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Bio-magnetostratigraphy and environment of the oldest Eurasian hominoid from the Early Miocene of Engelswies (Germany)

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ABSTRACT

The paleobiogeography of hominoids exhibits a puzzling pattern of migrations between and within Africa and Eurasia. A precise dating of hominoid-bearing localities is therefore essential to reveal the timing, direction and possible causes of dispersals. Here, we present a bio-magnetostratigraphic analysis of the section of Engelswies (Southern Germany, Upper Freshwater Molasse, North Alpine Foreland Basin) where the oldest Eurasian hominoid was found. Our paleomagnetic results reveal a very short normal and a reverse magnetic polarity for the entire section. The polarity record is correlated to the Astronomical Tuned Neogene Time Scale using an integrated stratigraphic approach. This approach follows the chronostratigraphic framework for the Upper Freshwater Molasse, which combines magnetostratigraphy with biostratigraphic, lithostratigraphic and ^{40}Ar/^{39}Ar dating results. According to this outcome, the reverse polarity of the Engelswies section most likely correlates to magnetochron C5Cr. The origin of the short normal polarity remains enigmatic. The magnetostratigraphic calibration and the evolutionary level of the Engelswies small mammal fauna suggest an age of 17.1–17.0 Ma (Early Karpatian, Early Miocene) for the oldest Eurasian hominoid, and roughly confirm the estimates of Heizmann and Begun (2001). The estimated age suggests that the first hominoids in Eurasia are contemporaneous with Afro-Arabian afropithecins, and dispersal may have been facilitated by intra-Burdigalian (∼18–17 Ma) sea-level low stands and the beginning of the Miocene Climate Optimum. The paleoclimatic and environmental reconstruction of the Engelswies locality indicates a lakeshore environment near dense subtropical rain forest vegetation, where paratropical temperatures (mean annual temperature around 20 °C) and humid conditions (mean annual precipitation > 1.100 mm) prevailed.

Introduction

The paleobiogeography of hominoids (afropithecids + hominids; the systematic framework follows Moyà-Solà et al., 2009) during the Neogene displays an intricate pattern of several dispersal events out of Africa, but also within Africa and Eurasia (Cameron and Groves, 2004; Andrews and Kelley, 2007). Many difficulties to disentangle these processes may be attributed to the complex paleogeographic history of these continents, especially during the Miocene, the scarce and incomplete fossil record, and also to inadequate dating of many fossil hominoid localities.

In this context, the first appearance of hominoids outside Africa is of particular importance. In 1973, Heinz Tobien excavated Miocene freshwater limestones of the South German locality Engelswies (Fig. 1), a site that was famous since the middle of the 19th century for the preservation of large mammal fossils (e.g., Schill, 1858). In the fossiliferous level 4 (Fig. 2), Tobien discovered a tooth fragment of a primate, which he later recognized as a left upper molar of a dryopithecin[1], on the 24th of June, 1973. A detailed investigation of this specimen by Heizmann and Begun (2001) identified a thickly enameled M3 with low dentine penetrance, which was referred to as cf. *Griphopithecus*. Both authors concluded, based on the biostratigraphic correlation of the mammal fauna, that the Engelswies section had to be of late Early Miocene age (17.0–16.5 million years ago, Ma). This discovery reinforces the hypothesis that thickly enameled molars were an adaptive key innovation that facilitated the early out

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[1] Unpublished manuscript of Heinz Tobien from the 8th January, 1985 (Staatliches Museum für Naturkunde, Stuttgart).

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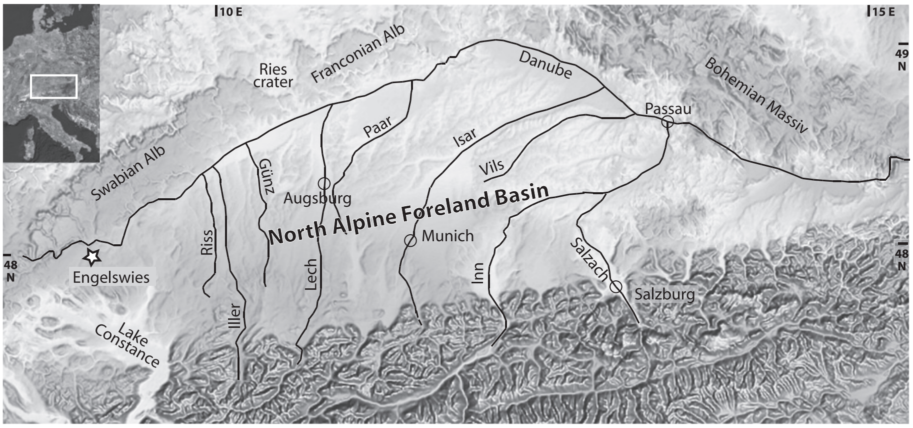

Figure 1. Digital elevation model of southern Germany (from Kuhlemann et al., 2006) with the geographic position of Engelswies (asterisk).

of Africa dispersal of hominoids (Heizmann and Begun, 2001; Begun, 2002; Alba et al., 2010). However, precise chronologic dating based on biostratigraphic long-distance correlation of mammal faunas can be disputable and some authors did not follow the stratigraphic concept of Heizmann and Begun (2001) and placed Engelswies in the Middle Miocene (e.g., Alba et al., 2010). In this paper, we present the first direct magnetostratigraphic calibration of the Engelswies section to the Astronomical Tuned Neogene Time Scale (ATNTS04; Lourens et al., 2004) and confirm earlier studies, which suggest age estimation of around 17 Ma, within the late Early Miocene.

Geologic setting

The Engelswies section (48°02.18′N and 9°07.43′E) is located in the western part of the North Alpine Foreland Basin (Fig. 1), in the state Baden-Württemberg, south of the city of Stuttgart. The outcrop is an abandoned limestone pit (Steinbruch am Talsberg), currently protected as a natural monument. In the 1920s, the exposed outcrops were more than 12 m thick (Kiderlen, 1931). Today, the studied sections are approximately 5 m thick (upper part of Kiderlen's profile) and comprise detrital limestone, oncolites, oncoidal crusts and stems, and *Potamogeton* rich carbonates (Fig. 2; for details see Rutte, 1953; Heizmann and Begun, 2001). According to borehole investigations, these freshwater carbonates lie directly above dark clays of the Kirchberg Formation (Hahn, 1968; Schweigert, 1992), suggesting that the section belongs to the lowest part of the Upper Freshwater Molasse, consequently corresponding to the Limnische Untere Serie lithostratigraphic unit (Doppler, 1989).

Small mammal biostratigraphy

The small mammals from Engelswies (fossiliferous levels 1–4, see Fig. 2) and Schellenfeld (a nearby locality of similar lithology and stratigraphy) are described by Ziegler (1995). Biostratigraphically most important are the cricetid rodents, especially the well elaborated chronospecies *Megacricetodon* aff. *M. bavaricus*

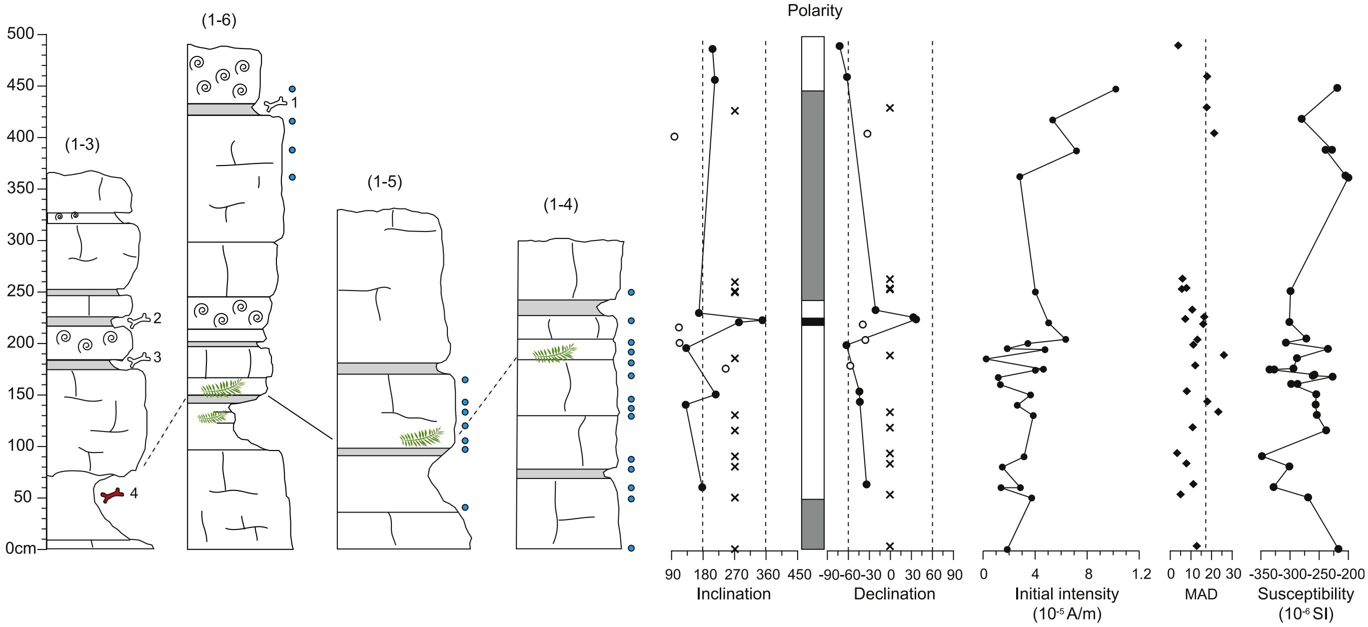

Figure 2. Lithological logs and paleomagnetic and susceptibility analyses results of Engelswies section. The paleomagnetic sampled positions are indicated with blue dots. The red bone (# 4) represents the hominoid-bearing level Engelswies 4 (bones 1–3 are additional small and large mammal levels, Engelswies 1–3) and green plant represents the *Potamageton* correlation level between the sections and the leaf and fruit-bearing horizons, respectively. Lithologic logs are redrawn after Schweigert (1996). The black (white) dots in the declination and inclination records represent reliable (uncertain) Characteristic Remanent Magnetization (ChRM) directions. Crosses are non-interpretable samples. In the polarity columns, black (white) zones indicate normal (reversed) polarity and gray zones undefined polarity. MAD indicates Mean Angular Deviation, the cut off is set at 15°. Intensity and susceptibility represent initial values measured at room temperature (20 °C).

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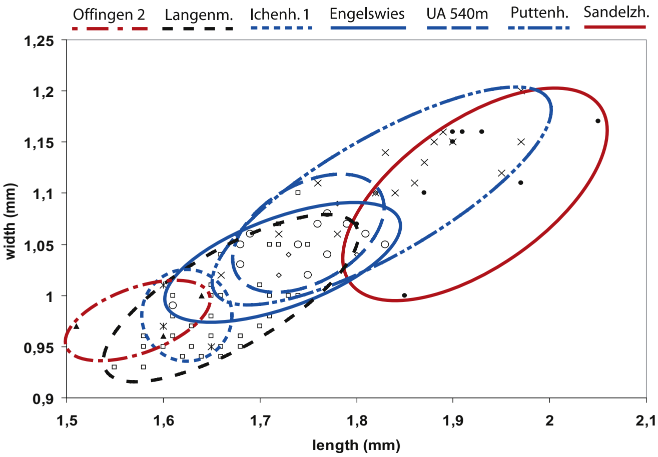

Figure 3. Scatter diagram of *Megacricetodon* aff. *M. bavaricus* (Fahlbusch, 1964) first lower molar size from Engelswies (data from Ziegler, 1995). The measurements are compared with *M. bavaricus* from Langenmoosen (Fahlbusch, 1964), Ichenhausen 1 and Offingen 2 (Abdul Aziz et al., 2010), and with *M.* aff. *M. bavaricus* from UA 540 m (Prieto et al., 2009), Puttenhausen classic (Wu, 1982), and Sandelzhausen (Wessels and Reumer, 2009). Red color indicates localities with normal magnetization correlated to chron C5Dn (Offingen) and C5Cn2n (Sandelzhausen), blue color indicates localities with inverse magnetization correlate to C5Cr, and black color indicates localities without palaeomagnetic information (Langenmoosen).

(Fahlbusch, 1964; Bolliger, 1992). The evolutionary history of the *M. bavaricus* lineage from the middle Ottnangian to the early Badenian is characterized by significant molar size increase (Fahlbusch, 1964; Abdul Aziz et al., 2010) of more than 60% in about three million years. This chronospecies therefore represents the most precise biostratigraphic tool around the Early to Middle Miocene transition in Central Europe (Heissig, 1990, 1997). Other small and large mammal taxa are of lesser importance for high-resolution biostratigraphy, because their rate of morphologic/morphometric evolution is by far lower.

The evolutionary level of the *Megacricetodon* aff. *M. bavaricus* reported from Engelswies is between the samples from the well-known localities of Langenmoosen (older than Engelswies; Fahlbusch, 1964) and Puttenhausen classic (Wu, 1982), as well as Sandelzhausen (both younger; Wessels and Reumer, 2009) (Fig. 3). Compared with the new data from western Bavaria (Abdul Aziz et al., 2010), the Engelswies fauna is younger than Offingen 2 and Ichenhausen 1 and slightly older than the level of UA 540 m (Untereichen-Altenstadt 540 m; Prieto et al., 2009; for detailed morphometric data see Supplementary Information). According to the local biostratigraphy, the Engelswies fauna corresponds to the earliest part of OSM C+D.

Magnetostratigraphy

Samples and methods

The Engelswies sections are sampled at regular intervals varying between five and 30 cm (average 19 cm). All samples were drilled using an electric water-cooled drill powered by a generator. The initial magnetic susceptibility of the samples was measured on a Kappa bridge KLY-2. The characteristic remanent magnetization (ChRM) was determined by thermal (TH) demagnetization, using incremental heating steps of 20 and 30 °C, carried out in a laboratory-built shielded furnace. To monitor changes in the mineralogical composition, the bulk magnetic susceptibility was measured after each thermal step on a Minikappa KLF-3 (Geofyzika Brno). The natural remanent magnetization (NRM) was measured on a vertically oriented 2G Enterprises DC SQUID cryogenic magnetometer (noise level 10^{-7} A/m) in a magnetically shielded room at the Niederlippach Paleomagnetic Laboratory of Ludwig-Maximilians-University Munich, Germany. Demagnetization results are plotted on orthogonal vector diagrams (Zijderveld, 1967) and ChRM directions are calculated using principle component analysis (PCA; Kirschvink, 1980).

Results

Paleomagnetic results

Twenty-four samples from the composite Engelswies section were analyzed. The results of the thermal demagnetization are of variable quality. The samples have low NRM intensities, between 0.012 and 0.1 mA/m (average 0.04 mA/m) (Fig. 2). Analysis of the Zijderveld diagrams revealed the presence of three magnetic

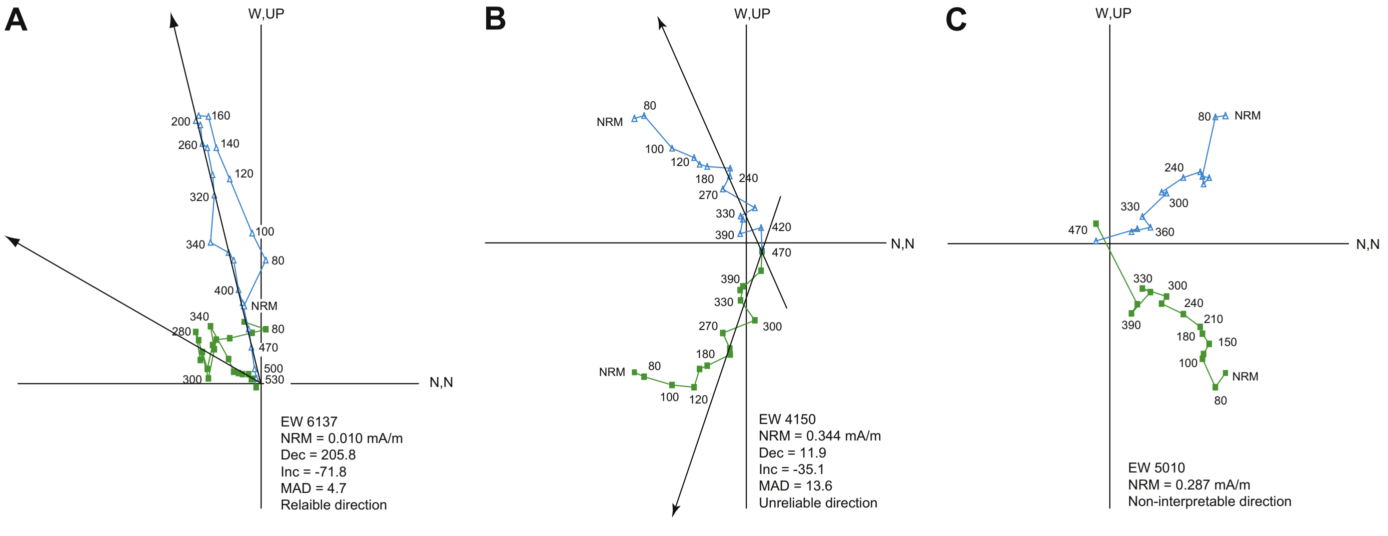

Figure 4. Thermal demagnetization diagrams. The Zijderveld diagrams denote the projection on the horizontal (filled squares) and vertical (open triangles) scales. Values along demagnetization trajectories indicate temperature steps in °C. Samples are shown of reliable (A), unreliable (B) and non-interpretable (C) ChRM directions.

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components. The first viscous component is removed at 100 °C and a second normal oriented component is removed around 210 °C. The third component is interpreted as the characteristic remanent magnetization (ChRM). Two unblocking temperatures have been distinguished. The majority of the samples have unblocking temperatures between 360 °C and 480 °C, suggesting that iron oxides are the main carrier of the ChRM (Fig. 4). A few samples have higher unblocking temperatures, between 500 °C and 560 °C, suggesting magnetite as the main carrier of the ChRM (Fig. 4).

The ChRM directions were calculated for more than six temperature steps in the range of 210–560 °C. The quality of the measurements and the line fitting were evaluated by visual inspection of Zijderveld diagrams and by calculating the maximum angular deviation (MAD). MAD values larger than 15° and/or samples with unconvincing ChRM directions were considered unreliable and are indicated with open circles in Fig. 2. Non-interpretable samples are shown as crosses in Fig. 2.

Magnetic susceptibility versus intensity

The magnetic susceptibility measured on selected samples from the Engelswies carbonates shows an average susceptibility value of -270×10^{-6} SI. Half of the samples show a progressive increase in susceptibility starting around 270 °C, however, the decay curve

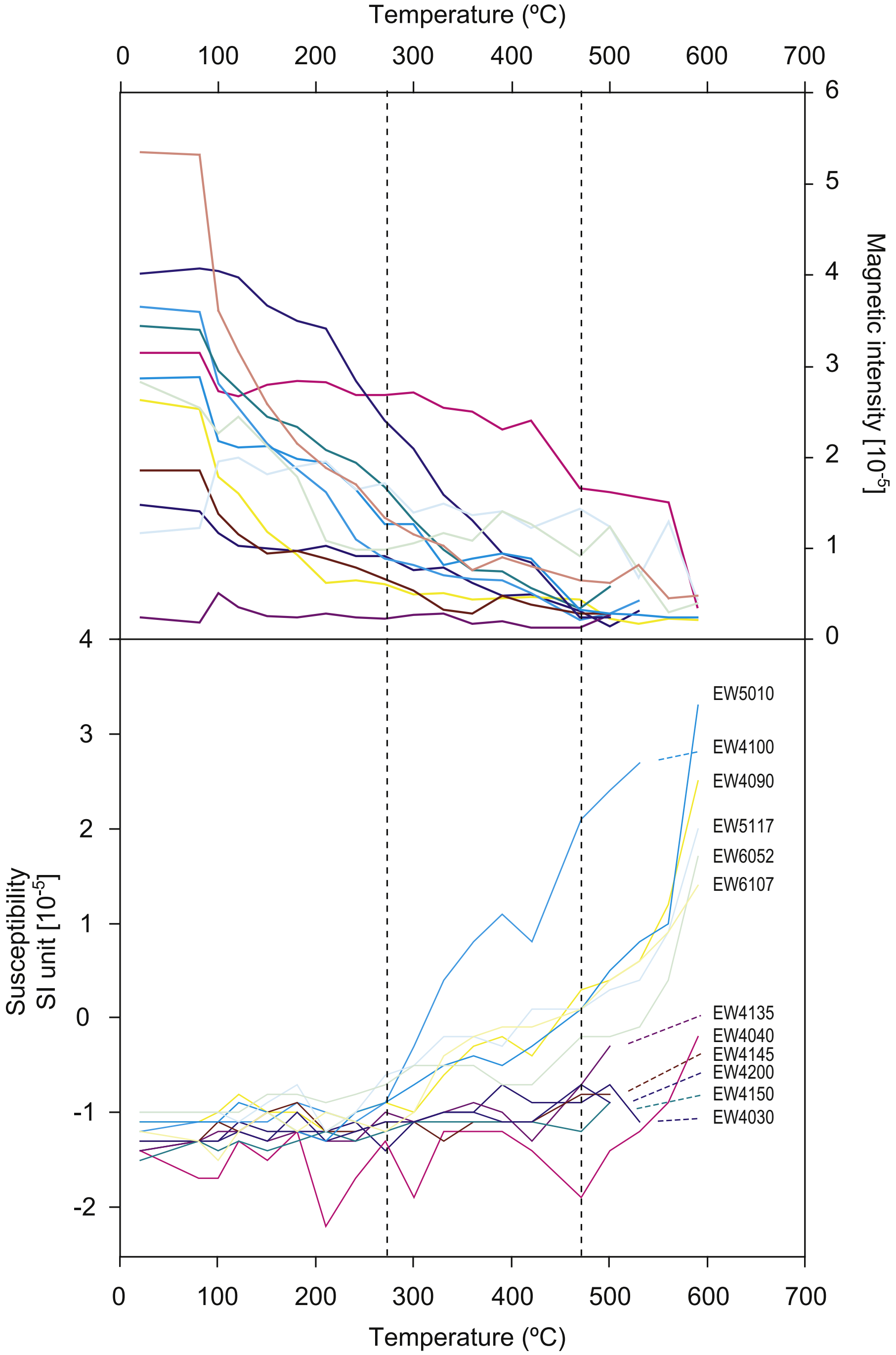

Figure 5. Susceptibility and intensity versus temperature of selected samples from Engelswies. See text for discussion.

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of the magnetization intensity does not seem to be affected (Fig. 5). Since the samples are freshwater limestones, which are usually rich in pyrite minerals, the susceptibility increase in the range 270–470 °C could be related to the oxidation of iron sulfides. At temperatures higher than 470 °C, the intensity decay curve shows that most of the analyzed samples are at a minimum. Also, several samples show a subsequent increase in susceptibility after 470 °C.

Discussion

Correlation to the ATNTS04

The declination and inclination results of the Engelswies composite section are plotted in stratigraphic order. The polarity record of Engelswies is dominantly reversed with a short normal (Fig. 2). Non-interpretable and intervals lacking data are represented by the gray shaded areas in the polarity record. The normal polarity has been found in two parallel sections (one sample from Section 1–4 the other from Section 1–5, see Fig. 2), suggesting that this normal direction is reliable. It must be noted that both samples come from the organic-rich *Potamageton* correlation level (see Fig. 2) and could have been remagnetized. However, no clear indications have been found for remagnetization. Correlation of the Engelswies polarity record to ATNTS04 has been achieved by comparing the bio-magnetostratigraphy of this locality to the established chronostratigraphic framework for the eastern and western Bavarian Upper Freshwater Molasse (UFM; Abdul Aziz et al., 2010).

Based on the first lower molar size (*m*/1) of *Megacricetodon* aff. *M. bavaricus* (Fig. 3), the Engelswies locality can be biostratigraphically placed between Puttenhausen classic and Ichenhausen 1, slightly below Untereichen-Altenstadt 540 m (UA 540) (Fig. 6). All three small mammal levels belong to a long reversed polarity interval that is correlated to chron C5Cr (Abdul Aziz et al., 2008, 2010). The next older normal chron C5Dn contains the level of Offingen 2 (Abdul Aziz et al., 2010), which is biostratigraphically more primitive (Fig. 3 and Supplementary information). Whereas Puttenhausen classic is situated in the late part of chron C5Cr (~16.8 Ma) and Ichenhausen 1 in the earlier part (~17.2 Ma), the position of UA 450 correspond to the middle portion of chron C5Cr (~17 ± 0.1 Ma; Abdul Aziz et al., 2010: Figs. 5, 14). Accordingly, the proposed magnetostratigraphic calibration of the Bavarian UFM sections to the ATNTS04 implies that the reversed polarity of the Engelswies section can be assigned to chron C5Cr, suggesting an age of approximately 17 Ma. The short normal polarity does not coincide with any known short normal polarity within subchron C5Cr in the ATNTS04 and its origin remains enigmatic. Thus, combined biostratigraphic and magnetostratigraphic information indicates a chronologic position of the Engelswies section in the

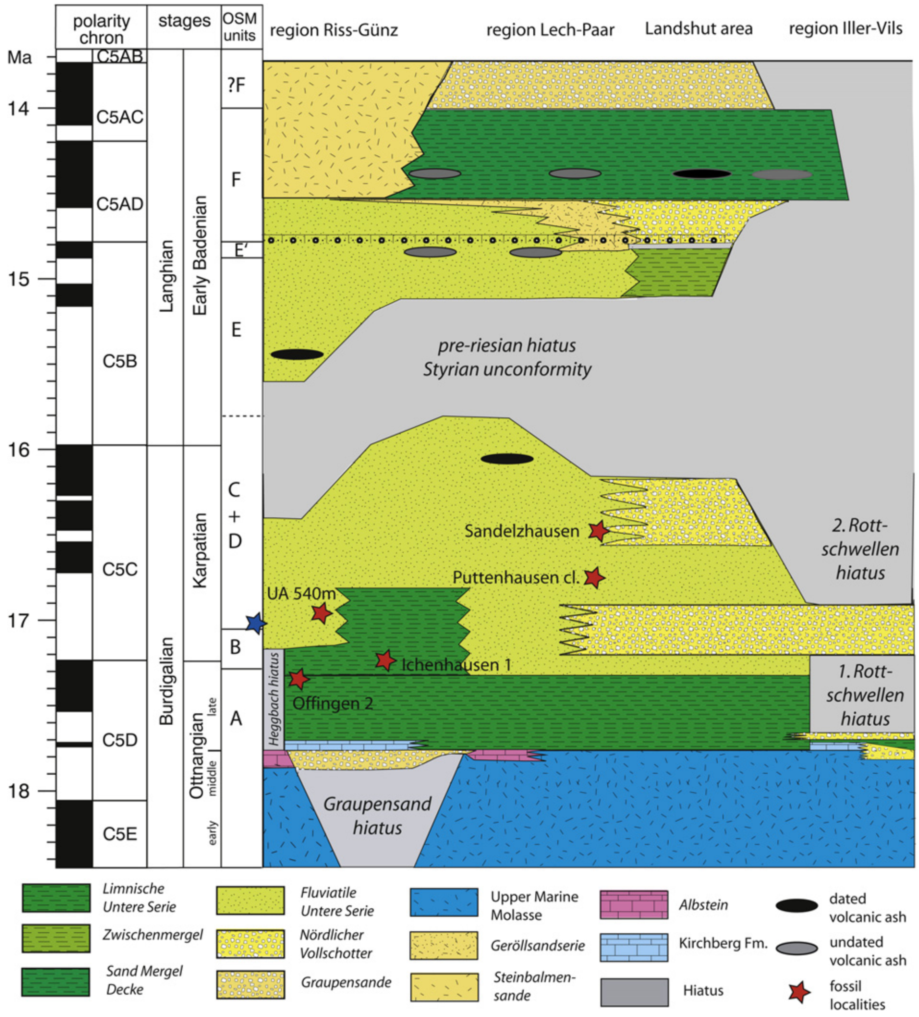

Figure 6. Synoptic chart of the chronology for the Lower to Middle Miocene sediments in the Bavarian part of the NAFB (according to Abdul Aziz et al., 2010), the stratigraphic position of biostratigraphic important localities (red stars) and of Engelswies (blue star, outside the area covered by the chart).

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lower third of chron C5Cr (17.235–16.721 Ma, Lourens et al., 2004), between 17.1 and 17.0 Ma (Fig. 6).

Chronologic comparison to Early and Middle Miocene hominoid localities

These results indicate that the Engelswies hominoid is stratigraphically significantly older than the European/Anatolian Middle Miocene *Griphopithecus* (and *Kenyapithecus*) localities (Fig. 7) of Klein Hadersdorf (late Early Badenian regression between the Upper Lagenid Zone and the *Spiroplectammina* Zone, 14.2 Ma; Strauss et al., 2006), Devínska Nová Ves Sandberg (highstand of Late Badenian transgression, 13.6–13.5 Ma; Kováč et al., 2007; for detailed stratigraphic information to Klein Hadersdorf and Devínska Nová Sandberg see Supplementary Information), Paşalar (based on rodents and suoids, 13.8–13.6 Ma; Pelaez-Campomanes and Daams, 2002; Made, 2003) and Çandır (based on suoids and magnetostratigraphy 13.5 Ma; Krijgsman, 2003; Made, 2003; for detailed stratigraphic information to Paşalar and Çandır see Supplementary Information), as well as the African *Equatorius*, *Nacholapithecus* and *Kenyapithecus* localities Kipsaramon BPRP#122 (15.58–15.36 Ma; Behrensmeyer et al., 2002), Maboko Formation bed 3 (~15 Ma; Feibel and Brown, 1991), Nachola unit 3 (14.77 ± 0.1 Ma; Nakatsukasa and Kunimatsu, 2009), and Fort Ternan (13.7 ± 0.3 Ma; Pickford et al., 2006).

Engelswies is also significantly older than the first European pliopithecids (*Pliopithecus antiquus*), which arrived in the NAFB in the earliest Middle Miocene (Early Badenian) at 15.0 Ma in the locality Ziemetshausen 1c (Heissig and Fiest, 1987; Abdul Aziz et al., 2010: Fig. 15).

Otherwise, the Engelswies hominoid is rather contemporary to thick enameled Afro-Arabian afropithecins like *Afropithecus* from Kalodirr (17.5 ± 0.2–16.8 ± 0.2 Ma; McDougall and Brown, 2009) and Locherangan (17.5 ± 0.3 Ma; Anyonge, 1991), and *Heliopithecus* from Ad Dabtiyah (~18–16 Ma; Whybrow and Clements, 1999).

Palaeoenvironmental context of the Engelswies hominoid

The reconstruction of the landscape surrounding the Engelswies Lake can be drawn by sedimentologic indications and the preserved fossil content (leaves and fruits, vertebrates). All botanical and zoological fossils come from a ~3 m thick portion of the exposed section (Fig. 2; contra Andrews and Kelley, 2007), representing probably a very short time-interval of a few thousand years. Unfortunately, all non-mammalian vertebrates of Tobien's excavations have been lost. Therefore, the paleoclimatic and environmental reconstruction is based only on paleobotanical data (Schweigert, 1992; Böhme et al., 2007), mammals and comparisons with contemporaneous sections of the UFM.

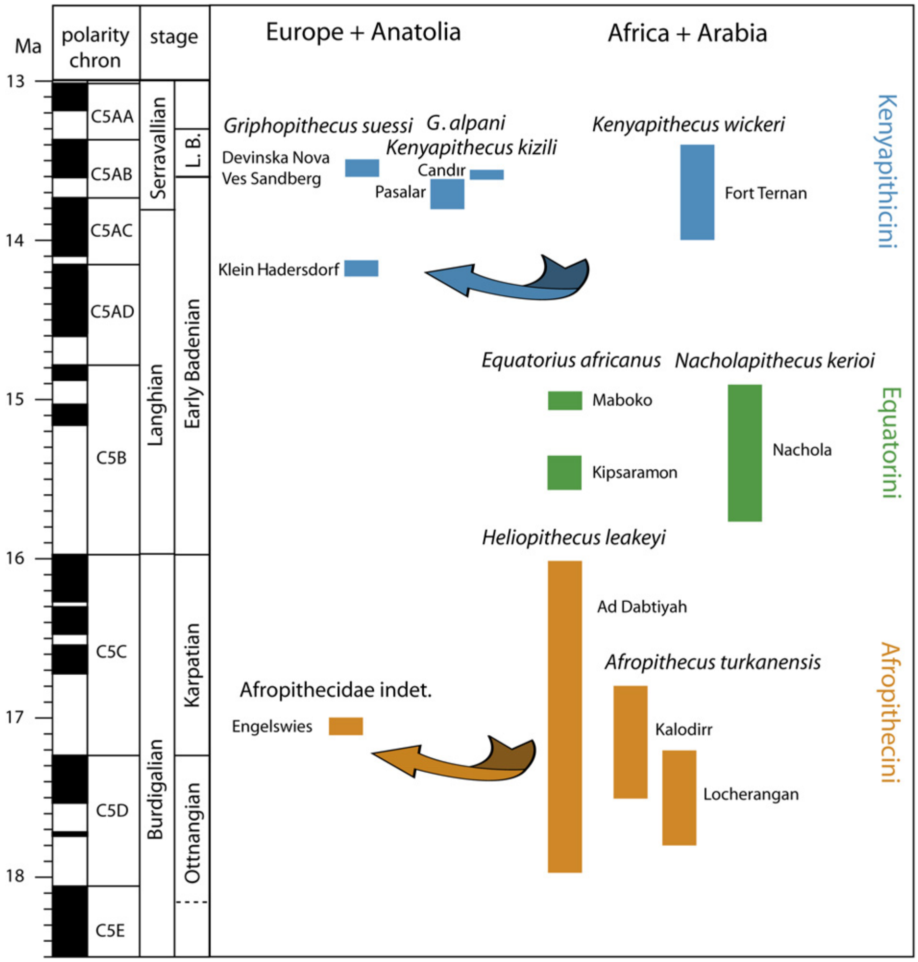

Figure 7. Stratigraphic distribution of Eurasian and African Afropithecinae. Arrows indicate possible migrations between Eurasia and Africa. The systematic framework is following Moyà-Solà et al. (2009).

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Schweigert (1996) interpreted the lithology (carbonate tufas, detrital limestones) and the carbonate microfacies (oncolites, cyanobacterial "reefs", etc.) as indicative of the littoral of a shallow lake, which was fed by carbonate saturated rivulets from the adjacent northerly situated karst plateau of the Suebian Alb.

He further described 36 macrofloral taxa (Schweigert, 1992) of which Lauraceae are dominant. The structure of the lake exhibits a zonality characterized by a reed-zone (encrusted stems) and a shallow-water pondweed-zone (*Potamogeton* rich carbonates). A probably narrow riparian-zone was covered with trees (*Salix*, *Alnus*, *Liquidambar*, *Glyptostrobus*), ferns (*Pteris*, *Pronephrium*), and herbs (*Heliconia*, *Zingiberoideophyllum*), indicating partly swampy conditions. The northern bank of the lake was relatively steep (palaeorelief due to erosion prior the sedimentation of the Kirchberg Fm, *Graupensand Hiatus* in Fig. 6) and covered with a lush evergreen broad-leaved forest. The dominated laurophyll tree taxa (*Daphnogene*, *Persea*, *Magnolia*, *Myrica*) are accompanied by climbing rattan palms (*Calamus*) and climbing ferns (*Lygodium*), forming a dense underbrush (Schweigert, 1992). Such a vegetation is in accordance with a dominance of arboreal and semi-arboreal, as well as frugivore and browsing large mammal species (Andrews and Kelley, 2007).

The floral composition and vegetation of Engelswies is unique in the NAFB (especially regarding the association of ferns, herbs and palms) and shows most botanical similarities to the palaeo-flora of Ipolytarnóc, northern Hungary (Schweigert, 1992), coming from the basal part of the Gyulakeszi Rhyolite Tuff Formation (Hably, 1985) for which an ^{40}Ar/^{39}Ar age of 17.13 ± 0.14 Ma is determined (Pálfy et al., 2007; recalibrated according to Kuiper et al., 2008). Nemejc and Knobloch (1973) describe a similar flora from Lipovany in southern Slovakia, which is only 7 km away from Ipolytarnóc and derives from the same basal layers within the Gyulakeszi Rhyolite Tuff Formation. According to Mai (1995), both floras belong to the floral complex of Ipolytarnóc-Luzern, characterized by a dominance of paleotropical elements and a high percentage of notophyll leaves, palms and ferns, which indicate a "subtropical rain forest vegetation" (Mai, 1995: 390). Palynological assemblages from coaly sediments directly overlying the Gyulakeszi Rhyolite Tuff (Pôtor beds of the Salgótarján Formation) are also indicative of a very warm climate (Planderova, 1990). Schweigert (1992) compared the Engelswies flora with the transition zone of southeast Asian paratropical rainforests to notophyllous broad-leaved evergreen forests.

Böhme et al. (2007) analyzed the contemporaneous (early Karpatian according to Abdul Aziz et al., 2010, contra late Karpatian as stated in the publication) xyloflora of the southern slope of the Franconian Alb, about 200 km to the northwest of Engelswies. The diverse flora point to subtropical semi-deciduous limestone forests dominated by legumes and Lauraceae, and the paleoclimatic analysis indicates (in contrast to Engelswies) a distinct dry season. Although the time-averaging for this composite xyloflora is large (~400 kyr) and edaphic condition may differ (oligotrophic rendzic leptosols at the Franconian Alp), the different vegetation at Engelswies may reflect fast changing climatic conditions in the early Karpatian.

Therefore, the uniqueness of the Engelwies floral composition within the NAFB is probably not only due to special site-related factors, such as high groundwater level and the southern slope of the Graupensand valley (Schweigert, 1992), but also due to favorable, but short-term climatic conditions.

Paleoclimate during the late Early Miocene in the NAFB

The paleoclimatic analysis of the Engelswies flora indicates in accordance with the flora from Ipolitarnóc (Hably, 1985) a mean annual temperature (MAT) of 20 °C or slightly more (Schweigert, 1992), whereas Mosbrugger et al. (2005; Coexistence Approach) quantified lower MAT values, ranging between 16.4 and 17.0 °C. The warmer estimates compares well with the MAT of the early Karpatian xyloflora from the Franconian Alb (Böhme et al., 2007, Coexistence Approach) of 15.7–20.5 °C and the late Karpatian estimates for the locality of Sandelzhausen (16.5 Ma) of 18.0–20.8 °C (Böhme, 2010; combined estimates from ectothermic vertebrates and xyloflora). Cold month temperature (CMT) estimates for Engelswies result in 5.0–5.6 °C (Mosbrugger et al., 2005), which is again cooler than results for the xyloflora (5.6–13.3 °C) and for Sandelzhausen (12.6–13.3 °C), suggesting a slight seasonality in temperatures and frost-free winters. These warm subtropical temperature estimates indicate that the Engelswies locality falls well into the Miocene Climatic Optimum (Böhme, 2003), however, postdates the Miocene Thermal Maximum in the early late Ottnangian (17.9–17.7 Ma), where MATs of 22.2–24.2 °C and CMT of 16.7 °C prevailed (Böhme et al., 2007; Böhme and Winklhofer, 2008).

Schweigert (1992) reconstructed for Engelswies a humid climate and the mean annual precipitation (MAP) has been quantified using the Coexistence Approach to 1122–1355 mm (Mosbrugger et al., 2005). These data are in good accordance with the MAP results based on Early Karpatian xyloflora (Böhme et al., 2007) and bioclimatic analysis of ectothermic vertebrates (Böhme et al., 2010).

In summary, the vegetation of Engelswies during the late Early Miocene resembles extant warm subtropical rainforests of southeastern Asia. The maximum rainfall occurred during the summer (Böhme, 2004; Böhme et al., 2007), however, in a meteorological sense, it was certainly not a monsoonal climate (contra Andrews and Kelley, 2007).

Conclusion

The Engelswies section reveals a reverse magnetic polarity and according to the chronostratigraphic framework of the UFM of the NAFB, the bio-magnetostratigraphic correlation indicates a position within the lower third of magnetochron C5Cr, suggesting an age between 17.1 and 17.0 Ma (Early Miocene, late Burdigalian, early Karpatian). The hominoid tooth from Engelswies therefore represents the oldest thickly enameled ape outside Africa, confirming earlier interpretations (Heizmann and Begun, 2001). This early hominoid predates the European and Anatolian *Griphopithecus* samples from the Middle Miocene (late Langhian/early Serravallian, late Early to Late Badenian) by at least three million years.

The chronologic relationships support the idea that the Engelswies hominoid was a descendent of Early Miocene Afro-Arabian afropithecins, as suggested by Heizmann and Begun (2001). If so, the temporary closure of the Tethys seaway during intra-Burdigalian (between ~18 and 17 Ma) global sea-level low stands (e.g., Bur3 and Bur4 sequence boundaries of Hardenbol et al.,1998; see also the discussion in Harzhauser et al., 2007) may have facilitated dispersal from Afro-Arabia into Eurasia during the beginning of the Miocene Climate Optimum (Böhme, 2003).

Paleobotanical data indicate that the first successful colonization of Eurasia by afropithecins in the Early Miocene may be favored by the temporary existence of dominantly evergreen subtropical rain forest vegetation during the early Karpatian. However, the significant gap between the Engelswies hominoid and later European kenyapithecines as well as paleoclimatic considerations lead us to speculate that this early out of Africa migration end up in a dead end. Possibly, a later dispersal event of African kenyapithecines around 14 Ma (Langhian regression and the Middle Miocene climate transition, Shevenell et al., 2004) gave rise to the long-term colonization of Eurasia by hominoids and the evolution of the first hominids (Dryopithecini).

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jhevol.2011.04.012.

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