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The oldest Eurasian hominoid

Engelswies is an early Miocene vertebrate locality in southern Germany with a rich assemblage of terrestrial mammals, invertebrates and fossil plants. It is dated to 16·5–17·0 Ma based on magneto-stratigraphy, biostratigraphy and lithostratigraphy, and includes among the faunal remains a hominoid upper molar fragment, the oldest hominoid so far identified from Europe. The evidence from Engelswies suggests that hominoids arrived in Eurasia about 17 Ma, roughly contemporaneously with pliopithecoids and *Deinotherium*, and before the last marine transgression to isolate Eurasia from Africa. Thick enamel and low dentine penetrance may have been key adaptations that contributed to the success of hominoids of dentally modern aspect in western Eurasia and ultimately to their ability to spread to eastern Eurasia and Africa in the middle and late Miocene.

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Introduction

Tertiary fossil localities in southwest Germany are numerous and critical to current interpretations of Cenozoic biostratigraphy, biochronology and paleoecology. Most of the Neogene localities in this region are associated with erosional and depositional regimes linked to the Alpine Orogeny and global climate changes that together resulted in periodic opening and closing of the seaway between the Atlantic and Indian Oceans. Many of these localities preserve a rich record of flora and fauna from the past, including the famous sites of Langenau, Steinheim and Höwenegg, all of which contain many nearly complete skeletons of terrestrial fossil mammals (Heizmann, 1992). Among these localities is Engelswies, near Sigmaringen, south of Stuttgart and east of Freiburg (Figure 1). The locality is situated in the Talsberg, southwest of the town of

Engelswies, which has been quarried for limestone since the nineteenth century. The quarry has long since been abandoned, and the site is covered in dense vegetation (the Talsberg is protected today as a natural monument). Several fossil localities (Engelswies 1–4) are known from quarry activities in the Talsberg and have been the subject of research since the late nineteenth century. It is particularly well known for its beautifully preserved plant remains and invertebrates, which include freshwater crabs and gastropods (Quenstedt, 1885; Engel, 1908; Fraas, 1910; Klähn, 1922, 1924, 1925, 1926; Rutte, 1953; Pretzmann, 1987; Schweigert *et al.*, 1997).

Neglected for many years, Engelswies was the subject of renewed excavations by Heinz Tobien (Mainz University) in the 1970s, during which the tooth described here was found. Tobien found the tooth, which he recognized as hominoid but never described, on 24 June 1973, in the lower part of the profile of the Scherer quarry (excavation horizon 4 in Figure 2), from which most of

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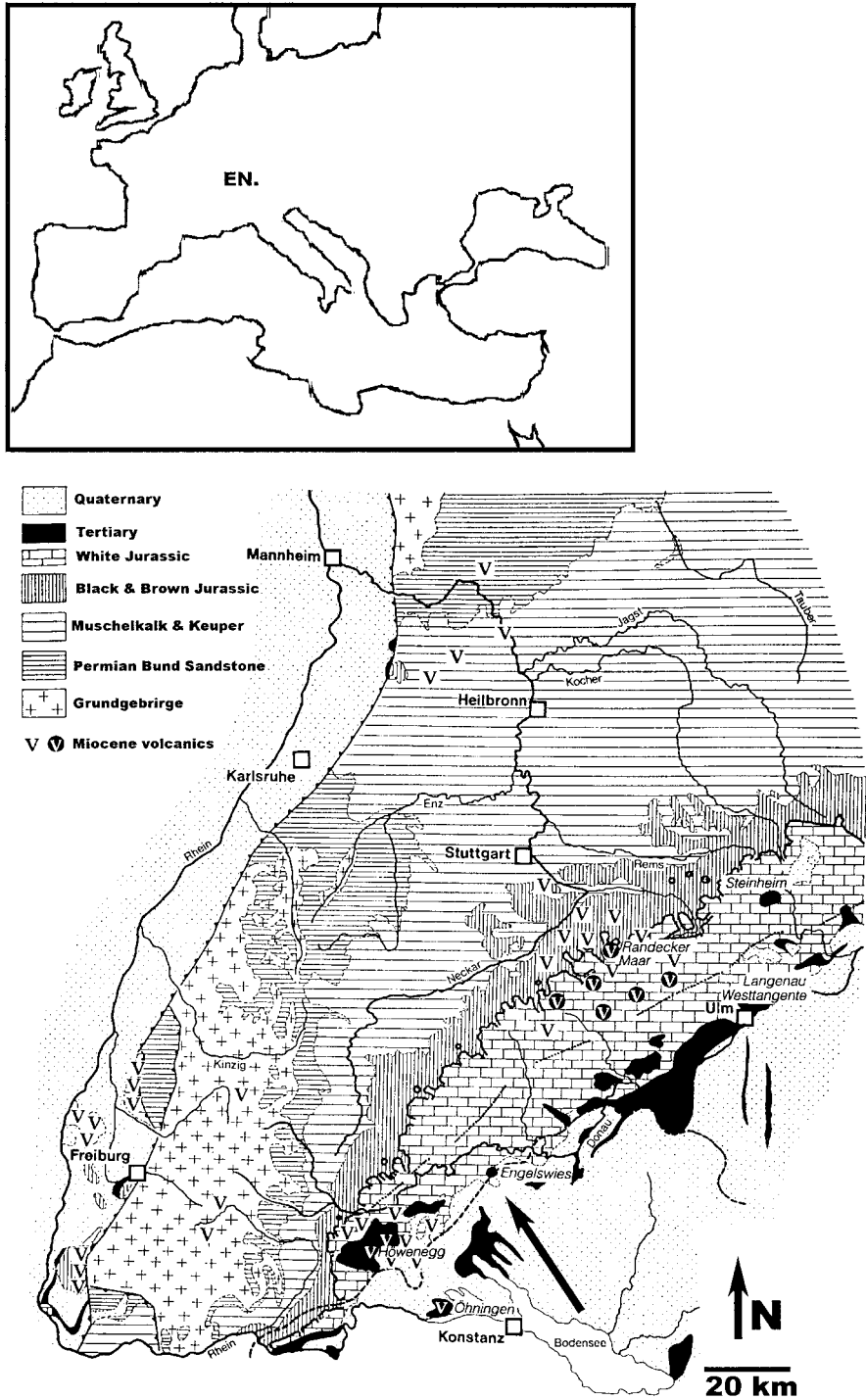
Figure 1. Geologic map with the locality of Engelswies (arrow) and other important localities, major rivers and large cities in the region. Inset shows the location of Engelswies in Western Europe.
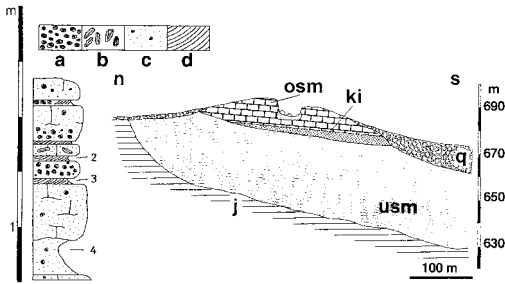
Figure 2. Geologic section and stratigraphy of the Engelswies locality. The hominoid tooth is from horizon 4. Stratigraphic column modified from Ziegler (1995; Abb. 2). Geologic section modified from Schweigert, 1992; Abb. 2). Legend: (a) oncolite (free rolling or mobile structures of algal origin) facies, (b) oncoidal crusts and plant fragments, (c) limestones with terrestrial detritus, (d) lake sediments. Abbreviations: n=north, s=south, osm=upper Freshwater Molasse, ki=Kirschenberger Schlichten, usm=lower Freshwater Molasse, q=Quaternary overburden, j=Jurassic limestone.

the large mammals are known (Schweigert, 1992). This horizon is 4 m below the level yielding the majority of the micromammals on which the biostratigraphic correlation is mostly based (Ziegler, 1995). In 1990, Tobien deposited the tooth in the Staatliches Museum für Naturkunde in Stuttgart (SMNS) along with the other mammalian fossils from Engelswies. This specimen has been noted in the literature (Heizmann, 1992; Andrews et al., 1996; Heizmann et al., 1996) but never described in detail, nor have its implications for Miocene hominoid biogeography been fully discussed.

Geology, biostratigraphy and paleoecology

The freshwater limestones of Engelswies represent an isolated outcrop of an originally widespread sedimentary stratum covering the northern rim of the Alpine Molasse Basin. Hahn (1968) in his detailed analysis of the regional geology took core samples at Engelswies and demonstrated the direct superposition of the fossil levels on the dark clays of the lower Miocene Kirchberger

Schichten (Figure 2). From these cores there is no evidence of any disconformity, indicating a continuous record of sedimentation. This, and the faunal content of the fossiliferous layers, indicates that these sediments correlate to the top of the Kirchberger Schichten, the basal facies of the OSM [Obere Süßwassermolasse (or Upper Freshwater Molasse in English)].

The molasse basin sediments of southern Germany and Switzerland are among the best studied of any Tertiary sediments in Europe, and the sequence of lower and upper marine and freshwater layers and numerous marker horizons, including the Kirchberger Schichten, are well established (Gall et al., 1977; Reichenbacher, 1989; Schlunegger et al., 1996; Bolliger, 1997; Heissig, 1997; Kempf et al., 1997; Reichenbacher et al., 1998; Kempf & Matter, 1999; Sach, 1999) (Figure 3). It has been demonstrated that the Kirchberger Schichten marks the transition between the upper marine molasse sediments (OMM) and the upper Freshwater Molasse sediments (OSM) (Heizmann et al., 1980; Heizmann, 1992; Schweigert, 1992; Reichenbacher, 1993; Ziegler, 1995; Reichenbacher et al., 1998). This transition occurs before the onset of the Langhian transgression, a stage in the Mediterranean marine sequence marked by the brief reconnection of the Atlantic–IndoPacific oceanic seaway (Rögl, 1999). The Langhian is well dated by magnetostratigraphic, radiometric, marine biostratigraphic and lithostratigraphic evidence to between 16·5 and 14·9 Ma (Steininger, 1999). At Engelswies the occurrence of *Megacricetodon bavaricus* and the evolutionary stage of *Democricetodon mutilus* allow a precise correlation to the lower part of MN 5 or late Orleanian (Ziegler, 1995), which we place in the early Miocene. There is currently a debate on the definition of the boundary between early and middle Miocene. We follow the proposal of Fahlbusch (1981), placing the limit

					M	CP	
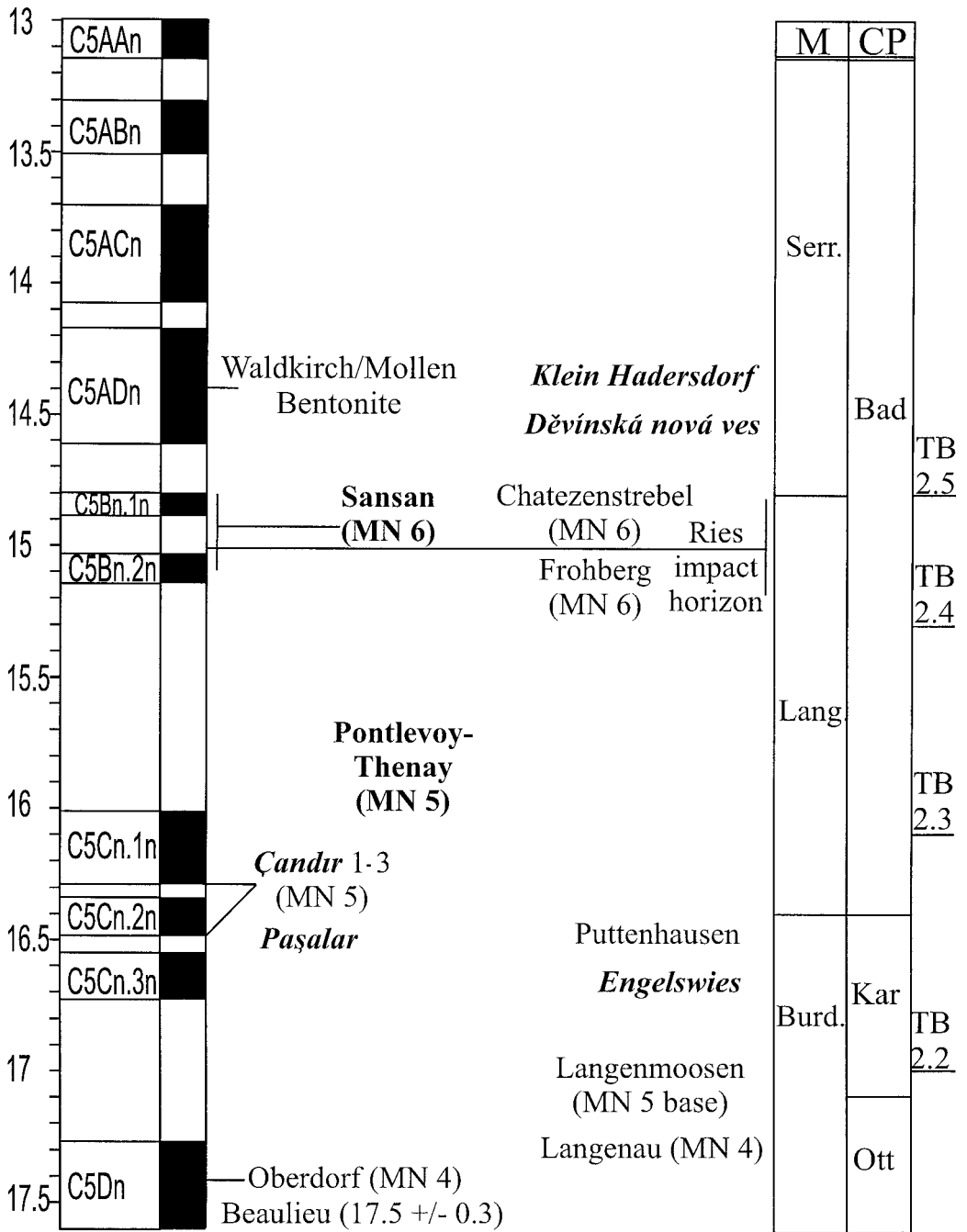
between MN 5 and MN 6. Steininger (1999), in contrast, sets the limit within MN 5. Either way, Engelswies, in the early part of MN 5, is in the early Miocene. The composition of the large mammal fauna is consistent with the biostratigraphy of the small mammals (Table 1). A study of *Anchitherium* (Abusch-Siewert, 1983) has suggested an age of MN 6 or older. The suids also imply an age of MN 5. *Hyotherium soemmeringi* is a typical species for MN 5, and the genus *Bunolistriodon* is extinct at the end of this zone. To summarize, based on regional geology, lithostratigraphy from core samples, and mammalian biostratigraphy and biochronology, Engelswies is between the base of the Langhian and the base of MN 5, or 16·5 to 17 Ma (Ziegler, 1995; Steininger, 1999) (Figure 3[1]).

[1]An important debate in European Miocene chronostratigraphy currently centers on the age of the late early Miocene and middle Miocene MN zones (MN 4–7/8). Evidence from Spain is interpreted to suggest an age for these zones 1 to 2 Ma younger than ages derived from evidence from elsewhere in Europe (Steininger, 1999; Daams et al., 1999). For a variety of reasons beyond the scope of this paper, including the fact that Engelswies predates the well dated Langhian transgression, we find the older ages suggested by Steininger (1999) to be more convincing, and these are used here.

The lithostratigraphic marker horizons of significance to a determination of the age of Engelswies are the OMM, OSM, Kirchberger Schichten and the Ries impact horizon. Based on the marine microfossil record and recent magnetostratigraphic, lithostratigraphic and radiometric work the ages of these horizons in Central Europe appear reasonably well established. Given the ages of these marker horizons, the MN 5 localities of Langenmoosen, Engelswies, and Puttenhausen are dated to between about 15 and 16·8 Ma (Steininger, 1999) (Figure 3). However, in the Calatayud-Daroca Basin of Spain, magnetostratigraphic and biostratigraphic evidence suggests that MN 5 is about 1 Ma younger (16–13·8 Ma, Daams et al., 1999). There are several possible resolutions to these divergent interpretations. The evidence from either Central Europe or Spain may be correct and the other misleading, for a number of technical reasons, or, there may be strong diachrony between Central Europe and Spain. The issue of the age of MN 5 is unresolved, and is in fact the focus of much attention today. Whatever the outcome, mammal localities in Central Europe including Engelswies that are traditionally assigned to MN 5 on the

Figure 3. Chronostratigraphy of the late early and middle Miocene with important fossil localities in their stratigraphic positions. Data from Heizmann et al. (1980), Ziegler & Fahlbusch (1986), Haq et al. (1988), Reichenbacher (1989), Heizmann (1992), de Bruijn et al. (1992, 2001), Reichenbacher (1993), Woodburne & Swisher (1995), Ziegler (1995), Schlunegger et al. (1996), Bolliger (1997), Heissig (1997), Kempf et al. (1997), Reichenbacher et al. (1998), Kempf & Matter (1999), Sach (1999), Sen & Ginsburg (2000), Steininger (1999), Begun et al. (2001). Columns on the left represent chronometric age and the GPTS (geomagnetic polarity time scale) with labeled normal subchrons. Columns on the right represent Mediterranean (M) and Central paratethys (CP) stages, abbreviated as follows: Mediterranean (Serr.=Serravallian, Lang.=Langhian, Burd.=Burdigalian); Central paratethys (Ott.=Ottnangian, Kar.=Karpatian, Bad.=Badenian). To the left, localities are correlated to the column based on radiometric or paleomagnetic data. Locality names in bold italics contain fossil hominoids. Locality names in bold only are reference faunas for the MN zonation (Sansan and Pontlevoy contain pliopithecids but no hominoids). Localities on the right are situated within the stratigraphic sequence on the basis of lithostratigraphic and biostratigraphic evidence. See text for discussion. Ages and paleomagnetic correlations for the European marine stage sequences follow Steininger (1999). The Ries impact horizon (Brockhorizont) is a meteor impact structure with associated detritus dated radiometrically to the range indicated in this figure (Reichenbacher et al., 1998). TB 2·2–2·5 refer to sea level low stands of Haq et al. (1988) and their recalibration by Woodburne & Swisher (1995). Note the TB 2·2 low stand at about 17 Ma that may have permitted hominoids to disperse into Eurasia from Africa.

Table 1 Faunal list from Engelswies

Insectivora	*Galerix* aff. *G. exilis*
	Plesiodimylus huerzeleri seu *chanterei*
Rodentia	*Chalicomys jaegeri*
	Spermophilinus aff. *S. bredai*
	Palaeosciurus sutteri
	?*Miopetaurista* cf. *M. dehmi*
	Bransatoglis cf. *B. cadeoti*
	Miodyromys sp.
	Glirulus aff. *G. conjunctus*
	Keramidomys thaleri
	Eumyarion weinfurteri
	Megacricetodon bavaricus
	Democricetodon mutilus
	Democricetodon gracilis
Primates	cf. *Griphopithecus* sp.
Carnivora	*Plithocyon stehlini*
	Ursavus intermedius
Perissodactyla	*Lartetotherium sansaniense*
	Hoploaceratherium tetradactylum
	Anchitherium aurelianense aurelianense
Artiodactyla	*Bunolistriodon lockarti*
	Hyotherium soemmeringi
	Dorcatherium naui
	Palaeomeryx bojani
	Lagomeryx cf. *L. parvulus*
	cf. *Procervulus* sp.
Proboscidae	*Gomphotherium angustidens*

Sources: Ziegler, 1995; authors, unpublished data.

basis of their fauna and that can be situated with reference to marine and other marker horizons appear to be between 15 and 16·8 Ma. The same appears to be the case for hominoid MN 5 localities in Anatolia (see below).

The varied flora of Engelswies, consisting of leaves and fruit, has been studied by Schweigert (1992) in detail. The high number of laurophyllous angiosperms indicates a warm, humid, subtropical or even tropical climate (Figure 4).

Hominoid anatomical description
(Figure 5)

Despite the fragmentary nature of the specimen, ENG. 4/1, there is no doubt that it is a hominoid upper molar fragment. The combination of features that are preserved on this specimen is unlike any nonhominoid tooth. Relatively bunodont teeth are known from a number of European Miocene mammals, but only fragments of suid and possibly a few carnivore (ursid, amphicyonid, some mustelid) teeth could conceivably mimic the anatomy of a primate molar as preserved in this specimen. However, the combination of simple occlusal morphology, thick enamel, occlusal outline in superior view corresponding exactly to that of a hominoid M^3, broad, rounded cusps on a vertically sided crown, and evidence of one lingual and one buccal root close to the cervix together clearly identifies this specimen as hominoid.

ENG. 4/1 is a worn upper molar preserving most of the distobuccal two thirds of the crown and a small portion of the roots. The specimen is fragmentary enough to make anatomical identification challenging [it has been identified previously as both an upper and a lower molar, though its hominoid affinities have not been at issue (Andrews et al., 1996; Köhler et al., 1999)]. It is in fact a left M^3 and is identified on the basis of the following features: strong occlusal wear, yet no distal interstitial facet; more strongly worn on the lingual half of the crown; occlusal surface inclined from buccal to lingual and then flattening lingually in distal view; lower crowned on the lingual side in distal view; buccal root cervix larger in section than the lingual root cervix; distal crown tapering; apparent reduction of the distal cusps relative to the mesial cusps; strongly convex and asymmetric distal margin; strongly distally flared distal crown surface. Any one of these features in isolation would not be unambiguously diagnostic to a left M^3, but their presence together on this specimen make identification clear.

Little anatomical detail is preserved on this specimen, but a few features are observable. The crown as preserved measures 10·3 mm mesiodistally and 12·1 mm buccolingually. We estimate the original
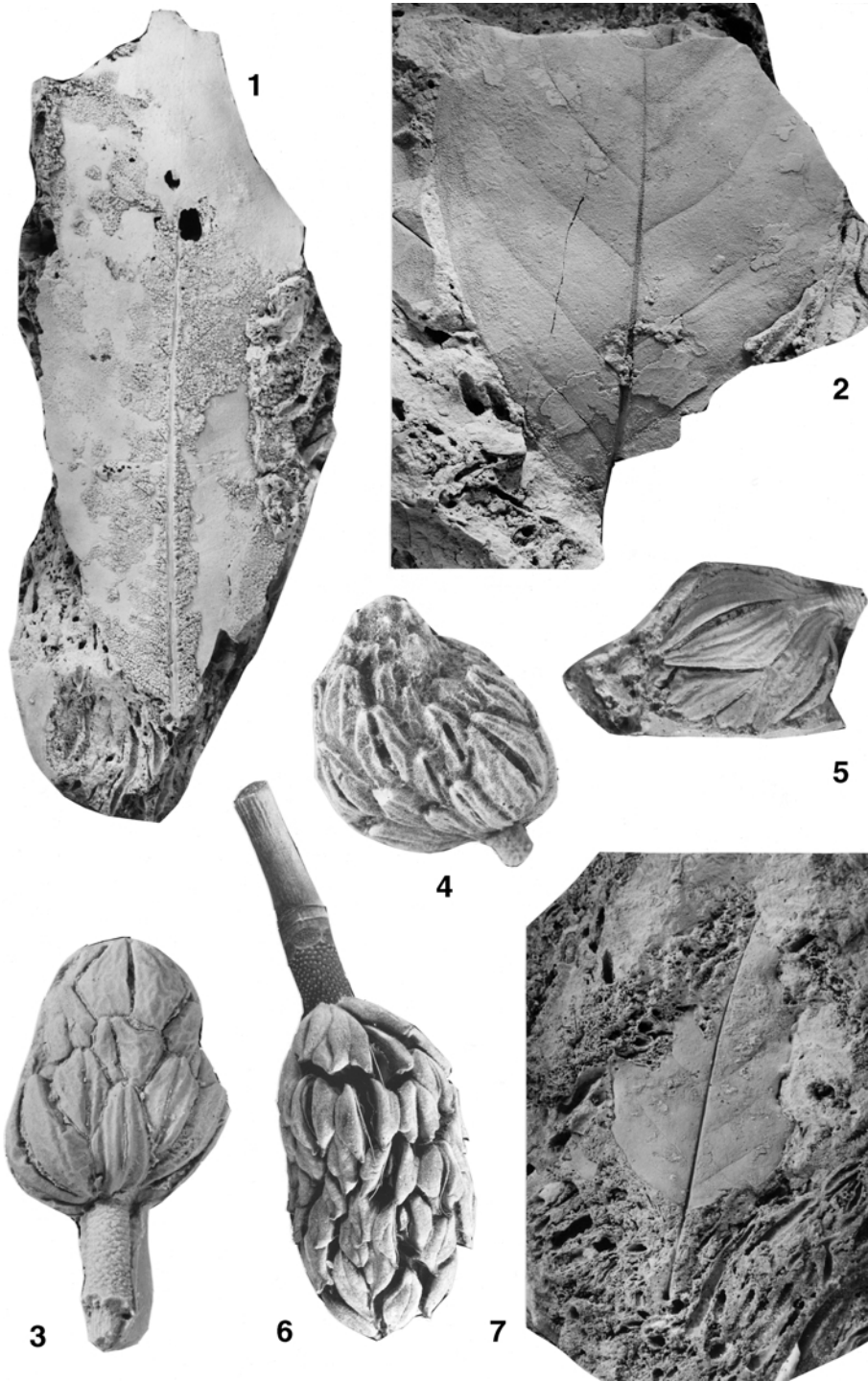
Figure 4. Macrofloral fossils from Engelswies. 1: *Magnolia dianae* leaf fragment, 2: *Magnolia mirabilis* leaf fragment, 3–5: *Magnoliaestrobus sigmaringensis* fruit, 6: *Magnolia grandiflora* (recent) fruit: *Symplocos* cf. *S. hallensis* leaf fragment. From Schweigert (1992), reproduced by permission.
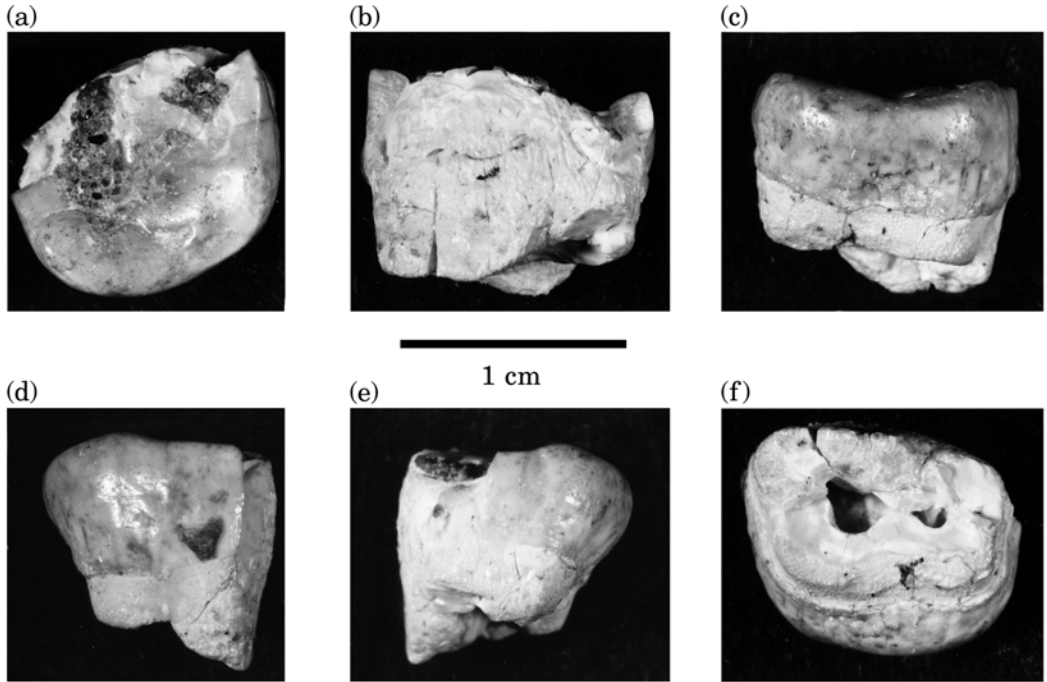
Figure 5. ENG 4/1, left M³ from Engelswies attributed to cf. *Griphopithecus* sp. (a) Occlusal (mesial edge facing up), (b) mesial (occlusal surface facing up), (c) distal, (d) buccal, (e) lingual, (f) cervical.

mesiodistal length to have been about 11 mm. Buccolingual breadth can be estimated more confidently at 12·2 mm. The cervix is well preserved, and the confluence of the roots at this point measures 7·9 × 11·5 mm. Though worn nearly flat, much of the occlusal surface enamel is retained, with dentine exposures confined to the cusps [Figure 5(a)]. The protocone is not preserved, but matrix fills a dentine exposure that appears to have coalesced between the distal portion of the protocone and the hypocone [Figure 5(a)]. The hypocone is well preserved, with the dentine pit at its center connected to the exposed dentine on the protocone. The distal marginal crista formed by the hypocone is thick, and the fissure between it and the postprotocone crista is still visible. This fissure, marking the mesial extent of the hypocone, is distally placed, as is more commonly seen in last molars, reflecting some degree of distal cusp reduction. The metacone is complete and bears a small dentine pit. The metacone is the smallest of the preserved cusps and is mesially placed relative to the hypocone. A thick postmetacone crista runs into the metacone's dentine pit, and a more subtly defined, low, rounded crista obliqua runs mesiolingually. This set of cristae defines a fovea distal to the postmetacone crista, a well defined fovea between the two metacone cristae, and the trigon basin mesial to the crista obliqua [Figure 5(a)]. This configuration is similar to that seen in other early or middle Miocene hominoid upper molars, such as the specimen described by Glässner (1931) from Neudorf Sandberg (now Děvínská Nová Ves, Slovakia) and some specimens from Paşalar (BP 19, 32, 34, 35, 37). The paracone is only partly preserved, mainly buccally and distally, and it retains evidence of dentine penetration in the form of a matrix-filled

pit. It is connected to the metacone by a sharp, well defined composite crista, a post-paracone crista and a premetacone crista, each of roughly equal length [Figure 5(a)]. There is almost no relief between the cusps and the trigon basin, yet little dentine is exposed in the trigon. A thin veneer of enamel remains at the most mesially preserved edge of the specimen. This surface is flat and is an additional indication that the dentine penetrance consisted of small, localized projections restricted to the cusp centers. In addition, the preserved or partly-preserved cristae are all thick and rounded. In mesial view a cross section of the enamel cap is visible [Figure 5(b)]. All of these observations are consistent with a tooth having thick enamel and low dentine penetrance. The patterns observed are similar to wear patterns on many thickly enameled Miocene hominoids, particularly the teeth from Paşalar, Turkey. It differs from other thickly enameled hominoid teeth, such as those of Proconsul and Afropithecus, which have enamel perforations exposing dentine at the cusp tips with relatively little wear, indicating the presence of relatively large and projecting dentine horns (Leakey & Walker, 1997; Beynon *et al.*, 1998).

The trigon appears to have been comparatively short and the hypocone displaced distally, consistent with the morphology of a hominoid M^3. No accessory cusps, grooves or cristae are preserved, although this is not surprising given the amount of wear. There is no sign of a lingual cingulum.

In distal, buccal and lingual views, it is clear that the crown was high [Figure 5(c), (d), (e)]. Despite the extreme occlusal wear, the crown is still about 5·2 mm from the cervix to the lowest point on the distal marginal crista [Figure 5(c)], 6·4 mm from the cervix to the tip of the metacone [Figure 5(d)] and about 4·8 mm from the cervix to the hypocone apex [Figure 5(e)]. In lingual buccal and basal views, a pronounced distal bulging of the crown is visible [Figure 5(d),

(e), (f)]. Basally the tooth is dominated by the walls and upper part of the canal of the buccal root, which was mesiodistally and buccolingually larger than the lingual root. The occurrence of single root canals suggests fused roots some distance from the cervix.

Taxonomy and biochronology

The specimen from Engelswies shares thick enamel and low dentine penetrance with several middle Miocene hominoids [*Kenyapithecus*, *Griphopithecus* (including *Equatorius*), and *Sivapithecus*]. It differs from these in its degree of hypsodonty and in the strong flare of the distal crown surface [Figure 5(d), (e)]. It also differs from early Miocene hominoids of similar size (*Proconsul*, *Afropithecus*) in lacking a cingulum [Figure 5(a)]. While some Paşalar M^3 specimens have a cingulum many do not, and in many of those that do it is confined to the mesiolingual corner of the tooth, which is not preserved on this specimen. While morphologically closest to the one permanent upper molar from Slovakia and the sample from Paşalar, the Engelswies specimen is distinguished by its crown height, its distal crown flare and the prominence of the distal marginal crista distally and lingually. For these reasons and because we hesitate to name a hominoid taxon based on a single molar fragment, we currently attribute this specimen to cf. *Griphopithecus*. The morphological similarities to *Griphopithecus* as defined by the samples from Děvínská Nová Ves and Paşalar are sufficient to be reasonably confident that the taxon is most similar to *Griphopithecus*. Given the morphological, temporal and geographic separation from other early and middle Miocene hominoids (see below) we think the Engelswies hominoid is probably a new genus, but the one known specimen is an unsuitable type.

Thickly enameled hominoids with low dentine penetrance first appear in the late

early to early middle Miocene within a relatively short time on three continents. In Africa they occur roughly contemporaneously at Maboko, Nachola, Kipsaramon and a number of other localities in Kenya (Ward et al., 1999). In Asia their first occurrence is recorded at Paşalar and Çandır, both in Turkey. In Europe, before the Engelswies discovery, thickly enameled hominoids were thought to first occur at the Sandhill locality (as opposed to the older fissures) of Děvínská Nová Ves, Slovakia. This is the type locality for *Griphopitheus darwini* (Abel, 1902). Indirect evidence based mainly on its primitive morphology suggests that the hominoid from Klein Hadersdorf in Austria is also *Griphopithecus*. This hominoid, originally named *Austriacopithecus*, is known only from ulnar and humeral fragments (two species were named by Ehrenberg (1938), one for each forelimb bone). *Austriacopithecus* has been synonymized with *Griphopithecus* on the basis of morphological similarities to *Griphopithecus* (or *Equatorius*) from Maboko, for which postcrania are known (Begun, 1992; Andrews et al., 1996). All of these localities are usually dated to either MN 6 (Paşalar, Çandır and Děvínská Nová Ves) or its chronostratigraphic equivalent (Maboko, Kipsaramon), but new data suggest that some revision to these ages are needed.

Benefit & McCrossin (1997) bracket Maboko between 14·7 and 16 Ma, which corresponds to mid MN 5 to early MN 6 in Central Europe based on biostratigraphic, radiometric and paleomagnetic evidence (Steininger, 1999). Paşalar, Çandır, and Děvínská Nová Ves Sandhill have traditionally been correlated to MN 6 on biostratigraphic grounds. Paşalar is considered to be basal MN 6 and Çandır upper MN 6 (Bernor & Tobien, 1990; Steininger et al., 1996), though Sen (1990) prefers an MN 5 date for Paşalar (see below). New evidence from Çandır indicates that this locality is more likely to be correlated with MN 5.

Most of the taxa from Çandır and Paşalar thought to be indicative of an MN 6 age are endemic to Anatolia and are not known from the MN zone reference localities, all of which are European. Among the Çandır taxa that are known from these reference faunas, nearly all occur before MN 6, and three taxa, *Keramidomys thaleri*, *Megacricetodon collongensis* and *Bunolistriodon* are extinct by MN 6 (de Bruijn et al., 2001; Begun et al., 2001). Paleomagnetic data consistent with this MN zone determination suggest an age of about 16·3 Ma (Krijgsman, 2001; Begun et al., 2001[2]). Paşalar is still considered slightly older than Çandır based on the stage of evolution of a number of taxa (Bernor & Tobien, 1990; Ünay, 1990; Gentry, 1990; Begun et al., 2001), but appears to be correlatable to MN 5, as suggested by Sen (1990). The Děvínská Nová Ves filled fissure deposits (Neudorf-Spalte) with *Epipliopithecus* are currently considered to date to upper MN 5 or the base of MN 6 (Rögl, 1999). The Děvínská Nová Ves sand hill locality is known from lithostratigraphic and tectonic evidence to be younger than this, and is currently considered to date to upper MN 6 (Rögl, 1999). Klein Hadersdorf is usually considered to be upper MN 6, and may well postdate Çandır (de Bruijn et al., 1992). In sum, Engelswies, reliably correlated to lower MN 5, is probably older than Makobo, based on radiometric dates from East Africa and the apparent age of MN 5 in Central Europe (see above). It may also be older than Paşalar and Çandır, though without the possibility of marine correlations or radiometric dates this cannot be definitively

[2]It should be noted that Krijgsman (2001), in his analysis of the paleomagnetic data from Çandır, concludes that the most likely age is about 13·4 Ma, based on the most likely correlation to the GPTS given an MN 6 age for the fauna. The 16·3 Ma age is based on the most likely correlation to the GPTS given an MN 5 age for the fauna, which is considered more likely by Sen (1990), de Bruijn et al. (2001) and Begun et al. (2001).

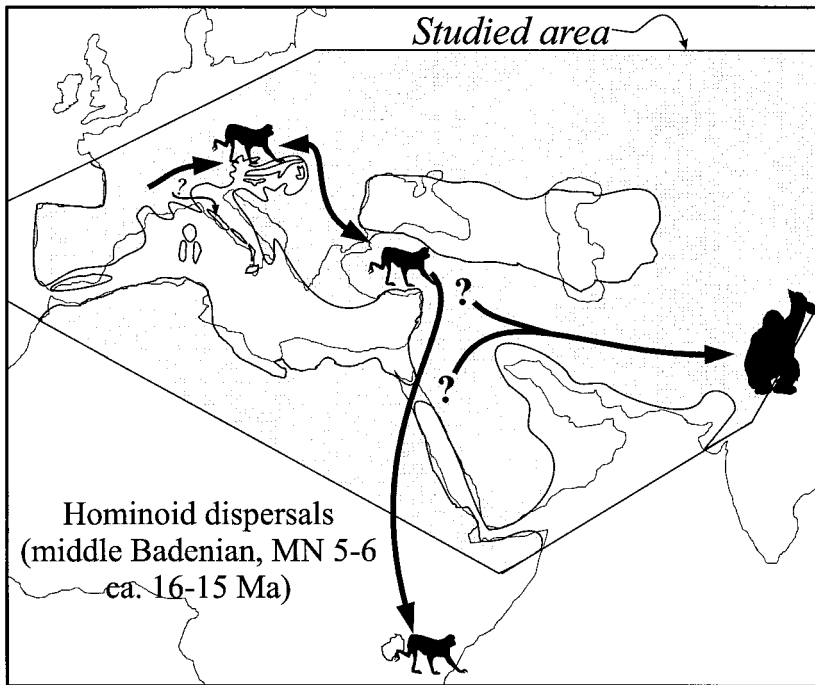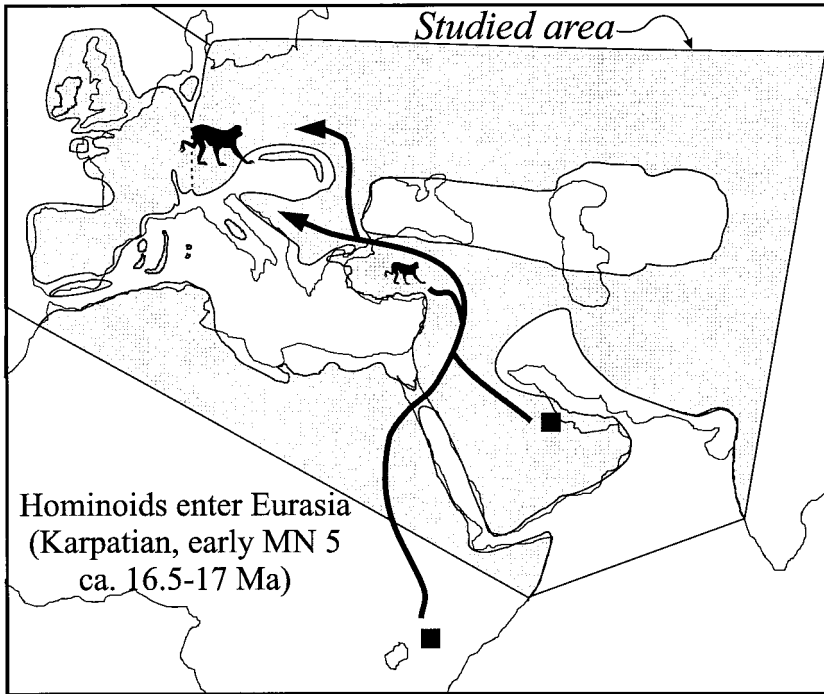determined at present. Engelswies is certainly older than Klein Hadersdorf and the Děvínská Nová Ves sands.

Discussion

The results of this analysis indicate that the first appearance datum for hominoids in Europe needs to be revised. The primate fossil from Engelswies, which is more valuable for its paleobiogeographic implications than for its phylogenetic or functional data, establishes the presence of a thickly enameled hominoid in Europe before the end of the early Miocene. Bernor & Tobien (1990) suggest that the first appearance of hominoids in Eurasia, at Paşalar, corresponds to the regression marking the end of the Langhian at about 15–15·5 Ma (Rögl & Steininger, 1983; Haq et al., 1987; Steininger et al., 1989), well into the middle Miocene. We present an alternative hypothesis, based on the newer evidence from Engelswies. The first occurrence of hominoids in Eurasia is older than 15·5 Ma and corresponds more closely to the pre-Langhian regression, ca. 16·5 Ma (Rögl & Steininger, 1983; Haq et al., 1987; Steininger et al., 1989; Bernor & Tobien, 1990; Rögl, 1999; Steininger, 1999).

Both regressions bracketing the Langhian transgressive event were characterized by extensive faunal exchange between Africa and Eurasia (Rögl & Steininger, 1983; Barry et al., 1985; Steininger et al., 1985; Thomas, 1985; Bernor et al., 1987, 1996; Mein, 1990; Bernor & Tobien, 1990; Harrison & Gu, 1999; van der Made, 1999; Rögl, 1999). It is likely that hominoids, and possibly also the ancestors of pliopithecids, migrated from Africa to Europe during the first of these regressions [see below and Figure 6(a)]. However, during and subsequent to the terminal Langhian regression there is much evidence for faunal exchange between Europe and Southwest Asia (Bernor et al., 1996; Begun et al., 2001).

Bernor & Tobien (1990) have characterized the Paşalar assemblage as being of mixed geographic origin. The overwhelming majority of taxa are of European, Asian or pan-Eurasian origin (Bernor & Tobien, 1990; Table 1, pp. 556–557; Begun et al., 2001). Only two taxa have any African distribution, and both of these (hominoids and the bovid Caprotragoides) are also known from Europe by at least MN 6 (Bernor & Tobien, 1990; Gentry & Heizmann, 1996; Andrews et al., 1996).

There is evidence from other mammals of a Central European source for many of the taxa found in Eastern Mediterranean early and middle Miocene faunas. Fahlbusch & Bolliger (1996) note the first occurrences of the eomyid rodents Eomyops and Keramidomys in Central Europe in MN 5. These genera first appear in Turkey at Çandır (de Bruijn et al., 2001). Among carnivores, the amphicyonid Amphicyon major, the ursid Plithocyon, the hyaenid Protictitherium and the felids Pseudailurus quadridentatus and Pseudailurus lorteti appear in Europe in MN 4/MN 5, probably before their occurrence at Paşalar in MN 5 (Werdelin, 1996; Werdelin & Solunias, 1996; Bernor & Tobien, 1990; Begun et al., 2001). At least one of these taxa, the primitive hyaenid Protictitherium, is considered to have been a partly arboreal omnivorous/insectivorous form (Werdelin & Solunias, 1996), which is ecologically consistent with hominoids and may suggest dispersal of both taxa under similar ecological conditions. The rhinoceros Brachypotherium brachypus occurs in Europe and Turkey in MN 5 (Heissig, 1996; Geraads & Saraç, 2001; Begun et al., 2001). This primitive rhino has broad, brachyodont molars and short limbs, and is considered to have had a diet of soft plants and possibly a preference for more wooded settings, which is also consistent with the supposed ecological preferences of middle Miocene hominoids (Andrews, 1990; Andrews et al., 1996, 1997). Heissig (1996) also notes the

Hominoids enter Eurasia
(Karpatian, early MN 5
ca. 16.5-17 Ma)

Studied area

Hominoid dispersals
(middle Badenian, MN 5-6
ca. 16-15 Ma)

Studied area

extreme rarity of African rhinos (*Diceros*) in Eastern Mediterranean faunas. Among suoids, the suids *Bunolistriodon* and *Conohyus* and the tayassuid *Taucanomo* occur first in Europe in MN 4/5 before appearing in Turkey in MN 5. The European taxa *Bunolistriodon lockharti*, which is known from Engelswies, and *Taucanomo sansaniense* are thought to be more primitive than their Turkish counterparts (Fortelius *et al.*, 1996). The giraffid *Giraffokeryx* and the bovid *Hypsodontus* also appear in Europe in MN 5 (Gentry & Heizmann, 1996). *Hypsodontus serbicus* from Europe is also thought to be more primitive than *Hypsodontus pronaticornis* from Paşalar (Gentry & Heizmann, 1996).

On the other hand, a number of other MN 5/6 mammals occur either first in the Eastern Mediterranean or contemporaneously in the Eastern Mediterranean and Central Europe, and in some cases the Eastern Mediterranean taxa appear to be more primitive than their European counterparts (Bollinger, 1996; Fahlsbusch, 1996; Fortelius *et al.*, 1996; Ünay, 1996; Werdelin, 1996). This latter case is especially true of a number of rodent groups, including eomyids, Cricetini and Cricetodontini (de Bruijn *et al.*, 1993, 2001; de Bruijn & Ünay, 1996). This indicates that the mammalian roadway between Europe and Western Asia was a two-way street and supports the view here of much more substantial amount of exchange between these regions during MN 5–6 than between Europe/Western Asia and Africa [Figure 6(b)].

What of the origins of African thickly enameled middle Miocene hominoids? A straightforward consideration of the biochronologic evidence presented here would suggest a Eurasian origin for African middle Miocene thickly enameled hominoids. Interestingly, there is evidence from other mammals of a Eurasian origin to a number of African lineages. Bovids such as *Eotragus* occur in Europe before they occur at Maboko (Gentry & Heizmann, 1996), and presumably migrated from either Europe or

Figure 6. Miocene land masses (gray) and marine basins (white) superimposed on modern coastal outlines for Europe, Western Asia and Africa to just south of the equator. Depicted are two hypotheses of hominoid dispersal consistent with the evidence discussed here. (a) Dispersal into Eurasia. Dark squares are early Miocene localities from which Eurasian hominoids may have dispersed (Kalodirr with *Afropithecus* in Kenya and Ad Dabtiyah with *Heliopithecus* in Saudi Arabia). The oldest Eurasian hominoid is known from Engelswies (large tailless catarrhine) but may have been present in Western Asia (small tailless catarrhine) and southern Europe as well. It is unclear whether this migration route passed north of the central Paratethys or by a more southerly route, although during the Karpatian a large marine connection linked the Mediterranean and central Paratethys (Rögl, 1999). The dotted line near the symbol representing Engelswies represents the Rhine Graben, which had connected the North and Mediterranean Swas during most of the Burdigalian but had closed by the end of the Karpatian (Rögl, 1999). (b) Serravallian dispersals of hominoids across the Old World. Note the reduced extent (regression) of the marine basins at this time. The central Paratethys remains connected to the Mediterranean by a comparatively narrow strait, the ''Transtethyan Trench Corridor'' (Rögl, 1999), and is considerably reduced in size. From the Molasse region, or possibly from southeastern Europe or Western Asia, hominoids disperse. Islands comprising the central portions of the Italian peninsula and portions of the larger modern islands of the present Mediterranean are more prominent, and it may have been at this time that some of the insular faunas of these regions appear, possibly including the ancestors of *Oreopithecus* (small arrow and ?). Tailless catarrhines in Europe represent the Děvínská Nová Ves sandhill locality (Slovakia) and Klein Hadersdorf (Austria). Tailless catarrhines in Anatolia and Kenya represent Paşalar/Çandır and Maboko/Kipsaramon. While the localities along the northern shore of the central Paratethys are probably younger, Engelswies and the Anatolian localities are close enough in age that the dispersal origin between central Europe and western Asia cannot be precisely situated. However, it appears that from somewhere in the central or subparatethyan realm hominoids dispersed into Asia (e.g. *Sivapithecus*) (large hominoid symbol) and Africa (*Equatorius* and *Kenyapithecus*). Maps modified from Rögl (1999).

South Asia to Africa before the end of MN 6. In contrast, bovids of Africa affinity do not reach Europe until the end of the Miocene (Gentry & Heizmann, 1996). Thomas (1985) suggests that gomphotheriids, amebelodontines, several carnivores and *Bunolistriodon* indicate Eurasian faunal influence on Afro-Arabian faunas before 16·1 Ma, which corresponds well to the possible entrance of a hominoid into East Africa suggested here. Tong & Jaeger (1993) also suggest that all African muroid rodents originated from Asia, with various lineages or their ancestors (*Democricetodon*, *Pronakalimys*, myocricetodontines, *Ternania*) migrating to Africa before Fort Ternan times (ca. 14 Ma). The pedetid muroid *Megapedetes*, which is known from both Fort Ternan and Maboko (Tong & Jaeger, 1993; Pickford, 1982), is also descended from a Eurasian immigrant, which must therefore predate Maboko.

It is beyond the scope of this paper to explore the morphological evidence for the origin of middle Miocene thickly enameled hominoids. However, it is worth noting that there is no agreement on the definitions of this clade, if it is a clade, nor on the position of this supposed clade relative to other Miocene hominoids (Pickford, 1986; Andrews, 1992; McCrossin & Benefit, 1997; Begun *et al.*, 1997; McCrossin *et al.*, 1998). *Afropithecus* bears some resemblance to *Kenyapithecus*, particularly in sharing thick enamel and a procumbent anterior dentition, and in masticatory robusticity (Leakey *et al.*, 1988; Leakey & Walker, 1997; McCrossin & Benefit, 1997). *Afropithecus* does not appear to share low dentine penetrance and reduced molar cingula with cf. *Griphopithecus* from Engelswies, or with *Griphopithecus* and *Kenyapithecus*. *Heliopithecus*, the thickly enameled hominoid from Saudi Arabia that may be congeneric with *Afropithecus*, also resembles *Griphopithecus* in the same features found in *Afropithecus* (Andrews & Martin, 1987). There are too few characters to perform a comprehensive phylogenetic analysis of the specimen from Engelswies [and the characters that are known, such as thick enamel, have proven to be very unreliable indictors of phylogeny (Begun *et al.*, 1997)]. However, nothing in the morphology of any of these taxa rules out a phylogenetic link between *Afropithecus*/*Heliopithecus* and *Griphopithecus*. *Griphopithecus* shares potentially derived characters with Engelswies in M^3 cingulum reduction and low dentine penetrance that suggest that they belong in the same clade to the exclusion of *Afropithecus* and *Proconsul*.

A number of scenarios are possible. The distribution of known fossil hominoids, of known migration and eustatic events, and the reconstruction of climate and paleoecology, all thought to explain the distribution patterns of Miocene terrestrial mammals, leads us to favor the following hypothesis. All the *Afropithecus*/*Heliopithecus* localities date to about 17 Ma (Leakey & Walker, 1997; Whybrow, 1987). It may be that a descendant of the *Afropithecus* clade expanded from an Africa–Arabia range to one that included Eurasia at about 16·5 Ma, during the pre-Langhian regression (TB 2·2 in Figure 3). We do not know if this taxon evolved into a *Griphopithecus*-like hominoid before entering Eurasia or upon colonizing it, but it seems to have radiated following its arrival in Eurasia and not in Africa. The first occurrence of this taxon is at Engelswies [Figure 6(a)]. Following the Langhian, with renewed sea level lowering, hominoids spread across western Eurasia (Slovakia, Austria, and Turkey) and back into East Africa (Ward *et al.*, 1999; Begun, 2000). This would account for the greater morphological similarities between Eurasian and East African latest early and early middle Miocene hominoids than between East African early and middle Miocene hominoids [Figure 6(b)].

This hypothesis is consistent with other inferred patterns of mammal migration

during the late early and early middle Miocene (Thomas, 1985; Bernor et al., 1987, 1996). It requires two intercontinental migration events and one cladistic event. These are the origin of thickly enameled middle Miocene hominoids from an *Afropithecus*-like taxon (in Africa or Eurasia), a migration of this taxon to Eurasia, followed by a radiation that included a migration of one descendant back to Africa. Though somewhat complex, this scenario is the most consistent with the current biochronologic evidence both for hominoids and other mammals. It is possible that an African taxon contemporaneous or even predating Engelswies and representing a better candidate for the ancestry of African middle Miocene hominoids remains to be found, but at this stage this is simply an additional assumption required of an alternative explanation. We currently favor a Eurasian origin of *Griphopithecus* (including *Equatorius*) and *Kenyapithecus*, which is most consistent with the biochronologic and morphological evidence [Figure 6(a)]. We recognize that the absence of evidence of older East African members of this clade is not necessarily evidence of the absence of these taxa. This hypothesis is testable through the recovery of more East African fossil hominoid material.

Summary and conclusions

The migration of thickly enameled hominoids into Eurasia at about 16·5 Ma was an important event in the evolutionary history of the hominoids (see also Bernor et al., 1996; Andrews et al., 1996). This *Griphopithecus* event, named for the senior taxonomic nomen among all thickly enameled middle Miocene hominoids, represents the origin of the diverse clade of Eurasian hominoids, and possibly even the origin of all living hominoids (Begun, 1996; Begun et al., 1997; Stewart & Disotell, 1998). While there is no pre-Pleistocene record of the

fossil relatives of gibbons, fossil taxa with clade affinities to living Asian and African hominids have been identified by many researchers, and the vast majority of these are Eurasian (Pilbeam, 1982; Andrews, 1992; Begun, 1996; Begun et al., 1997; Moyà-Solà & Köhler, 1995; Andrews et al., 1996; de Bonis & Koufos, 1993). Thickly enameled molars with bunodont cusps and low dentine penetrance may represent a key innovation that led to the radiation of hominoids of modern aspect. The evidence currently suggests that most of this evolutionary history occurred in Eurasia, with the direct ancestors of *Pongo* on the one hand and the African apes and humans on the other moving south into the tropics only towards the end of the Miocene (Begun, 1996, 2001).

Acknowledgements

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