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# Dispersal patterns of Eurasian hominoids: implications from Turkey

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A key to understanding the complex pattern of hominoid dispersals, origins, and extinction is the fossil evidence from Turkey. Miocene localities in Turkey are known to contain taxa from across Eurasia and Africa, and even North America. Three or four separate hominoid clades are identified in Anatolia, more than in any other place except Kenya. Each of these clades has its closest affinities with hominoids from different continents. Hominoids disperse into Eurasia at the beginning of MN 5, ahead of the Langhian transgression, probably as a result of the key adaptation of thick occlusal enamel and robust jaws and teeth, first observed in *Afropithecus* and *Heliopithecus* from Kenya and Saudi Arabia. Subtropical and mainly forested conditions encourage rapid dispersal and diversification of hominoids in Eurasia, while trends toward more open conditions in sub-Saharan Africa lead to the reduction in diversity and eventual extinction of African pre-modern hominoids. Toward the end of the Vallesian, Eurasian hominoids undergo a series of extinction events that begin in the northwestern end of their range (*Dryopithecus* from Western and Central Europe) and end near the end of the Miocene in Southern China (Lufeng and Hudieliangzi, Yunnan Province). Of the last surviving Eurasian hominoids, the Yunnan taxa appear to have affinities to *Pongo* while the latest forms from Europe and western Asia are most closely related to the African apes and humans. Localities in Turkey document the earliest evidence of hominoids in Eurasia, the spread of hominoids across Eurasia, and, perhaps, the return to Africa in the Turolian of the common ancestor of the African apes and humans.

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## INTRODUCTION

At least three and perhaps four clades of hominoids occur in Turkey between about 16.5 and 7 Ma. These clades represent separate dispersal events at various times between Africa, Asia, Europe and Anatolia, and can be

associated with dispersals of other mammalian taxa, circum-Mediterranean changes in sea levels during the middle and late Miocene, and global climate changes toward the end of the Miocene.

The first hominoids in Turkey appear about

16 to 16.5 Ma, and are among the earliest outside of Africa (Begun *et al.* 2002). They are represented by a large sample of isolated teeth and a few larger fragments from the western Anatolian site of Pasalar, near Bursa, and by a single mandible from the central Anatolian site of Çandır, north of Ankara. Of close to the same age is the hominoid from Engelswies in southern Germany (Heizmann & Begun 2001). All of these hominoids share characters of the dentition that distinguish them from early Miocene hominoids from East Africa, and link them to more modern hominoids. The principal synapomorphy of middle Miocene Eurasian and more modern hominoids is thick occlusal enamel on the

postcanine teeth. This morphology is associated with robust mandibles and some reduction in the relative size of the anterior dentition (incisors and canines). Most researchers assign these samples of hominoids to the genus *Griphopithecus* (Fig. 1) (Paşalar and Çandır) or cf. *Griphopithecus* (Engelswies) (Heizmann 1992; Heizmann *et al.* 1996; Andrews *et al.* 1996; Güleç & Begun 2002; Heizmann & Begun 2001). Recently some researchers have suggested that a second genus of hominoid with close affinities to *Kenyapithecus* (Fig. 1) from Fort Ternan, Kenya may be represented in the sample from Paşalar (Ward *et al.* 1999; Kelley *et al.* 2000; Begun 2000). Most researchers hold that

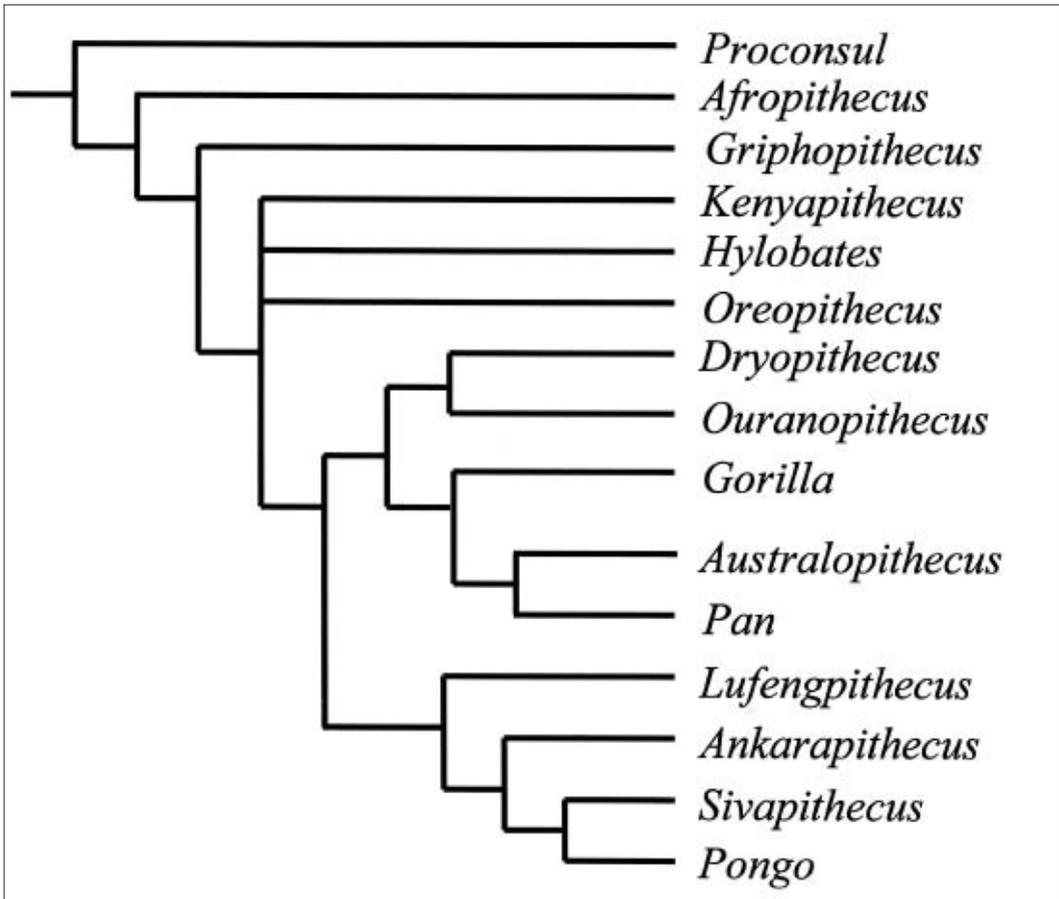


Figure 1 A phylogeny of some hominoid taxa modified from Begun (2001). *Griphopithecus* is the outgroup to the Euhominoidea, the clade that includes all living hominoids and all Eurasian fossil hominoids. The node leading to *Kenyapithecus*, *Hylobates*, *Oreopithecus* and the Hominidae is unresolved.

*Kenyapithecus* is a more modern hominoid than *Griphopithecus* (Fig. 1), sharing with later Miocene hominoids compressed canines and a higher position of the root of the zygomatic process of the maxilla (Harrison 1992; Begun 2001; but see McCrossin & Benefit 1997 for an opposing view). If *Kenyapithecus* or a related taxon is also present at Paşalar it would represent evidence of a second clade of middle Miocene hominoid in Turkey.

The second or third clade of hominoid from Turkey is represented by *Ankarapithecus* (Fig. 1) from the Sinap Formation of central Anatolia. *Ankarapithecus* is known from a partial mandible, a male maxilla with a portion of the face, and a female partial skull (Ozansoy 1965; Alpagut *et al.* 1996; Begun & Güleç 1998). The evolutionary relations of *Ankarapithecus* are being debated, but the most comprehensive analysis to date indicates a close relationship to Asian great apes (see below). There is no evidence of a direct relationship to the middle Miocene hominoids of Turkey.

Finally, another hominoid clade is represented in Turkey by a newly discovered maxilla from Çorakyerler, in the northern Çankırı-Çorum basin near the town of Çankırı (Sevim *et al.* 2001). While the relations of this taxon remain to be worked out, it has affinities with European and African late Miocene to Pliocene taxa and not to the Asian great apes. Each of these fossil hominoids is associated with faunas and paleoecological settings that are distinct from the others, and each probably represents a separate migration rather than in situ evolution of Anatolian hominoids. For the remainder of this paper we will describe in more detail evidence for the evolutionary relations of Anatolian hominoids and their implications for understanding broader issues of migration and dispersal of hominoids across Eurasia and to and from Africa.

## GRIPHOPITHECUS

The earliest hominoids from Anatolia are known primarily from the middle Miocene

locality of Paşalar and a great deal has been written about the age and paleoecology of this locality. Less is published about Çandır, although the analysis of this locality is now complete (Güleç *et al.* 2002; Begun *et al.* 2002). Results of these analyses suggest a slightly different picture from that presented by many but not all researchers on the Paşalar site (e.g., Bernor & Tobien 1990; Andrews 1990; Sen 1990). Here we briefly review the major conclusions of our research at Çandır in so far as it relates to an understanding of the relations of Anatolian middle Miocene hominoids to other hominoids, and the timing of hominoid dispersal events.

The holotype of *Griphopithecus darwini* is a lower molar from Devínská Nová Ves, Slovakia (Abel 1902). The long history of this nomen is reviewed elsewhere (Andrews *et al.* 1996; Güleç & Begun 2002). The primate mandible from Çandır (Fig. 2) is the holotype of *Griphopithecus alpani* (Tekkaya 1974). It is indistinguishable from the Slovakian sample of four isolated teeth, mostly because the latter is inadequate for detailed comparisons. Most researchers have also concluded that the Çandır taxon is the same as the more abundant of the two hominoid taxa from Paşalar (Alpagut *et al.* 1990; Ward *et al.* 1999; Güleç & Begun 2002). *Griphopithecus* is characterized by thickly enameled molars with broad, rounded cusps, shallow occlusal basins, blunt occlusal crests and a shallow topography of the enamel-dentine junction. The Çandır specimen preserves most of the mandibular corpus, which is low and robust in transverse dimensions, both of which are functionally consistent with thickly enameled molars. It also preserves the premolars, which have a simple occlusal morphology, and the alveoli for the canines and incisors, which must have been quite small. The symphysis is strongly reinforced by superior and inferior transverse tori (Güleç & Begun 2002). The sample of mostly isolated teeth with a few gnathic fragments from Paşalar is broadly consistent with this morphology, and together these samples indicate that the first

hominoid from Anatolia was a hard object feeder with dental characters most similar to middle and late Miocene *Sivapithecus* from South Asia, *Ouranopithecus* from Greece, and Pliocene hominids from East and South Africa (*Australopithecus* and early *Homo*). This is probably the primitive morphological complex for hominids (great apes and humans) and represents the earliest appearance of these characters. Given its primitive nature, the relations of *Griphopithecus* are unclear, except that it is derived relative to early Miocene hominoids such as *Proconsul* and primitive relative to most middle and late Miocene and recent great apes (Andrews *et al.* 1996; Güleç & Begun 2002). In Begun (2002) *Griphopithecus* is placed in its own family (Griphopithecidae). Andrews *et al.* (1996) classification of *Griphopithecus* and other middle-late Miocene hominoids is paraphyletic by the authors' admission and is thus not considered further here.

Central Anatolia is near the geographic center of the distribution of middle Miocene

hominoids, which range from France east to India and Pakistan and south to Namibia, and most Çandır and Paşalar taxa, at least at the genus level, are found in all three Old World continents in the middle part of the Miocene. Many migration routes between South and East Asia, Europe and Africa appear to have passed through Anatolia, contributing to the unique character of this assemblage compared to faunas "typical" of specific biogeographic provinces (Geraads *et al.* 2002). Reconstructing the timing of the original dispersal of hominoids into Eurasia, and its correlation to other events, such as climate and sea level changes and the biochronology of other taxa, depends on the assessment of the age of Çandır and Paşalar.

Based in large part on their preliminary analysis of the Paşalar fauna, Bernor & Tobien (1990) concluded that Paşalar and Çandır belong in MN 6, with Paşalar slightly older than Çandır. However, most of the large mammals from Çandır and Paşalar that also occur in Europe first occur there by MN5 or before (Begun *et al.* 2002). Of the large mammals that have an FAD in MN 6, nearly all are known only from Turkey (mainly Paşalar and Çandır). *Griphopithecus alpani* and *Orycteropus seni* have congeners or close relatives from pre-MN 6 localities in Germany and East Africa (Güleç & Begun 2002; Van der Made 2002), and the rhinos from Çandır appear to be closely related to MN 4-5 taxa (*Aceratherium* to *Plesioacera-therium* from MN 4-MN 5 and *Beliajevina* to *Hispanotherium*, which disappears in late MN5 or early MN6 in Europe, (Geraads & Saraç 2002). *Bunolistriodon* becomes extinct before MN6 in Western Europe. *Turcocerus*, which is given an MN 6 FAD based on its occurrence in Anatolia, is not known from Europe at all, while *Giraffokeryx* and *Hypsodontus*, both unknown from Western Europe but with records in Eastern Europe, have MN 5 distributions. *Heteroprox* is known from MN 5-MN 6 in Western Europe. Only three large mammal taxa from Paşalar or Çandır are considered to be MN 6 taxa as



Figure 2 Lingual (a) and occlusal (b) views of the Çandır mandible. Note the massive corpus, doubled symphyseal tori and broad, rounded molar cusps.

determined by their presence in localities other than Paşalar or Çandır. These are *Percrocuta miocenica*, *Listriodon splendens* and *Anchitherium aurelianense hippoides*. Each of these taxa is represented at Çandır by small numbers of isolated teeth (and some postcrania, in the case of *Anchitherium*, which however differ from those of the same subspecies at Sansan) (Güleç & Geraads 2002; van der Made 2002; Nagel 2002).

Among the micromammals from Çandır only the flying squirrels have a FAD from Europe later than MN 5. *Forsythia* is said to have an MN 7/8 distribution in Europe (De Bruijn *et al.* 2002; De Bruijn 1999) but has been recently reported in MN 6 at Sansan (Mein 1999). The generally primitive nature of the micromammal fauna from Çandır and Paşalar however suggests that those taxa may have come to Europe from Western Asia. *Cricetodon candirensis* is only known from Çandır, and De Bruijn *et al.* (1993) and De Bruijn & Ünay (1996) suggest that the *Cricetodon* from MN 4 in Turkey is ancestral to that from Spain, and that a migration event took place in MN 5. Of the two widespread and biostratigraphically important cricetini, *Megacricetodon collongensis* is extinct by MN 6, and *Democricetodon* aff. *D. gaillardi* from Çandır is thought to be primitive relative to the sample from Sansan (De Bruijn *et al.*, 2002). *Desmanodon* is extinct in Europe before MN 6 and *Dinosorex* has a range from MN 4 to MN 9 in Europe (Ziegler 1999). *Keramidomys thaleri* is extinct by MN 6, and in fact is primarily known from MN 5 (De Bruijn *et al.* 2002 and pers. comm., Engesser 1999). *Eomyops* from Çandır is identified as *E. cf. E. catalaunicus* (MN 9), but only 2 teeth are known from Çandır and the genus is notoriously slow to evolve (De Bruijn, personal communication). *Eomyops* is thought to first occur in Europe in MN5, though Engesser (1999) suggests that it may have been present as early as MN 2/3. Engesser (1999) also stresses the slow pace of evolution in the molars of *Eomyops*, suggesting that the two teeth from Çandır are difficult to

assign to a species.

In sum, few taxa from Çandır and Paşalar have a FAD in MN 6 as determined by their presence outside Turkey (3 of 25 large mammals and 2 of 19 small mammals), and most have a FAD in MN 5 or earlier (Begun *et al.* 2002). Given the extinction of *Keramidomys thaleri* and *Megacricetodon collongensis* in MN 5 and that all other taxa known outside Turkey originate in MN 5 or earlier, it is likely that the few apparently MN 6 taxa from Çandır and Paşalar actually originated in MN 5 or earlier in Turkey and do not appear in Europe until MN 6. We conclude therefore that Çandır and Paşalar belong to MN 5, which we believe to be between 15 and 17.3 Ma in Turkey and central Europe (Steininger 1999; Begun *et al.* 2002; see an extensive discussion in the latter on the issue of the age of MN 5). Based on faunal similarities to localities from central Europe and somewhat ambiguous paleomagnetic results from Çandır (Krijgsman 2002) we place this locality at about 16.2 Ma, and Paşalar slightly older, following Bernor and Tobien (1990). With regard to other hominoid localities, Çandır and Paşalar are roughly contemporaneous with Engelswies and older than Klein Hadersdorf and Devínská Nová Ves (Fig. 3) (Begun *et al.* 2002; Heizmann & Begun 2001).

The *Gomphotherium* Landbridge came into being at about 18.5 Ma and appears to have been crossed in two phases preceding the Langhian Transgression that temporarily separated Eurasia and Africa (Rögl 1999). Mastodons appear to cross into Eurasia from Africa first, followed by *Deinotherium*. It may be that primates accompanied the latter into Eurasia at about 17 to 16.5 Ma. This would correspond roughly to the base (low stand) of TB 2.2 (Fig. 3) of the sea level cycles of Haq *et al.* (1988) (Woodburne & Swisher 1995). At this time many of the mammals known from Çandır Paşalar crossed into Eurasia from Africa (Hominoidea, *Deinotherium*, *Bunolistriodon*, *Chalicotheriinae*, *Brachypotherium*, *Orycteropus*), or

into Africa from Eurasia (hypodontines, Amphicyon, Hemicyon) (Fig. 4). Starting also at this time and continuing into the middle Miocene taxa present at Çandır moved between Western Asia and other parts of Eurasia (*Democratodon*, *Megacricetodon*, *Cricetodon*, *Tamias*, *Pliospalax*, *Alloptox*, *Beliajevina*, *Tethytragus*, *Turcocerus*, *Schizochoerus*, petauristids, hominoids) or from Europe to Western Asia (*Palaeomeryx*, *Heteroprox*, *Hoploacetherium*,

*Protictitherium*, *Percrocuta*, *Pseudaelurus*, *Ischrictis*, eomyids, sciurids, and glirids). A number of these taxa also appear to disperse into North America at this time as well (petauristids, eomyids and *Pseudaelurus* (Woodburne & Swisher 1995). All these pathways potentially take land mammals through Central Anatolia.

This scenario of dispersal events differs somewhat from others that have been recently proposed, but mainly in combining impor-

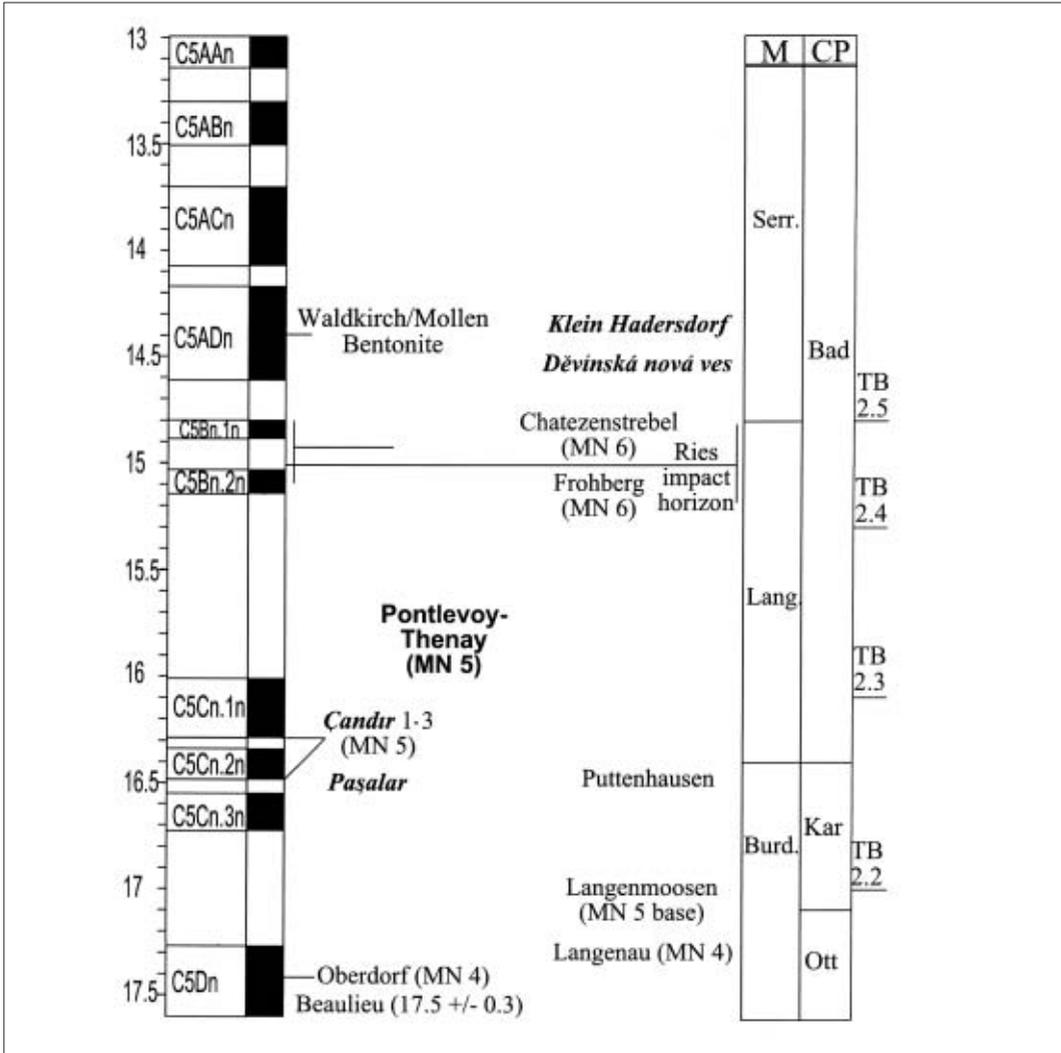


Figure 3 Chronology of important middle Miocene hominoid localities in Eurasia. Chron (left column), and Mediterranean and Central Paratethys ages (right column) correlations from Steinger (1999) and references therein (see also Begun et al. (2002) and Heizmann & Begun (2001)).

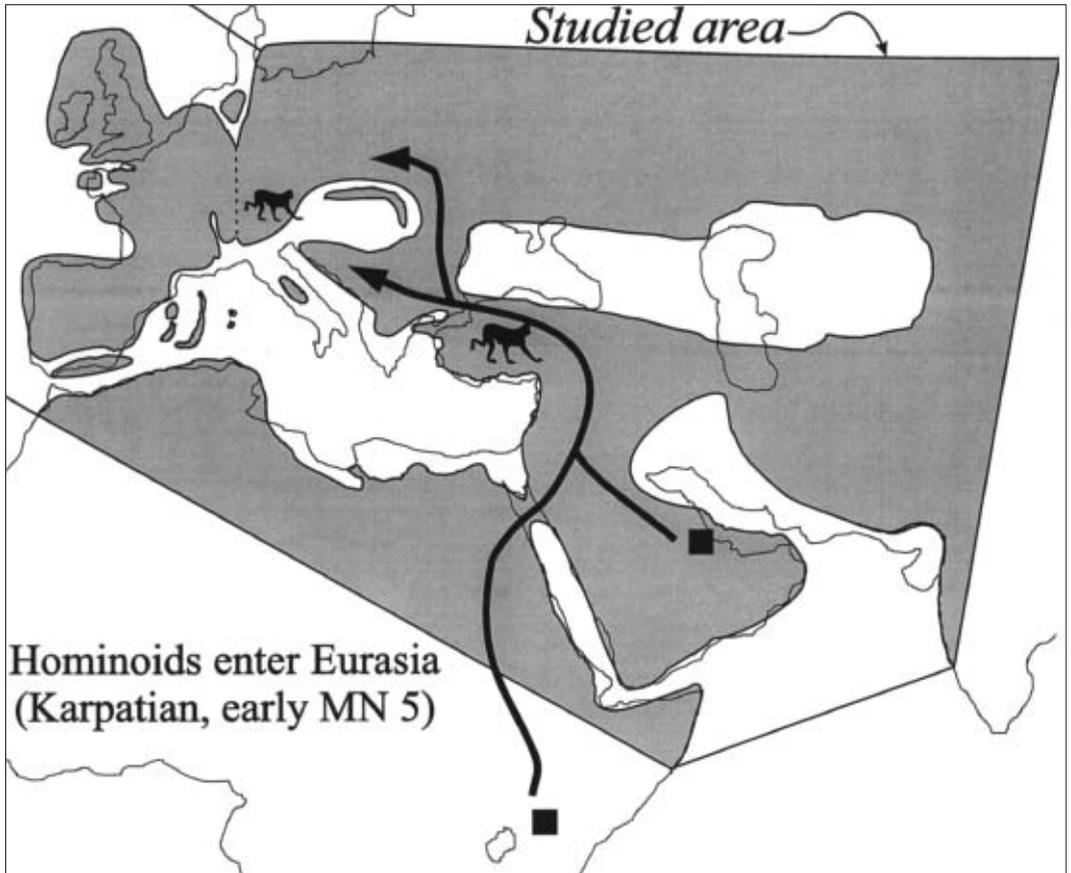


Figure 4 Paleogeography and hominoid migration routes in pre-Langhian MN 5. Map modified from Rögl (1999). Tailless catarrhine symbols represent localities in Anatolia (Paşalar and Çandır) and Germany (Engelwies). Squares represent localities in Kenya (Kalodirr) and Saudi Arabia (Ad Dabtyyah) from which early Miocene hominoids with thickly enameled molars are known.

tant dispersal events (late Burdigalian and early Serravallian events of Rögl 1999, or TB 2.2-2.5 cycle events of Van der Made 1999). This is a consequence of the earlier age we attribute to the Çandır fauna, but it is also consistent with the data on dispersals between the Old World and North America, which are concentrated at this time in the earlier parts of the TB 2 supercycle (Woodburne & Swisher 1995). It is also consistent with the model proposed by Pickford & Morales (1994), who correlate faunal exchanges between African and Eurasia and increases in generic diversity, to shifts in the northern boundary of the tropical biogeographic realm. Their early peak at about 17 to 18 Ma fits our

scenario well.

Hominoids are rare in late early or early middle Miocene faunas (Paşalar being a notable exception), and may have dispersed from Africa toward the end of this period of intercontinental migration events, in early to mid MN 5. They appear at about the same time in Turkey (Çandır and Paşalar) and Germany (Engelwies) at 16 to 16.5 Ma (Fig. 3), and somewhat later in East Africa (Maboko, Kipsarimon, Nachola), and the Vienna Basin (Devinská Nová Ves [Neudorf] Sandberg and Klein Hadersdorf) (Fig. 3) (Matsuda *et al.* 1986; Pickford 1986; Heizmann 1992; Heizmann & Begun 2001; Sawada *et al.* 1998; Ward *et al.* 1999; Rögl 1999; Begun *et*

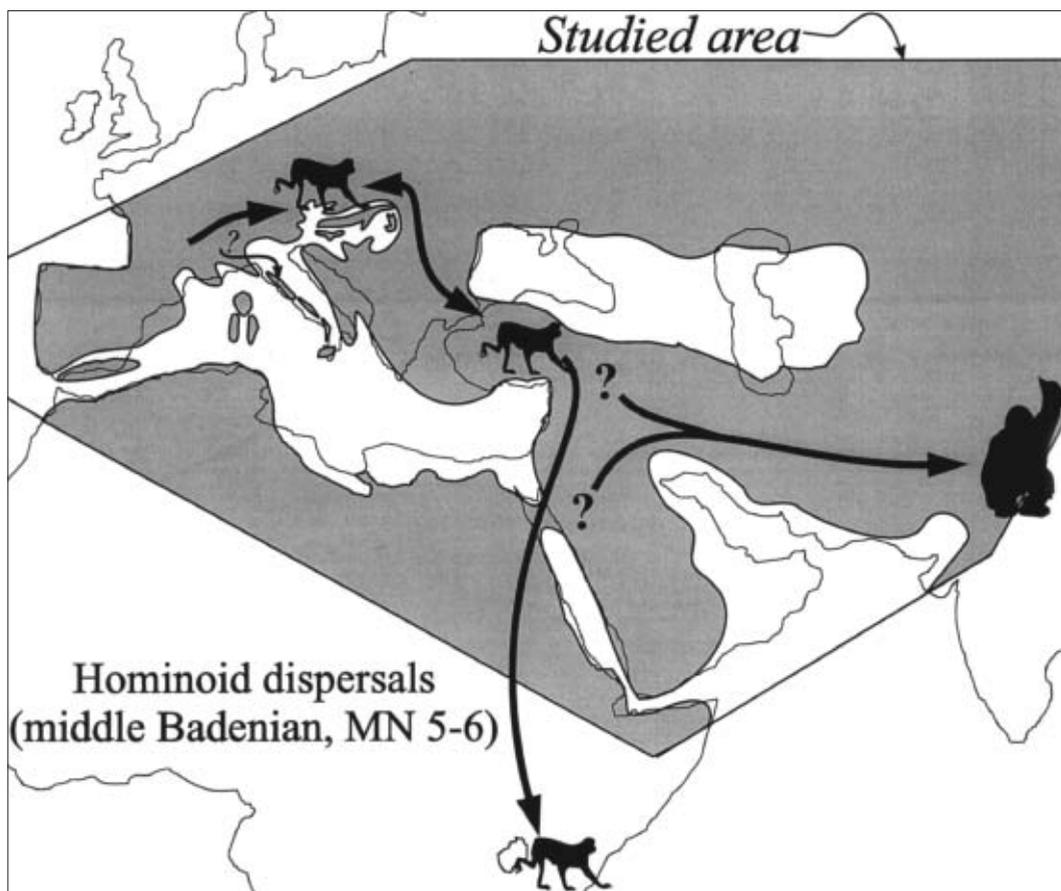


Figure 5 Paleogeography and hominoid migration routes in post-Langhian MN 5-6. Map modified from Rögl (1999). Tailless catarrhine symbols represent localities in Anatolia (Pasalar and Çandır) and Slovakia (Devínská Nová Ves). The ape grasping a branch represents localities in the Siwalik Hills. The precise pattern of dispersal among these localities is not completely clear, though the Anatolian and German sites are almost certainly older than the Slovakian one. Siwalik hominoids may originate from a Mediterranean source or from an African one.

al. 2002). It is possible that the first hominoid of modern dental aspect, *Griphopithecus*, evolved in Eurasia and that the presence of dentally very similar taxa in East Africa 1 Ma or more later represents an early Serravallian return of hominoids to Africa, contemporaneous with the spread of *Griphopithecus* to the Vienna Basin (Begun 2000, 2001) (Fig. 5). This migration would correspond to the TB 2.5 lowstand (Fig. 3). Interesting in this regard also is the fact that another middle Miocene primate, represented by one specimen from Fort Ternan, KNM-FT 20, attributed to cf. *Limnopithecus legetet* (Andrews 1978) has affinities with the other-

wise exclusively Eurasian Pliopithecoidea (Begun 2002b). Both primates from Fort Ternan (cf. *Limnopithecus* and *Kenya-pithecus*) could be immigrants from Eurasia, of which there appear to have been several. Along with other Western Asian taxa present at Çandır (*Tethyragus*, *Turcocerus*, *Schizochoerus*, *Pliospalax*, *Cricetodon*, *Cricetini*, and possibly the flying squirrels) hominoids radiate from the northern and eastern Mediterranean and diversify into a number of clades from China to Spain (Begun 2002a).

Evidence from Anatolia, central Europe and East Africa suggests that hominoids of

modern aspect originate in Eurasia from a more primitive African form about 17 Ma. Several early Miocene hominoids from this time, such as *Afropithecus* from northern Kenya and *Heliopithecus* from Saudi Arabia, share features with the earliest Eurasian hominoids, particularly the presence of thick occlusal enamel, that may have provided one of them with the key adaptation necessary to exploit the more northerly subtropical environments. Between the late Burdigalian (Karpatian) dispersals and the late Miocene fewer migration events between Eurasia and Africa are recorded although several lineages of rodents move from Asia to Africa, as does *Percrocuta* and possibly *Kenyapithecus* (Tong & Jaeger 1993, Van der Made 1999, Begun 2000 and above). It is during this time that the hominids (great apes) evolve *in situ* in Eurasia.

### ANKARAPITHECUS

The earliest hominid from Turkey is *Ankarapithecus* from deposits at Sinap Tepe, Kayıncak, and Delikayıncak Tepe, near Yassıören, Central Anatolia. Unlike the middle Miocene localities, the Yassıören localities are well dated biostratigraphically and by paleomagnetic correlation to about 10 Ma (Sen 1991; Alpagut *et al.* 1996; Pekka Lunkka *et al.* 1999). They are thus roughly contemporaneous with *Dryopithecus* from the Vallesian of central Europe and Spain and *Sivapithecus* from the Potwar Plateau (Pilbeam *et al.* 1979; Kordos 1982, 1991; Raza *et al.* 1983; Barry *et al.* 1985; Kappelman *et al.* 1991; Agustí *et al.* 1996). *Ankarapithecus meteai* is the only species of the genus, and is known cranially from three specimens, but two of them are relatively complete. A number of postcrania have also been reported but they are unpublished, other than a brief reference to their relative robusticity and indications of some degree of adaptation to terrestrial locomotion (Köhler *et al.* 1999). Like *Griphopithecus*, *Ankarapithecus* is thickly enameled with low, rounded cusps, blunt crests and shallow basins (Fig. 6), but it

is much larger than *Griphopithecus*. In addition the mandible is taller and less robust than in *Griphopithecus alpani* and the symphyseal morphology is very different (Begun & Güleç 1998). *Ankarapithecus* molars lack cingula that sometimes appear on *Griphopithecus* molars, and are very similar in morphology and dental proportions to *Sivapithecus* and *Ouranopithecus*, two taxa with which *Ankarapithecus* has been confused in the past (Andrews & Tekkaya 1980; Martin & Andrews 1984). Like both of these taxa, it is likely that *Ankarapithecus* was also a hard object feeder.

Unlike *Griphopithecus*, the face of *Ankarapithecus* is well preserved and reveals a number of unambiguous synapomorphies both of the Hominidae and the Ponginae (the Asian great ape clade including *Sivapithecus* and *Pongo*) (Fig. 1). The maxilla is massive with roots of the zygomatic processes placed high on the alveolar process, and a broad nasal aperture at its base, both being hominid characters (Fig. 6). The premaxilla is robust and elongated, as in hominids, but lacks the highly derived morphology of *Sivapithecus*. Details of the nasal fossa also distinguish *Ankarapithecus* from *Pongo* and *Sivapithecus* (Begun & Güleç 1998). Like *Ouranopithecus* the premaxilla is biconvex and less horizontally oriented than in *Sivapithecus* (Fig. 6). Like *Sivapithecus* the zygoma are broad and laterally flared, and face anteriorly. The mid-face is prognathic and not flat as in *Sivapithecus* and *Pongo*, but very tall, as in the Asian taxa. The orbits are squared, not elongated as in *Sivapithecus*, and the interorbital space is relatively narrow, again, like Asian great apes (Alpagut *et al.* 1996; Begun & Güleç 1998). The nasal bones are extremely elongated, as in *Sivapithecus*. Supraciliary arches contour the superior edges of the orbits, but they do not meet in the midline to form a true torus. They are robust but closely resemble those of large *Pongo*, and to a lesser extent *Sivapithecus* and large *Cebus* (Alpagut *et al.* 1996; Begun & Güleç 1998). These arches have been interpreted as supraorbital

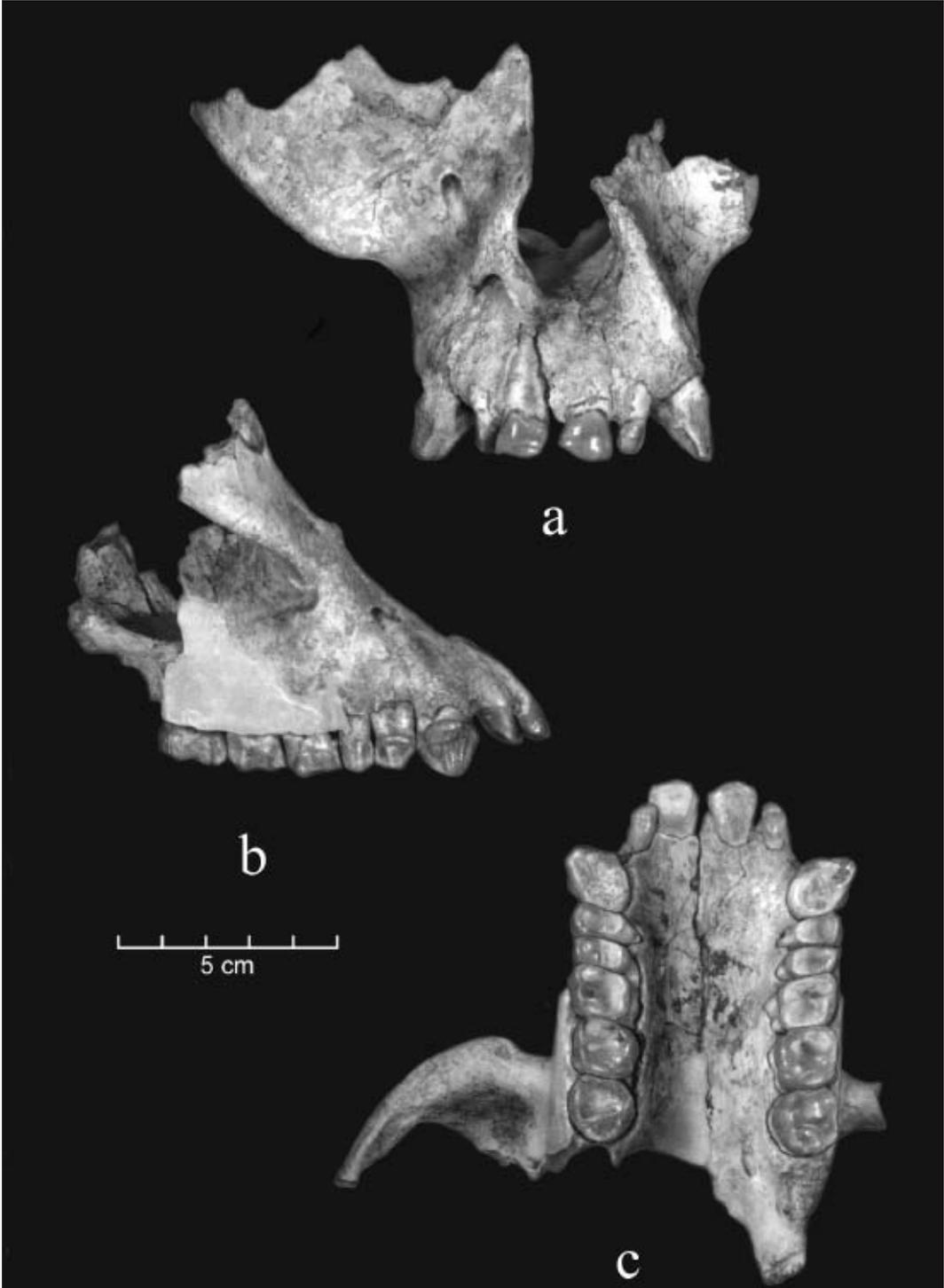


Figure 6 (a): Frontal view of the palate of a male of *Ankarapithecus meteai*. Note the broad and widely flared zygoma. (b): Lateral view. Note the midfacial prognathism, with the nasal aperture margin projected anteriorly relative to the zygomatic. (c): Occlusal view.

tori (Alpagut *et al.* 1996), which are otherwise only found in *Dryopithecus*, *Ouranopithecus*, and African apes and humans, but their condition in *Ankarapithecus* is unlike a true torus that meets in the midline and does not follow the orbital contours (Begun 2002a). Overall the morphology of *Ankarapithecus* is strongly suggestive of cladistic affinities with *Sivapithecus* and Pongo (Fig. 1), but lacking some of the derived characters of these hominids. It has been interpreted as a basal hominid by Alpagut *et al.* (1996) and but a more detailed analysis strongly indicates pongine affinities as the sister taxon to the *Sivapithecus*-Pongo clade (Begun and Güleç 1998).

Like *Griphopithecus* and other taxa from earlier deposits in the middle Miocene of Anatolia, *Ankarapithecus* is primitive compared to its closest relatives. Begun & Güleç (1998) have noted that while *Ankarapithecus* is primitive relative to contemporary and later *Sivapithecus* from the Siwaliks, a number of older (Chinji Formation) specimens attributed to *Sivapithecus* are in fact undiagnostic, and may ultimately be attributable to *Ankarapithecus*. It is possible that *Ankarapithecus* in Anatolia is a relict population of the *Sivapithecus*-Pongo clade that survived in Turkey after the initial appearance of *Sivapithecus* in the Siwaliks. Another scenario accounts for the diversity of *Sivapithecus* in the Siwaliks and the evidence of faunal exchanges between African and Eurasia in the middle and late Miocene. The late Miocene sediments at Sinap and in the Siwaliks have a primarily Eurasian character (Sen 1991; Pilbeam *et al.* 1979). This is especially true of the more recent Siwalik faunas (Pilbeam *et al.* 1979), while the older Siwalik faunas, including Chinji, have closer affinities to East African faunas (Pilbeam *et al.* 1979; Raza *et al.* 1983; Kappelman *et al.* 1991). Pongines may first appear in South Asia, represented by the Chinji specimens of uncertain taxonomy (Begun & Güleç 1998). *Ankarapithecus* may represent an early branch, migrating southwest to Turkey, while

*Sivapithecus* radiated *in situ* into a diversity of species (Kelley & Pilbeam 1986; Kelley 1988) (Fig. 7).

*Ankarapithecus* is one of many hominids that appears in Eurasia between MN 7/8 and MN 10. These include *Dryopithecus*, *Oreopithecus*, and *Ouranopithecus* in Europe and *Sivapithecus*, *Lufengpithecus* and *Gigantopithecus* (or *Indopithecus*) in Asia. It was the golden age of the great apes, and yet no hominids are known from this time in Africa. In fact, no hominids are known from Africa until *Orrorin tugenensis*, of uncertain cladistic affinities, from the latest Miocene (6 Ma) of Kenya (Senut *et al.* 2001; Pickford & Senut 2001). The middle Serravallian isolation of Eurasia from Africa (Fig. 7) may explain the absence of great apes south of Anatolia and west of south Asia at this time.

## A TUROLIAN HOMINID FROM ANATOLIA

In August of 2000 a team of excavators led by Dr. Ayla Sevim under the direction of the second author (EG) discovered the first Turolian hominid from the eastern half of the Mediterranean basin (Sevim *et al.* 2001). This specimen, a large male palate, is under analysis, but it is clear from preliminary work that it represents a separate clade of hominid from those previously known from Turkey. Its affinities are with other eastern Mediterranean taxa such as *Ouranopithecus* and *Graecopithecus*, but also early Pliocene taxa such as *Australopithecus anamensis* and *Ardipithecus ramidus* (Sevim *et al.* 2001). Either way, the presence of a Turolian hominid in Anatolia is a surprise, given earlier reconstructions of climate change and hominid evolutionary dynamics (Andrews *et al.* 1996; Andrews & Bernor 1999), and its clear affinities to the Afro-European clade supports earlier suggestions of a close relationship among the hominids from these two regions (De Bonis & Melentis 1987, De Bonis *et al.* 1991; De Bonis & Koufos 1993, 1997; Koufos 1995; Begun & Kordos 1997; Begun 2001; Begun 2002). It also supports the paleobiogeographic hypothe-

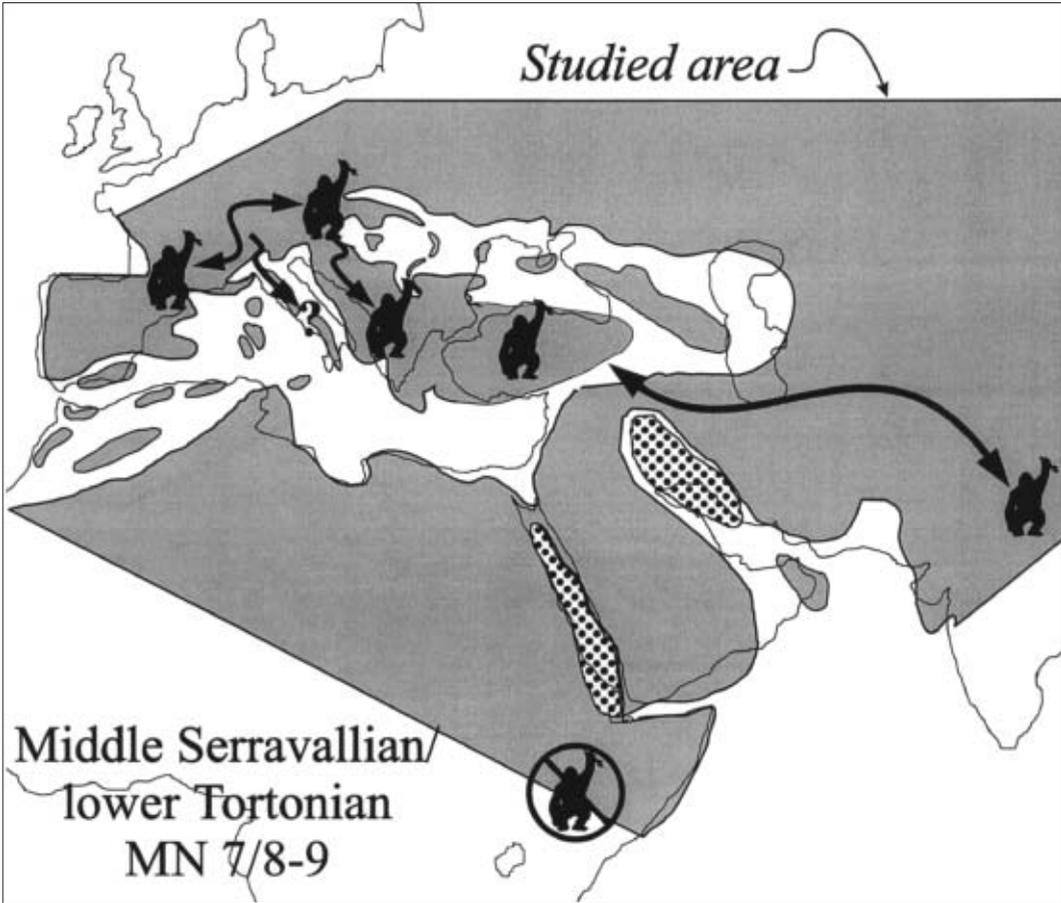


Figure 7 Paleogeography and hominoid migration routes in the late middle and early late Miocene. Map modified from Rögl (1999). The ape grasping a branch represents hominid localities in the Siwalik Hills, Spain, France, Germany, Austria, Hungary, Greece, and Turkey. There are no hominids in Africa at this time.

sis depicted in Figure 8. While hominids are becoming extinct in most of Eurasia one or more populations manages to find refuge in southeast Asia (*Pongo*) and another in Africa (African apes and humans) (Begun 2001).

## CONCLUSIONS

Not surprisingly given its central location, Turkey samples much of great ape evolutionary history, and with its comprehensive record of mammal migrations offers the best evidence to date of the dynamics of hominoid migrations leading to the origin of the modern lineages of the great apes and humans. The first hominoids of modern

aspect appear in Turkey and central Europe shortly before Eurasia was isolated from Africa during the Langhian transgression. It is probably a combination of this geographic isolation, the presence of a key adaptation in robust chewing structures, and the new challenges of existence in Eurasia that lead to the evolution of *Griphopithecus* and its spread across the central and eastern Mediterranean region in MN 5-6. Subsequent *in situ* evolution of hominids in Eurasia is likely, given their absence in Africa until the end of the Miocene and their tremendous diversity in the middle and late Miocene of Eurasia. The only possible exception is *Kenyapithecus*,

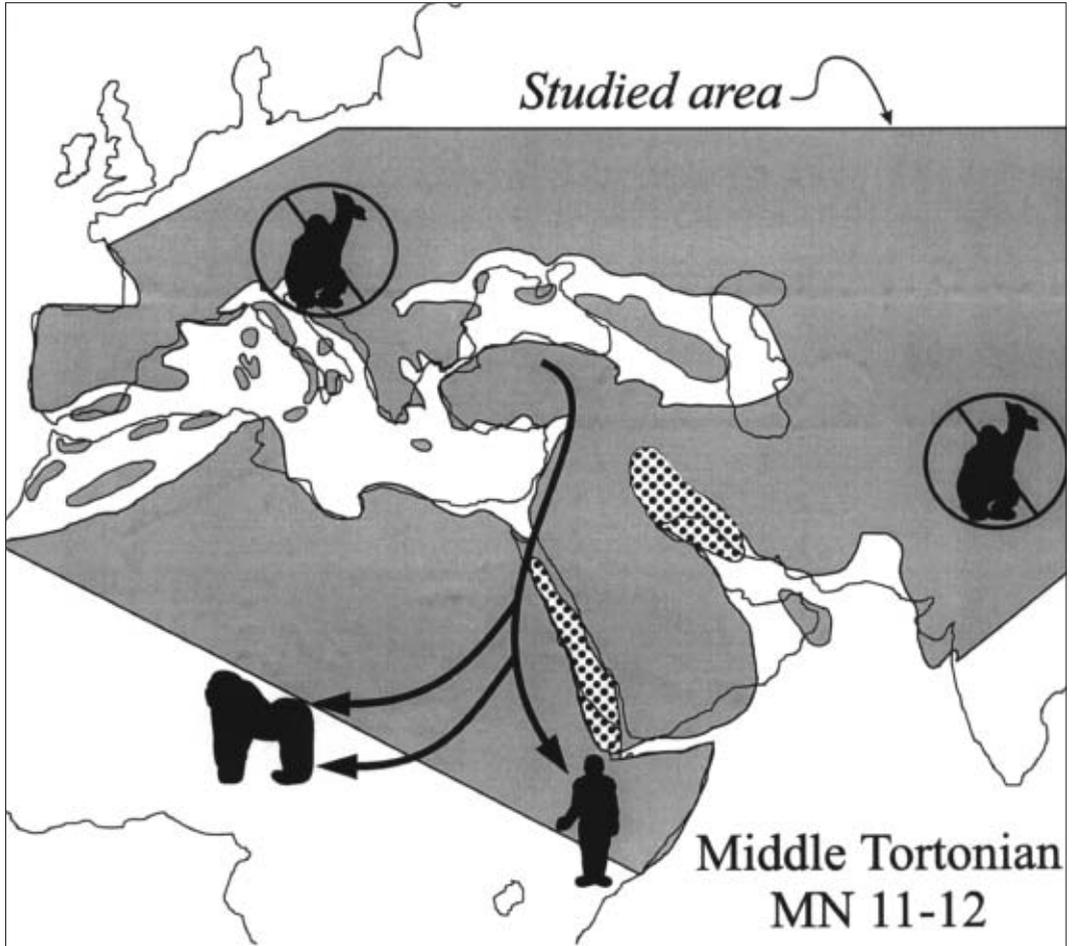


Figure 8 Paleogeography and hominoid migration routes in the late Miocene. Map modified from Rögl (1999). Hominids become extinct in Eurasia at this time and first occur in Africa, suggesting a Eurasian origin for the African apes and humans. Symbols in Africa represent 2 clades of knuckle-walking African apes (*Gorilla* and *Pan*) and fossil humans, the sister taxon to the latter:

which may well be of Eurasian origin as well. During this time period the modern clades of the Asian great apes (represented today only by *Pongo*) and the African apes and humans diverge and radiate across Eurasia, from Spain to China. Turkey samples two branches of this radiation, the Asian great ape *Ankarapithecus* and an Afro-European hominid with affinities to taxa from both continents. All of these taxa are probably derived from a *Griphopithecus*-like ancestor. By beginning of the Messinian (ca. 7 Ma) all hominids living north of the Tropic of Cancer are extinct (Begun 2001). Two comparatively

trivial branches, in terms of peak species diversity, survived whatever conditions led to the extinction of the great radiation of Eurasian hominids. These vestiges remain today in Southeast Asia and Central Africa, still representing the two principle lineages of late Miocene Eurasian hominids.

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## REFERENCES

- Abel, O., 1902 - Zwei neue Menschenaffen aus den Leithakalkbildungen des Wiener Beckens - Sitzungsberichte Akademie der Wissenschaften, mathematik-naturwissenschaft K.1, Abteilung I, 111: 1171-1202
- Agustí, J., Köhler, M. & Moyà-Solà, S., 1996 - Can Llobateres: the pattern and timing of the Vallesian hominoid radiation reconsidered - *Journal of Human Evolution* 31: 143-155
- Alpagut, B., Andrews, P., Fortelius, M., Kappelman, K., Temizsoy, I. & Lindsay, W., 1996 - A new specimen of *Ankarapithecus meteai* from the Sinap formation of central Anatolia - *Nature* 382: 349-351
- Alpagut, B., Andrews, P. & Martin, L., 1990 - New Miocene hominoid specimens from the middle Miocene site at Paşalar - *Journal of Human Evolution* 19: 397-422
- Andrews, P., 1978 - A Revision of the Miocene Hominoidea from East Africa - *Bulletin of the British Museum of Natural History (Geology)* 30: 85-224
- Andrews, P., 1990 - Palaeoecology of the Miocene fauna from Paşalar, Turkey - *Journal of Human Evolution* 19: 569-582
- Andrews, P. & Bernor, R. L., 1999 - Vicariance biogeography and paleoecology of Eurasian Miocene hominoid primates - in: Agustí, J., Rook, L. & Andrews, P., (ed.) - *The Evolution of Neogene Terrestrial Ecosystems in Europe* - pp. 454-487, Cambridge University Press, Cambridge
- Andrews, P., Harrison, T., Delson, E., Bernor, R. L. & Martin, L., 1996 - Distribution and biochronology of European and Southwest Asian Miocene Catarrhines - in: Bernor, R. L., Fahlbusch, V. & Mittmann, H.-W., (ed.) - *The Evolution of Western Eurasian Neogene Mammal Faunas* - pp. 168-295, Columbia University Press, New York
- Andrews, P. & Tekkaya, I. 1980 - A revision of the Turkish Miocene hominoid *Sivapithecus meteai* - *Palaeontology* 23: 85-95
- Barry, J. C., Johnson, N. M., Raza, S. M. & Jacobs, L. L., 1985 - Neogene mammalian faunal change in southern Asia: correlations with climatic, tectonic, and eustatic events - *Geology* 13: 637-640
- Begun, D. R., 2000 - Middle Miocene hominoid origins - *Science* 287: 2375a.
- Begun, D. R., 2001 - African and Eurasian Miocene hominoids and the origins of the Hominidae - in: Andrews, P., Koufos, G. & De Bonis L., (ed.) - *Hominoid Evolution and Environmental Change in the Neogene of Europe* - pp. 231-253, Cambridge University Press, Cambridge
- Begun, D. R., 2002a - European Hominoids - in: Hartwig, W., (ed.) - *The Primate Fossil Record* - pp. 339-368, Cambridge University Press, Cambridge
- Begun, D. R., 2002b - The Pliopithecoida - in: Hartwig, W., (ed.) - *The Primate Fossil Record* - pp. 221-240, Cambridge University Press, Cambridge
- Begun, D. R. & Güleç, E., 1998 - Restoration of the Type and Palate of *Ankarapithecus meteai*: Taxonomic, Phylogenetic, and Functional Implications - *American Journal of Physical Anthropology* 105: 279-314
- Begun, D. R., Güleç, E. & Geraads, D., 2002 - The Çandır hominoid locality: Implications for the timing and pattern of hominoid dispersal events - *Courier Forschungsinstitut Senckenberg* 240: 251-265
- Begun, D. R. & Kordos, L., 1997 - Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominids - in: Begun, D. R., Ward, C. V., & Rose, M. D., (ed.) - *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations* - pp. 291-316, Plenum, New York
- Bernor, R. L. & Tobien, H., 1990 - The mammalian geochronology and biogeography of Paşalar (Middle Miocene, Turkey) - *Journal of Human Evolution* 19: 551-568
- De Bonis, L. & Koufos, G., 1993 - The face and mandible of *Ouranopithecus macedoniensis*: description of new specimens and comparisons - *Journal of Human Evolution* 24: 469-491
- De Bonis, L. & Koufos, G., 1997 - The phylogenetic and functional implications of *Ouranopithecus macedoniensis* - in: Begun, D. R., Ward, C. V. & Rose, M. D., (ed.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations* - pp. 317-326, Plenum, New York
- De Bonis, L., Bouvrain, G., Geraads, D. & Koufos, G., 1991 - New hominoid skull material from the late Miocene of Macedonia in northern Greece - *Nature* 345: 712-714

- De Bonis, L. & Melentis, J., 1987 - Intérêt de l'anatomie naso-maxillaire pour la phylogénie de l'Hominoidea - Comptes Rendus de l'Académie de Science Paris 304: 767-769
- De Bruijn, H., 1999 - Superfamily Sciuroidea - in: Rössner, G. E. & Heissig, K., (ed.) -The Miocene Land Mammals of Europe - pp. 271-280, Dr. Friedrich Pfeil, München
- De Bruijn, H., Fahlbusch, V., Saraç, G. & Ünay, E., 1993 - Early Miocene rodent faunas from the Eastern Mediterranean area Part III. The genera *Deperetomys* and *Cricetodon* with a discussion of the evolutionary history of the Cricetodontini – Proceedings Koninklijke Nederlandse Akademie van Wetenschappen Series B 96: 151-216
- De Bruijn, H., Hoek Ostende, L. Van den, Kristkoiz-Boon, E., Rummel, M., Theocharopoulos, C. & Ünay, E., 2002 - Rodents, lagomorphs and insectivores from the middle Miocene hominoid locality of Çandır (Turkey) - Courier Forschungsinstitut Senckenberg 240: 51-87
- De Bruijn, H. & Ünay, E., 1996 - On the evolutionary history of the Cricetodontini from Europe and Asia Minor and its bearing on the reconstruction of migrations and the continental biotope during the Neogene - in: Bernor, R. L., Fahlbusch, V. & Mittmann, H.-W., (ed.) - The Evolution of Western Eurasian Neogene Mammal Faunas - pp. 227-234, Columbia University Press, New York
- Engesser, B., 1999 - Family Eomyidae - in: Rössner, G. E., & Heissig K., (ed.) - The Miocene Land Mammals of Europe - pp. 319-335, Dr. Friedrich Pfeil, München
- Geraads, D., Begun, D. R. & Güleç, E., 2002 - The middle Miocene hominoid site of Çandır, Turkey: general paleoecological conclusions from the mammalian fauna – Courier Forschungsinstitut Senckenberg 240: 241-250
- Geraads, D. & Saraç G., 2002 - Rhinocerotidae from the Middle Miocene Hominoid Locality of (Turkey) - Courier Forschungsinstitut Senckenberg 240: 217-231
- Güleç, E. & Begun, D. R., 2002 - Functional morphology and affinities of the hominoid mandible from Çandır - Courier Forschungsinstitut Senckenberg
- Güleç, E. & Geraads, D., 2002 - Anchitherium from the middle Miocene hominoid locality of Çandır (Turkey) - Courier Forschungsinstitut Senckenberg
- Güleç, E., Geraads, D. & Begun, D. R., 2002 - Geology and Vertebrate Paleontology of the Middle Miocene Hominoid locality Çandır (Central Anatolia, Turkey) - Courier Forschungsinstitut Senckenberg 240: 1-265
- Haq, B. U., Hardenbol, J. & Vail, R. R., 1988 - Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level changes- in: Wilgus, C. K., Hastings, B. S., Ross, C. A., Posaentier, H., Wagoner, J. van & Kendall, C. G. S. C., (ed.), - Sea-Level Changes: An integrated approach - Special Publication 42 pp. 71-108, Society of Economic Paleontologists and Mineralogists, Tulsa
- Harrison, T., 1992 - A reassessment of the taxonomic and phylogenetic affinities of the fossil catarrhines from Fort Ternan, Kenya - Primates 33: 501-522
- Heizmann, E., 1992 - Das Tertiär in Südwestdeutschland - Stuttgarter Beiträge zur Naturkunde, Serie C 33: 1-90
- Heizmann, E. & Begun, D. R., 2002 - The oldest European Hominoid - Journal of Human Evolution 41: 463-481
- Heizmann, E., Duranthon, F. & Tassy, P., 1996 - Miozäne Grossäugetiere -Stuttgarter Beiträge zur Naturkunde, Serie C 39: 1-60
- Kappelman, J., Kelley, J., Pilbeam, D., Sheikh, K. A., Ward, S., Anwar, M., Barry, J. C., Brown, B., Hake, P., Johnson, N. M., Raza, S. M., & Shah, S. M. I., 1991 - The earliest occurrence of *Sivapithecus* from the middle Miocene Chinji Formation of Pakistan - Journal of Human Evolution 21: 61-73
- Kelley, J., 1988 - A new large species of *Sivapithecus* from the Siwaliks of Pakistan - Journal of Human Evolution 17: 305-325
- Kelley, J. & Pilbeam, D. R., 1986 - The Dryopithecines: taxonomy, comparative anatomy, and phylogeny of Miocene large homionoids - in: Swindler, D. R. & Erwin, J., (ed.) – Comparative Primate Biology, volume 1: Systematics, Evolution and Anatomy- pp. 361-411, Alan R. Liss, New York
- Kelley, J., Ward, S., Brown, B., Hill, A. & Downs, W., 2000 - Middle Miocene hominoid origins - Science 287: 2375a
- Kordos, L., 1982 - The prehominid locality of Rudabánya (NE Hungary) and its neighbourhood: A paleogeographic reconstruction – A Magyar Állami Földtani Intézet Évi Jelentése az 1980-évről: 395-406
- Kordos, L., 1991 - *Le Rudapithecus hungaricus* de Rudabánya (Hongrie) - L'Anthropologie (Paris) 95:

- 343-362
- Koufos, G. D., 1995 - The first female maxilla of the hominoid *Ouranopithecus macedoniensis* from the late Miocene of Macedonia, Greece - *Journal of Human Evolution* 29: 385-389
- Köhler, M., Moyà-Solà, S. & Andrews, P., 1999 - Order Primates - in: Rössner, G. E. & Heissig, K., (ed.) - *The Miocene Land Mammals of Europe* - pp. 91-104, Dr. Friedrich Pfeil, München
- Krijgsman, W., 2002 - Magnetostratigraphic dating of the Çandır fossil locality (middle Miocene, Turkey) - *Courier Forschungsinstitut Senckenberg* 240: 41-87
- Martin, L. & Andrews, P., 1984 - The phyletic position of *Graecopithecus freyberi* Koeningswald - *Courier Forschungsinstitut Senckenberg* 69: 25-40
- Matsuda, T., Torii, M., Makinouchi, T., Mitsushia, H. & Ishida, H., 1986 - Geochronology of Miocene hominoids east of the Kenya Rift Valley - in: Else, J. G. & Lee, P. C., (ed.) - *Primate Evolution* - pp. 35-45, Cambridge University Press, Cambridge
- McCrossin, M. L. & Benefit, B. R., 1997 - On the relationships and adaptations of *Kenyapithecus*, a large-bodied hominoid from the middle Miocene of eastern Africa - in: Begun, D. R., Ward, C. V. & Rose, M. D., (ed.) - *Function, Phylogeny and Fossils: Miocene Hominoid Origins and Adaptations* - pp. 241-267, Plenum Press, New York
- Mein, P., 1999 - European Miocene Mammal Biochronology - in: Rössner, G. E. & Heissig, K., (ed.) - *The Miocene Land Mammals of Europe* - pp. 25-38, Dr. Friedrich Pfeil, München
- Nagel, D., 2002 - Carnivora from the middle Miocene Hominoid locality of Çandır (Turkey) - *Courier Forschungsinstitut Senckenberg*
- Ozansoy, F., 1965 - Étude des gisements continentaux et des mammifères du Cénozoïque de Turquie - *Memoires de la Société Géologique de France Nouvelle Série*. 44: 1-92
- Pekka Lunkka, J., Fortelius, M., Kappelman, J., & Sen, S., 1999 - Chronology and mammal faunas of the Miocene Sinap Formation, Turkey - in: Agustí, J., Rook, L. & Andrews, P., (ed.) - *The Evolution of Neogene Terrestrial Ecosystems in Europe* - pp. 238-264, Cambridge University Press, Cambridge
- Pickford, M., 1986 - Geochronology of the Hominoidea: A summary - in: Else, J. G. & Lee, P. C., (ed.) - *Primate Evolution* - pp. 123-128, Cambridge University Press, Cambridge
- Pickford, M. & Morales, J., 1994 - Biostratigraphy and palaeobiogeography of East Africa and the Iberian peninsula - *Palaeogeography, Palaeoclimatology, and Palaeoecology* 112: 297-322
- Pickford, M. & Senut, B., 2001 - Contexte géologique et faunique des restes d'hominidés du Miocène supérieur de Lukeino, Kenya - *Comptes Rendus de l'Académie de Science, Paris - Series IIA - Earth and Planetary Science* 332: 145-152
- Pilbeam, D. R., Barry, J. C., Behrensmeyer, A. K. & Shah, S. M. I., 1979 - Miocene sediments and faunas of Pakistan - *Postilla* 179: 3-45
- Raza, S. M., Barry, J. C., Pilbeam, D., Rose, M. D., Shah, S. M. I., & Ward, S., 1983 - New hominoid primates from the middle Miocene Chinji Formation, Potwar Plateau, Pakistan - *Nature* 306: 52-54
- Rögl, F., 1999 - Circum-Mediterranean Miocene Paleogeography - in: Rössner, G. & Heissig, K., (ed.) - *The Miocene Land Mammals of Europe* - pp. 39-48, Dr. Friedrich Pfeil, München
- Sawada, Y., Pickford, M., Itaya, T., Makinouchi, T., Tateishi, M., Kabeto, K., Ishida, S. & Ishida, H., 1998 - K-AR ages of Miocene Hominoidea (*Kenyapithecus* and *Samburupithecus*) from Samburu Hills, Northern Kenya - *Comptes Rendus de l'Académie de Science, Paris - Series IIA - Earth and Planetary Science* 326: 445-451.
- Sen, S., 1990 - Middle Miocene lagomorphs from Paşalar, Turkey - *Journal of Human Evolution* 19: 455-461
- Sen, S., 1991 - Stratigraphie, faunes de mammifères et magnétostratigraphie du Néogène du Sinap Tepe, Province d'Ankara, Turquie - *Bulletin du Muséum National d'Histoire Naturelle Paris 4e série.*, 12: 243-277
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. & Coppens, Y., 2001 - First hominid from the Miocene (Lukeino formation, Kenya). - *Comptes Rendus de l'Académie de Science, Paris - Series IIA - Earth and Planetary Science* 332: 137-144
- Sevim, A., Begun, D. R., Güleç, E., Geraads, D. & Pehlevan, Ç., 2001 - A new late Miocene hominid from Turkey. - *American Journal of Physical Anthropology Supplement* 32: 134-135
- Steininger, F. F., 1999 - Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)" - in:

- Rössner, G. E. & Heissig, K., (ed.) - The Miocene Land Mammals of Europe, - pp. 9-24, Dr. Friedrich Pfeil, München
- Tekkaya, I., 1974 - A new species of Tortonian anthropoids (Primates, Mammalia) from Anatolia - Bulletin of the Mineral Research and Exploration Institute of Turkey 83: 1-11
- Tong, H. & Jaeger, J.-J., 1993 - Muroid rodents from the middle Miocene Fort Ternan locality (Kenya) and their contribution to the phylogeny of muroids - *Palaeontographica* 229: 51-73
- Van der Made, J., 1999 - Intercontinental relationship Europe-Africa and the Indian subcontinent - in: Rössner, G. E. & Heissig, K., (ed.) - The Miocene Land Mammals of Europe - pp. 457-472, Dr. Friedrich Pfeil, München
- Van der Made, J., 2002 - The aardvark from the Miocene hominoid locality Çandır, Turkey - Courier Forschungsinstitut Senckenberg
- Ward, S., Brown, B., Hill, A., Kelley, J., & Downs, W., 1999 - *Equatorius*: a new hominoid genus from the middle Miocene of Kenya - *Science* 285: 1382-1386
- Woodburne, M. O., & Swisher, C. C., 1995 - Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance - *Geochronology time Scales and Global Stratigraphic Correlation* SEPM Special publication 54: 335-364
- Ziegler, R., 1999 - Order Insectivora - in: Rössner, G. E. & Heissig, K., (ed.) - The Miocene Land Mammals of Europe - pp. 53-74, Dr. Friedrich Pfeil, München

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