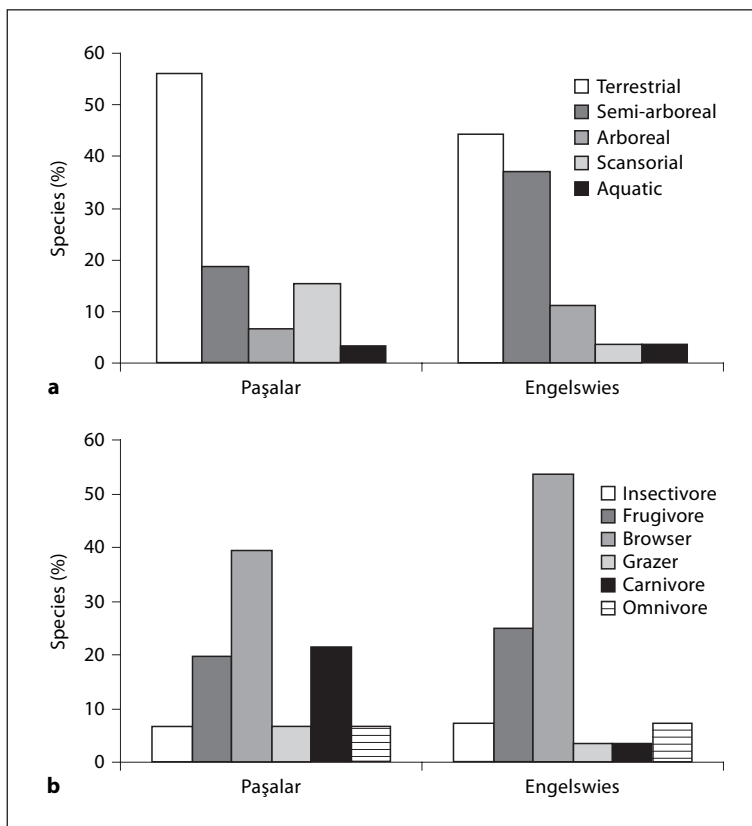


Fig. 2. Distributions of locomotor (a) and dietary categories (b) in the faunas from Paşalar and Engelswies. The vertical axis shows the percentage numbers of species in each category. See text for explanation.

vide evidence of an evergreen laurophyllous flora [Schweigert, 1992] growing in a subtropical humid climate. This is a relic of the oak-laurel-palm forests that extended across southern Europe during the Palaeogene and early Neogene [Axelrod, 1975], which suggest monsoonal climates, with warm, wet summers and frost-free winters. Lower temperatures across Europe and the change to a pattern of winter rainfall have resulted in the replacement of laurel forests with sclerophyllous evergreen and broad-leaved deciduous forests, but during the middle Miocene it is inferred that subtropical conditions persisted, at least in places such as Engelswies.

Analysis of the community structure of the fauna from Engelswies [Heizmann and Begun, 2001] has been based on a composite fauna of large and small mammals, even though they are found in different levels. Even combining the two sets, the Engelswies fauna is small and only partially representative of the original fauna, and there is no information on the taphonomic bias affecting the fossil assemblages. Bearing these limitations in mind, figure 2 compares the Engelswies fauna with that

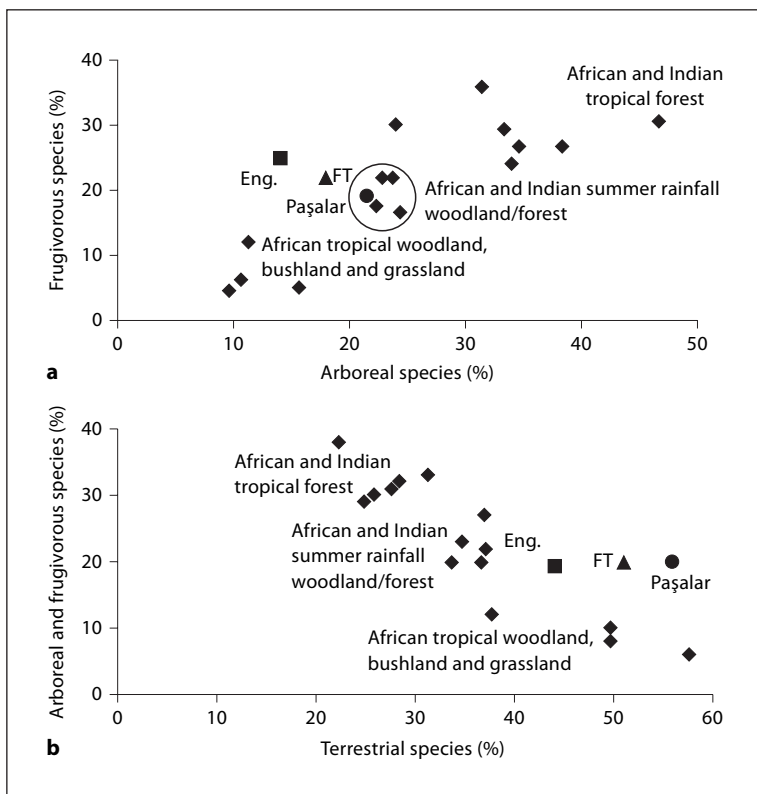


Fig. 3. Bivariate plots comparing dietary guilds with locomotor functions. Proportions of frugivorous species are plotted against proportions of arboreal species (a), and arboreal frugivores are plotted against proportions of terrestrial species (b). Both show a series of recent faunas ($n = 15$, diamonds) and fossil faunas (squares): Eng. = Engelswies, FT = Fort Ternan, and Paşalar. The 15 points for the recent faunas are averages derived from 44 single faunas listed in Andrews and Humphrey [1999, table 20.1].

from Paşalar. Terrestrial species have highest representation in both faunas but only slightly higher than semi-arboreal species in the Engelswies fauna. Arboreal species are relatively abundant in both. Browsing herbivores dominate, with few grazers, but frugivores are also well represented. The similarities between the two fossil faunas are shown in figure 3, where they are shown to fall into an intermediate position between tropical forest and open bushland or grassland, and closest to subtropical or summer rainfall woodlands and forest. These patterns suggest an environment with plentiful fruit and browse but little grass. They also suggest substrates with trees, but not multi-canopied as in tropical forest. They instead indicate more open canopies, with movement of arboreal species probably being mainly along the ground. This is consistent with the evidence from the Engelswies flora for monsoonal (i.e. seasonal summer rainfall) forests which are generally single canopied and which have a long dry season.

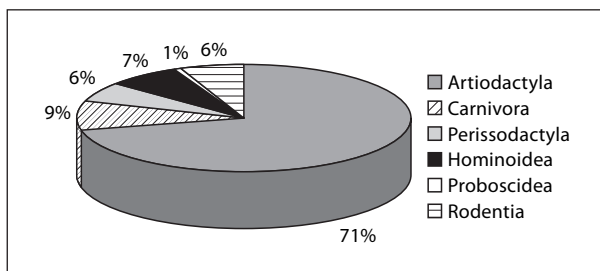


Fig. 4. Distribution of major taxonomic units in the Paşalar fauna based on numbers of specimens ($n = 24,885$).

There are no plant remains at Paşalar, but there is a large mammalian fauna from a single stratigraphic horizon, with good evidence from taphonomy, sedimentology and isotopes. The fauna [Andrews, 1990; Bernor and Tobien, 1990] contains 59 species and is dominated by terrestrial species, but also with many arboreal species (fig. 3). The most common species was the artiodactyl *Caprotragoides stehlini*, which constitutes nearly half of the specimens. Bovids, giraffids, rhinos and horses were also abundant and contribute to the high terrestrial component of the fauna (fig. 4). The distribution of dietary categories of the Paşalar fauna is similar to that of Engelswies, both dominated by browsing herbivores but with substantial numbers of frugivores as well. On the other hand, there were at least 2 species at Paşalar with hypsodont teeth, and the isotope signals from dental enamel indicate that both were mixed feeders inclining more towards C_4 plants [Quade et al., 1995]. The adaptive profile of the Paşalar fauna is closest to present-day faunas from subtropical monsoon forests of India (fig. 3), with intermediate levels of arboreal and frugivorous species. The structure of the carnivore guild at Paşalar supports the same conclusion [Viranta and Andrews, 1995]. The sedimentology of the fossiliferous sediments at Paşalar also suggests a highly seasonal climate, with gleyed horizons indicating seasonal waterlogging and abundant calcareous nodules indicating a pronounced dry season [Bestland, 1990].

The conclusion from several independent lines of inquiry is therefore that the environment in middle Miocene times at Paşalar was a subtropical woodland or forest – with a single tree canopy, abundant ground vegetation and incorporating open areas – set in highly seasonal environments with summer rainfall (monsoon) and a long dry season. Whether the vegetation was taxonomically similar to the laurel forests of Engelswies we cannot say in the absence of plant fossils at Paşalar, but structurally the types of vegetation would have been similar at the two sites. It may also be inferred that the availability of food would have been similar, with the degree of seasonality restricting soft fruit availability to the wetter months so that other foods would have had to be consumed during the cooler dry season [Richards, 1957; White, 1983]. Likewise, the mixture of substrates would have been similar at the two sites, with the single canopy restricting tree-to-tree movement for larger arboreal animals and the existence of more open areas making necessary some degree of movement on the ground.

Evidence from Africa during the Middle Miocene

Evidence of fossil apes from the middle Miocene of Africa is considered for 3 sites of approximately similar age, Maboko Island, Fort Ternan and Kipsaraman. These are the only fossil ape sites that have adequate analyses of palaeo-ecology, although a fourth site, Nachola, has good fossil material [Ishida et al., 1999]. Maboko Island is the type site of *E. africanus*, represented by a mandible, maxilla, some postcrania and isolated teeth [Benefit and McCrossin, 1989, 1993]. Formerly attributed to *Kenyapithecus* [Leakey, 1967], it was assigned to a new genus by Ward et al. [1999] when new material from Kipsaraman in northern Kenya was described. *E. africanus* is a species with robust mandibles having an elongated symphysis, upper central incisors that are relatively broad with a low, broad lingual tubercle and cingulum, asymmetrical upper lateral incisors, enlarged premolars and molar teeth with thick enamel, traces of cingulum and a low dentine relief. *E. africanus* is similar to *K. wickeri* from Fort Ternan in postcanine dental morphology, but there are many differences in other aspects of dental and maxillary morphology that we interpret to be phylogenetically significant [Ward et al., 1999; Kelley et al., 2000; Kelley et al., in press]. The upper central incisor of *K. wickeri* is relatively very broad, with large lingual mesial and distal marginal ridges bounding a thickened central area and no lingual tubercle or pillar, the lower canine crown is slender and high-crowned, the upper premolars are relatively symmetrical, and P_3 has a continuous lingual cingulum. These are considered to be derived characters relative to *E. africanus* based on the morphology seen in early Miocene African apes with the possible exception of the P_3 cingulum.

The nature of the differences between *E. africanus* and *K. wickeri* strongly suggest that they belong to two separate lineages [Ward et al., 1999; Kelley et al., 2000; Ward and Duren, 2002]. *E. africanus* shares many characters with slightly earlier fossil apes such as *Nacholapithecus* as well as with *Proconsul* from the early Miocene, differing mainly in the greater robusticity of the jaws, enlarged premolars and thicker enamel and reduced cingulum on the molars. *K. wickeri* shares few characters with earlier Miocene apes, differing from them in the same suite of dental characters that distinguish it from *E. africanus*. On present evidence, therefore, the species of *Equatorius* and *Kenyapithecus* provide the best evidence of possible middle Miocene relationships with European immigrant apes (see also Guleç and Begun [2003]). The question can now be addressed of the possible phylogenetic links between the African and European middle Miocene apes. This is presented here as two comparisons for which environmental evidence is sufficiently complete.

Kenyapithecus wickeri and *Kenyapithecus* New Species from Paşalar

Some of the characters described above distinguishing *K. wickeri* from *E. africanus* were identified as derived relative to the earlier Miocene apes, namely the characters of I^1 , lower canines and the P_3 . These characters of the dentition are however shared with the species of *Kenyapithecus* from Paşalar and are part of the basis for assigning the new Paşalar species to this genus. Many additional characters of *Kenyapithecus* sp. from Paşalar are known that appear to be primitive retentions, such as the short naso-alveolar clivus, broad incisive foramen and the morphology of the mandible. The degree of similarity is such that it is difficult to distinguish the Paşalar species from *K. wickeri* except on minor details of dental morphology [Kelley et al., in press], the main characters being I^1 marginal ridges that meet in a dis-

tinct V close to the base of the crown, I² with symmetrical mesial and distal margins, I₁ and I₂ with distinct mesial and distal marginal ridges that join at the base of the crown in a sharp V, upper canines with a distinct buccal cingulum, P³ and P⁴ with transverse ridges linking the buccal and lingual cusps.

The sharing of a suite of derived characters provides evidence of a *phylogenetic link* between the fossils from Fort Ternan and Paşalar and is the basis for their being congeneric. In addition, they provide evidence for a geographic connection between East Africa and Europe during the earliest middle Miocene. The lack of fossil evidence of hominoids in Europe prior to the middle Miocene, despite large numbers of richly fossiliferous sites, leads to the conclusion that this phylogenetic/palaeogeographic connection was the result of dispersal from Africa to Europe during the earliest middle Miocene or late early Miocene.

Equatorius africanus and *Griphopithecus* Species

In contrast to the comparison of the two *Kenyapithecus* species, *E. africanus* and *G. alpani* have not been found to share uniquely any derived morphological characters. They share many primitive characters of the dentition with each other, and many of the characters, such as robust mandibles and maxillae, thick enamel on the molars and enlarged premolars, are also shared with the African clade Afropithecinae [Andrews, 1992]. There is therefore no evidence of sister group relationship of *Equatorius* and *Griphopithecus* species. On the other hand, Afropithecinae, as indicated here, had a range spanning Africa and Europe and also provides evidence of migrations between the two continents during earliest middle Miocene or late early Miocene.

Palaeo-Ecology of the African Middle Miocene Apes

Having established the phylogenetic and/or geographic links between middle Miocene apes in Africa and Europe, the ecological background within which these migrations took place will now be examined. There are three stages that can be recognized in the ecological record of East Africa.

Stage 1

The early Miocene flora from Mfwangano Island has many forest affinities in association with fossil remains of *Proconsul* and *Rangwapithecus* species. The flora is dominated by the forest genus *Celtis*, with *Terminalia*, *Antrocaryon* and species of Rubiaceae; large emergent forest trees are represented in the flora by *Entandrophragma* and *Sterculia* [Collinson, 1985]. The general conclusion for the Mfwangano flora, which is located in the Kiahara Formation and is dated to earlier than 19.5 Ma [Bishop et al., 1969], is that it represents multi-canopied evergreen forest in large part, with areas of semi-evergreen forest. Slightly later in time are two sites younger than 19.6 Ma, Songhor and Koru. Both have several species of fossil ape, notably *Proconsul major* and *Rangwapithecus gordonii*, as well as smaller species of *Micropithecus* and *Limnopithecus*. Their environments have been reconstructed as evergreen multi-canopied forest [Evans et al., 1981; Andrews, 1992, 1996; Andrews et al., 1997] on the basis of the community structure of their mammalian faunas.

Stage 2

The flora from the Hiwégi Formation on Rusinga Island contrasts with that of Mfwangano Island in that no species have yet been found that are unequivocally large forest trees [Collinson, 1985]. There is a large and diverse flora of trees, shrubs and climbing plants [Chesters, 1957]. Plants with thorns make up a small percentage (3.5%) of specimens at the so-called 'fruit and nut bed', a site rich enough to enable a full quantitative analysis to be made, and grasses were absent. The dominant genera are similar to those found in the same area today, representing the deciduous woodlands fringing Lake Victoria, e.g. species of *Ziziphus*, *Terminalia*, *Lannea*, *Grewia*, *Cordia*, with several genera of herbaceous and woody climbers. The conclusion from this flora, which is dated to approximately 18 Ma [Van Couvering and Miller, 1969] is that it represents disturbed woodlands bordering a large river, disturbance perhaps by volcanic activity. Structurally, the woodlands were single-canopied with a dense ground vegetation of herbs and bushes. It may also represent a river flood plain, as the sediments are overbank deposits on a large flood plain [Bestland and Retallack, 1993]. Numerous fossil apes and primitive catarrhines in at least 4 genera (*Proconsul*, *Nyanzapithecus*, *Limnopithecus*, *Dendropithecus*) have been found in the Rusinga deposits, although none associated directly with the fruit and nut bed. The *Proconsul* species from Rusinga are *P. heseloni* and *P. nyanzae*, different from the stage 1 species *P. africanus* and *R. gordonii*, although *P. nyanzae* is common to both.

Stage 3

The third ecological stage is the one associated with the middle Miocene apes from East Africa discussed above. The Fort Ternan fauna (approx. 14 Ma) appears to have been derived from mixed sources [Shipman, 1986] and the main part of the fauna, including *K. wickeri*, is dominated by large terrestrial mammals. Two species of bovid make up over 50% of the mammal assemblage, with browsing and frugivorous herbivores being the two most abundant dietary categories (fig. 5). A minor component of the fauna has different taphonomic modifications, including the fragmentary remains attributed to *Proconsul*, and was probably transported from some distance from the site. The majority of specimens represent the habitat close to the fossil site, which has been identified as 'open habitat or savannah' [Shipman et al., 1981; Shipman, 1986]. Analysis of the ecological diversity indicates that the vegetation type within the savannah biome was deciduous woodland [Andrews et al., 1979; Evans et al., 1981; Shipman, 1986; Cerling et al., 1991; Kappelman, 1991], and it is clear from the work of Retallack [1991, 1992] that a variety of wooded grassland and early successional woodland was present at the site, with perhaps some tropical montane forest nearby.

The fauna from Maboko Island is too incomplete to analyse its community structure. The abundance of monkeys at the site [Benefit and McCrossin, 1989] suggests some form of seasonal wooded environment, while the analysis of habitat spectra based on all available species suggests woodland with some forest patches [Evans et al., 1981]. On the other hand, the adaptations for terrestriality of the fossil monkeys and possibly also the fossil apes [Benefit and McCrossin, 2002] suggest a more open environment for this site, but even the most terrestrial of monkeys living today cannot survive far from trees/cliffs for protection from predators. There is no indication of tropical forest at any stratigraphic horizon at Maboko based on present evidence.

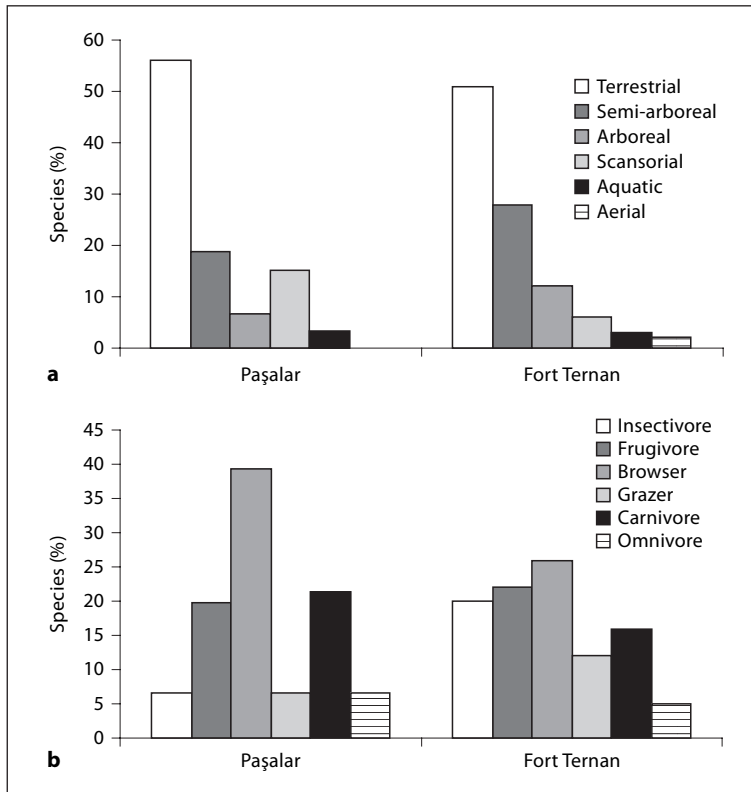


Fig. 5. Distributions of locomotor (a) and dietary categories (b) in the faunas from Paşalar and Fort Ternan. The vertical axis shows the percentage numbers of species in each category. See text for explanation.

There is little direct evidence of the environments at Kipsaraman, despite extensive excavations there [Pickford, 1988; Hill, 2002]. The fauna from the main bone bed is moderately diverse (21 species) and has many similarities with the Maboko fauna, dated to 15.6 Ma [Behrensmeyer et al., 2002]. The bone bed at Kipsaraman is interpreted as a fluvial influx into a shallow lake, the fossils having accumulated upstream as an attritional assemblage [Behrensmeyer et al., 2002]. The original accumulation, which includes the *E. africanus* remains, evidently sampled different environments, since pedetid spring hares are associated with anomalurid flying squirrels. The most that can be said is that there are indications of both open habitat (favoured by spring hares) and forest (favoured by anomalurids).

There are several explanations possible for the observed environmental change from evergreen tropical forest in stage 1, to deciduous woodland with gallery forest in stage 2 and to seasonal woodland in stage 3. One is that it is coincidence, that the earliest Miocene sites happen to sample forest habitats while middle Miocene sites sample woodland habitats. There is no way of testing this other than to include many additional sites. Conversely, the observed change could reflect a real temporal change in

climate, but what kind of change? Emphasis has been placed on global cooling [Vrba, 1985], but there is increasing recognition now that the amount and seasonality of rainfall are more critical for both animals and plants [O'Brien, 1993, 1998; Andrews and O'Brien, 2000]. Reduction in rainfall, or an increase in the seasonality of rainfall, could be implicated in the environmental change observed in East Africa from the early to middle Miocene [Kingston, 2005]. Temperature reduction alone would not appear to be the cause of these changes, for reduced annual temperatures would actually increase water availability in tropical ecosystems by reducing evaporation and transpiration in plants. Nevertheless, the fact remains that fossil apes in the middle Miocene have been found associated only with non-forest environments, deciduous woodlands that *structurally* would have had many similarities with the single-canopied subtropical woodlands and forests present at that time in the middle Miocene of Europe [Suc, 1999].

Direction and Nature of Dispersals

Two lines of evidence suggest that the initial dispersal of apes occurred at the beginning of the middle Miocene and was an emigration out of Africa. The fossil record demonstrates an extensive radiation of apes in Africa before approximately 17 Ma, and phylogenetically these early Miocene apes retain certain characters predicted for the common ancestor of apes and monkeys. Ecologically they have been found associated with tropical forest environments of a kind that had not existed in Europe since the Eocene [Collinson, 1983; Collinson and Hooker, 1987]. The faunas from Europe and Asia during the early Miocene are devoid of fossil apes. On this evidence, it appears that *Kenyapithecus* and *Griphopithecus*, or their ancestors, originated in Africa and dispersed into Europe at the beginning of the middle Miocene, an event made possible by the adaptive shift in early Miocene hominids from being forest dependent to being adapted for life in more open, seasonal woodland and forest. This may have involved both taxa, but it is more likely that the first dispersal was restricted to the more primitive *Griphopithecus* (from Africa to Europe) and was followed by the return to Africa of the more derived *Kenyapithecus* (Europe to Africa; fig. 6). In other words, *Kenyapithecus* could have emerged in Europe, specifically perhaps in Turkey and perhaps from some member of the afropithecine clade, and it then re-entered Africa after the Langhian transgression (approx. 14 Ma) to appear about 2 Ma later at Fort Ternan. We have no evidence one way or the other on this issue, for the species of *Kenyapithecus* appear equally derived in both the African and the Eurasian fossil ape radiations, but the similarities in the environment in both regions make movement between them possible, and evidence on timing of the African and European sites makes it necessary to consider this point further [Begun et al., 2003].

A final point concerns the late Miocene disparity in the ape fossil record. After the Fort Ternan fossil record (14 Ma), fossil apes are represented in the African Miocene by a few fragmentary fossils: single teeth from Ngorora and Lukeino, the maxilla of *Samburupithecus*, and a number of specimens presently attributed to Hominini such as *Orrorin* and *Sahelanthropus* [Ward and Duren, 2002]. In contrast, there is an abundance of fossil apes in the late Miocene of Europe and Asia [Kelley, 2002], including the postcranially derived species of *Dryopithecus*. This has led to the suggestion that the great ape and human clade originated in Eurasia and that members of this clade dispersed from there into Africa towards the end of the late Miocene [Begun,

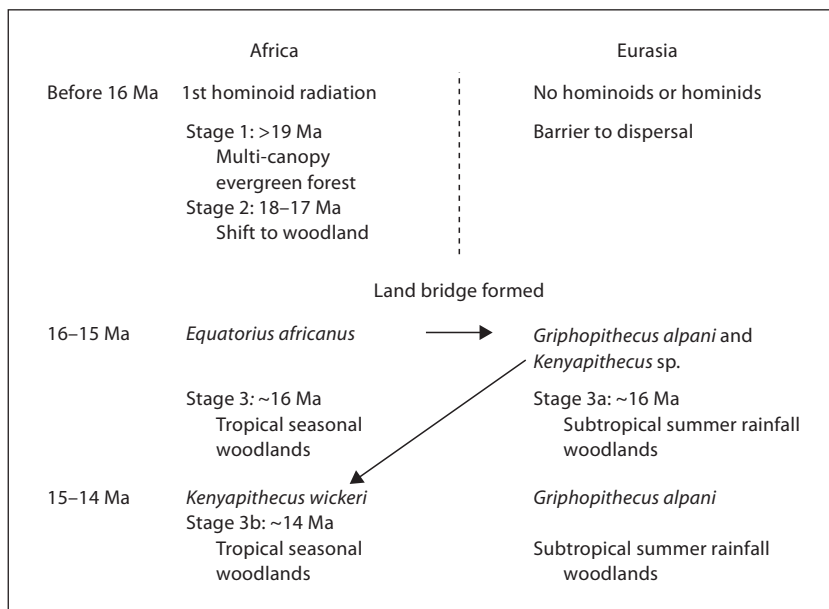


Fig. 6. Probable dispersals of middle Miocene apes between Africa and Europe. The lines indicate directions of dispersal and do not necessarily imply phylogenetic links.

1992, 1994, 2000]. This suggestion cannot be dismissed out of hand, but it should be pointed out that the absence of evidence from Africa during the late Miocene does not necessarily support this idea, for this absence may be due to a paucity of fossil sites, not absence of apes from an abundant fossil record (but see Begun [2001, 2005]).

Conclusions

E. africanus from Africa and *G. alpani* from Turkey appear to be part of a single hominid radiation, perhaps part of the Afropithecinae clade, which includes earlier Miocene apes such as *Afropithecus* and *Nacholapithecus* [Andrews, 1992]. The presence of a European member of this clade in deposits postdating African species suggests emigration out of Africa into Europe during the latest early Miocene. The exact date of this event is uncertain, but it may have preceded the Langhian transgression (16.5–14.9 Ma [Steininger, 1999]), when the brief expansion of the Tethys cut off Africa from Eurasia [Heizmann and Begun, 2001].

Kenyapithecus provides clearer evidence for a phylogenetic link between middle Miocene apes from Africa and Europe, with closely related species of this genus from both Kenya and Turkey. The Kenyan site of Fort Ternan is dated to 1–2 Ma later than Paşalar in Turkey, but because the fossil ape record prior to the middle Miocene was exclusively African, it is generally assumed that this similarity is due to emigration of apes, including *Kenyapithecus*, from Africa to Europe early in the middle Miocene.

While the appearance of apes in Europe in the earliest middle Miocene is certainly the result of African emigration, it is possible that *Kenyapithecus* was not part of this emigration, but instead the genus evolved as a derived taxon in Europe, e.g. at Paşalar, and re-entered Africa in post-Langhian times as suggested by Begun et al. [2003].

Evidence available at present on the environments associated with fossil apes in Africa appears to show a shift from multi-canopied evergreen forest in the earliest Miocene (floras and faunas from Mfwangano Island, Songhor and Koru, all in Kenya) to deciduous woodlands, with forest patches and riverine vegetation later in the early Miocene (floras and faunas from Rusinga Island, Kenya), and finally to the middle Miocene seasonal woodlands at Fort Ternan and Maboko Island.

The middle Miocene environments at Fort Ternan and Maboko Island have been shown to be similar to those of the European sites at Engelswies and Paşalar in terms of their inferred vegetation structure. Climate seasonality would have been greater in the subtropical European sites, and fruit availability would have been more highly seasonal, but the environments in Africa and Europe were sufficiently similar for the morphologically and adaptively similar pairs of apes (*Equatorius/Griphopithecus* and *K. wickeri/Kenyapithecus* sp.) to have moved between them with no impediment. Apart from the initial movement of apes out of Africa, there is no direct indication as to the direction of dispersal, but we recognize the possibility of origin of *Kenyapithecus* in Europe and its later dispersal to Africa, which finds some indirect support at least in the patterns of movement of other mammals during this period [Begun et al., 2003].

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