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A Middle Miocene large Hominoid from Thannhausen (MN 5-6) Germany

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Abstract

An isolated lower central incisor from the freshwater molasse deposits at Thannhausen (late MN 5 or basal MN 6), Swabia, Germany, is described and interpreted as belonging to a large-bodied hominoid. It is most likely to represent *Griphopithecus suessi* or a closely related species. The specimen helps to fill what used to be a lengthy gap in the fossil record of hominoids in Germany stretching from MN 5 (Engelswies) to MN 9 (Vallesian karst deposits in the Swabian Alb and fluvial sediments in the northern Rhine Graben). The specimen poses interesting biogeographic questions.

Key words: Hominoid, incisor, Germany, upper freshwater molasse, Middle Miocene Palaeoenvironment.

Zusammenfassung

Aus der oberen Süßwassermolasse bei Thannhausen (obere MN 5 oder basale MN 6), Schwaben, Deutschland, wird ein einzelner, unterer zentraler Schneidezahn beschrieben. Der Zahn gehört zu einem großen Hominoiden, vermutlich *Griphopithecus suessi* oder eine nahe verwandte Art. Das Fossil hilft dabei, eine Lücke im Fossilbefund der Hominoiden in Deutschland – von MN 5 (Engelswies) bis MN 9 (Karst-Ablagerungen aus dem Vallesian der Schwäbischen Alb und fluviatile Sedimente des nördlichen Rheingrabens) – zu füllen. Darüber hinaus wirft das Fossil intertessante biogeographische Fragen auf.

Schlüsselwörter: Hominoid, Schneidezahn, Deutschland, obere Süßwassermolasse, Mittelmiozän, Paläoumwelt

1. Introduction

Thannhausen is a Middle Miocene fossil locality (late MN5 or early MN 6) in Swabia, Germany (Dehm 1980; Eronen & Rössner 2007) (Fig. 1). The fossiliferous deposits occur in the upper freshwater molasse (obere Süßwassermolasse). For many years fossil vertebrates were collected by Mr. Geiselmann during operations at the Thannhausen Garden Centre (label with the fossils), and most of the specimens have been housed in the BSPG, Munich (Dehm 1980), but some are also kept at the Heimatsmuseum Thannhausen. The mammalian fauna from Thannhausen comprises a diversity of carnivores, proboscideans, perissodactyls and artiodactyls (Tab. 1), all with characteristic late Middle Miocene affinities.

There has been debate about the correlation of the various fossiliferous localities in the upper freshwater molasse, but the regional marker horizon (main bentonite) provides a useful key for placing many of the localities (Kälin & Kempf 2009; Abdul-Aziz et al. 2010). Thannhausen is beneath this horizon (OSM F in Heissig 1997, 2006), which would place the site into MN 5 according to Heissig (1997, 2006), who correlates post-Ries faunas with MN 6. Whatever the final outcome of the debate in terms of correlation to the MN zonation may be, Thannhausen is younger than Engelswies, which correlates with basal levels of MN 5, and it probably is older than Sansan, France, the niveau répère of MN 6.

2. Material and methods

BSPG 1968 I 171, hominoid right i/1 in light wear, collected by Mr. Geiselmann at Thannhausen Gärtnerei (23.5.1968). The specimen was measured with sliding callipers to the nearest 0.1 mm, and images were captured with a Sony 10.2 megapixel cybershot camera and processed using Photoshop Elements 3

Table 1: Mammal list of the Thannhausen Fauna (Data from Dehm 1980; Rössner 2002; Eronen et al. 2007, and personal observation of fossils in the BSPG).

Carnivora	
	Amphicyon cf. *steinheimensis*
	Miohyaena certa
	Pseudaelurus cf. *quadridentatus*
Primates	
	Griphopithecus suessi
Proboscidea	
	Deinotherium bavaricum
	Gomphotherium angustidens
Perissodactyla	
	Chalicotherium grande
	Metaschizotherium aff. *bavaricum*
	Lartetotherium sansaniense
	Brachypotherium brachypus
	Dicerorhinus steinheimensis
	Plesiaceratherium fahlbuschi
	Prosantorhinus germanicus
	Anchitherium aurelianense
Artiodactyla	
	Hyotherium soemmeringi bavaricum
	Choeromorus sansaniensis
	Palaeomerycidae indet.
	Dorcatherium crassum
	Dorcatherium guntianum
	Dorcatherium peneckei
	Micromeryx flourensianus
	Stehlinoceros elegantulus
	Dicroceros elegans
	Eotragus clavatus

to increase contrast and eliminate background. The scale was added manually in order to avoid distortion due to parallax and other optical and digital effects.

3. Systematic palaeontology

Order Primates Linnaeus, 1758
Superfamily Hominoidea Gray, 1825

Genus *Griphopithecus* Abel, 1902

Species *Griphopithecus suessi* Abel, 1902

Material: BSPG 1968 I 171, right i/1 in light wear, lacking the apex of the root.

Locality, Stratigraphy and Age: Thannhausen, Swabia, Germany, upper freshwater molasse, late MN 5 or basal MN 6 (ca 14 Ma)

Description: The tooth is peg-like, with the crown posed in continuity of curvature with the root (Fig. 2). The crown has been slightly eroded and is pitted with small patches of chemical damage. In labial view the mesial and distal margins of the crown are sub-parallel for most of the height of the crown, the mesio-distal length decreasing gently from crown apex towards the cervix, the enamel curving quite abruptly at the cervix. In labial and lingual views the crown and root lie in a straight line, unlike i/2s of hominoids in which the root is angled with respect to the crown. In lingual view, the cutting edge of the incisor slopes gently from mesial to distal. The lingual surface is marked by narrow enamel wrinkles but not to the extent of forming a prominent central lingual ridge. The mesial and distal margins of the lingual surface of the crown are bordered by shallow, narrow grooves. In mesial and distal views, the cervix forms an inverted V-shape, slightly further towards the apex of the crown mesially than distally, but the offset between the level of the V's is not great. The enamel extends rootwards slightly further labially than lingually. In distal view, there is a shallow longitudinal depression in the crown into which the i/2 would fit (Fig. 2c). In mesial and distal views the crown increases in breadth from apex to cervix, producing a markedly concave lingual surface and a less curved convex labial surface. Immediately beneath the cervix, the root shows signs of abrasion at gingival level, especially pronounced on the lingual aspect, but passing onto the mesial and distal parts of the root. There is a shallow but broad groove on the mesial and distal surface of the root, deeper distally than mesially. Measurements of the tooth are provided in Table 2.

4. Discussion

The tooth described in this study was previously identified as a right i/2 of *Hyotherium soemmeringi bavaricum*, but there are several features which reveal that it does not represent a suid incisor. First, in suid second lower incisors the enamel extends much farther rootwards on the lingual side of the tooth than on the labial side – in hominoid central lower incisors the opposite is the case – the enamel extends slightly further rootwards labially than lingually. Second, in suids the central lingual ridge is strongly developed, is inclined distally and extends the entire height of the crown – in hominoids the central lingual pillar is usually low when present, and seldom if ever reaches the apex of the crown. Third, in suid lower second incisors, the inverted V-shape of the cervix is considerably further rootwards distally than mesially – in hominids the offset between the two V's is much less. Fourth, in suids the crown tends to be

Figure 1: Geographic location of Thannhausen (snowflake symbol) within the upper freshwater molasse and other German localities that have yielded large hominoids (Circle – fluvial deposits in the northern Rhine Graben, Starburst symbol – karstic deposits in the Swabian Alb, Diamond symbol – Engelswies marls with travertine).

longer relative to breadth than is the case in hominoids. Fifth, in labial view, the crown of lower incisors of *Hyotherium* narrow gradually towards the cervix – in hominoids the mesial and distal margins are subparallel for most of the height of the crown. Sixth, in suid incisor roots the labial and lingual breadths tend to be similar – in hominoids the root tends to be broader labially than lingually.

Based on these six features and on the overall aspect and dimensions of the tooth, there can be little doubt that the specimen represents a large-bodied hominoid, about the size of a female gorilla. The tooth is far too large to belong to the Pliopithecidae.

4.1 Affinities of the Thannhausen hominoid incisor

There are several potential candidates to which the Thannhausen incisor could be attributed. The tooth is evidently that of a large hominoid of approximately the dimensions of a female gorilla. It is similar in dimensions to large lower incisors of *Ugandapithecus major* from the Lower Miocene of East Africa (Pickford et al. 2009), *Afropithecus turkanensis* from Kalodirr, Kenya (Leakey et al. 1988), as well as an unidentified hominoid from Can Llobateres, Spain (Fig. 3). The Middle Miocene locality at Paşalar in Turkey has yielded three taxa, *Griphopithecus suessi*, *Griphopithecus alpani* and *Kenyapithecus kizili* (Kelley et al. 2008; Pickford 2012). The first has larger incisors than the other two taxa (form 2 in Kelley et al. 2008), but all Paşalar incisors are smaller than the Thannhausen specimen. Lower central incisors are not known for the Middle Miocene *Pierolapithecus catalaunicus* Moyà Solà et al. (2004) from Spain and La-Grive-St-Alban, France (MN 7/8) (Pickford 2012), but those of *Anoiapithecus brevirostris* (Moyà-Solà et al. 2009) are smaller than the Thannhausen specimen. Another European Miocene hominoid, *Dryopithecus fontani*, known from Spain, France and Germany, has smaller incisors than the Thannhausen specimen, as does the Rudabánya hominoid, *Rudapithecus hungaricus*. The enamel of the Thannhausen incisor appears to be quite thick, which accords with *Griphopithecus suessi*, the molars of which are endowed with thick enamel (Abel 1902). Of all these European taxa, the Thannhausen specimen is closest to *Griphopithecus suessi*, but until more informative fossil material is discovered at the site, such an identification must remain provisional.

4.2 Implications of the identification of a large hominoid in the Middle Miocene of Germany

Large hominoid remains have been encountered in the Middle and Late Miocene of several European countries (Alba et al. 2010; Alpagut et al. 1990; Andrews et al. 1996; Begun 2002). Most of the German Miocene hominoids are of Late Miocene age (Pickford 2012), although there is a damaged and deeply worn upper molar from Engelswies (MN 5) attributed to *Griphopithecus* sp. by Heizmann & Begun (2001).

In view of the fact that only a single large hominoid tooth has been reported from the Middle Miocene of Germany to date (Heizmann & Begun 2001), the specimen from Thannhausen takes on special significance. It confirms the presence of members of the superfamily Hominoidea in the Middle Miocene of the country. The Engelswies specimen was recovered from marls with travertine in the Swabian Alb (Schweigert 1992; Ziegler 1995; Böhme et al. 2011). The Thannhausen specimen in contrast, is from the fluvial deposits of the upper freshwater molasse, and thus from a different sedimentological and geomorphological setting. The associated fauna at Thannhausen (Tab. 1) attributes the locality to the latter part of MN 5 or the lower part of MN 6, probably somewhat older than hominoid sites in Austria at Klein Hadersdorf (Ehrenberg 1938), Slovakia at Neudorf Sandberg (Devinska Nova Ves) (Holec & Emry 2003) and Turkey at Çandir (Tekkaya 1974). Thannhausen is somewhat younger than the Engelswies specimen (MN 5), and appreciably older than the Vallesian (MN 9 – MN 10) specimens from the Swabian Alb karst deposits at Neuhausen, Salmendingen, Melchingen, and Trochtelfingen and the specimens from the flu-

Table 2: Dimensions of BSPG 1968 I 171, right i/1, large hominoid from Thannhausen.

Measurements	mm
Mesio-distal length (greatest)	6.6
Labio-lingual breadth (greatest)	9.6
Labial height of enamel cap (cervix to apex of crown)	17.5
Lingual height of enamel cap (cervix to apex of crown)	16.5

vial deposits of the Rhine Graben (MN 9) at Ebingen, Eppelsheim and Wissberg Gau-Weinheim (Pickford 2012). As a result, the Thannhausen specimen helps to fill a considerable stratigraphic gap that used to separate the Engelswies specimen (MN 5) from the material from the other German localities (MN 9).

4.3 Biogeography

The Engelswies and Thannhausen hominoids, which probably belong to *Griphopithecus*, have closer affinities to fossils from Austria, Slovakia and Turkey where this genus has been reported (Abel 1902, 1903; Alpagut et al. 1990; Holec & Emry 2003; Tekkaya 1974) than to fossils from Spain and France from which the genus has not been reported to date. In sharp contrast, the Vallesian hominoids from Germany (Swabian Alb, Rhine Graben) show strong affinities with Spanish forms (Pickford 2012). This could be due to a difference in age of the hominoid records from the two areas because the Franco-Iberian hominoid record is overall younger than the Engelswies-Thannhausen one. However, the Swabian Alb hominoids have almost the same age as those from France and Spain, suggesting that a change occurred in the biogeographic affinities of southern Germany, which were more closely related to Anatolia-Austria (i.e. Paratethyan) during the Middle Miocene, but became more closely related to western Europe (Franco-Iberia) during the Vallesian. This shift in biogeographic affinities of mid-latitude Europe witnessed the influx by dispersal of many new lineages of mammals from the Far East and Africa (e.g., *Propotamochoerus*, *Hippopotamodon* among the suids), and the disappearance by extinction of many lineages from Europe (e.g., *Listriodon*, *Conohyus* among the suids). The Hominoidea were probably part of this biogeographic activity, with old lineages such as *Griphopithecus* vanishing locally, to be replaced by incoming lineages from Africa such as those that gave rise to *Dryopithecus* and *Anoiapithecus*. The faunal changes were thus most probably predominantly by replacement rather than by autochthonous evolution.

4.4 Palaeoenvironment

During the Middle Miocene, southern Germany, in particular the Molasse Basin between the Alps in the south and the Jurassic Limestone Plateau in the north, enjoyed a sub-tropical climate, although it is clear that the palaeoclimate was not stable and uniform throughout the period, especially after the Mid-Miocene cooling phase (Rössner 2002; Eronen & Rössner 2007; Böhme et al. 2006, 2008; Prieto et al. 2011). Thannhausen has yielded a highly diverse perissodactyl assemblage (five species of Rhinocerotidae, two chalicotheres and an anchithere) and a rich artiodactyl fauna (three species of tragulids, a primitive bovid, a Palaeomerycidae, a Moschidae and two deer) (Tab. 1). Eronen & Rössner (2007) described the palaeoenvironment as a “Wetland Paradise” characterised in the build-up phase by a high abundance of small-sized browsers and mixed feeders, giving way later to a declining phase dominated by larger mammals and fewer mixed feeders. The dominance of browsers in the Thannhausen fauna indicates that leaves were probably available on a year-round basis, implying evergreen woodland to forest conditions (Böhme et al. 2007). Under these circumstances it seems surprising that large-bodied hominoids have not previously been recognised in the many Middle Miocene faunas of the German Molasse Basin, although they have been recognised in the Austrian part further east (Abel 1902; Ehrenberg 1938). However, hominoid fossils tend to be generally rare in the European fossil record (Casanovas-Vilar et al. 2011) and this might also explain their scarcity in Germany. In contrast, smaller bodied Pliopithecidae are well known from the upper freshwater molasse at localities such as Ziemetshausen Ib, Gallenbach 2b, Stätzling, Hohenraunau Tiefenried and Burg-Balzhausen that are of approximately the same age as Thannhausen (Heissig 1997) and at Mörgen and Kirrberg-Tongrube that are younger than Thannhausen (Seehuber 2009).

5. Conclusions

In a paper on the Neuhausen hominoids, Pickford (2012) raised the question as to “How many other dryopithecine teeth are lying incorrectly identified in collections in the various institutions in Germany and elsewhere in Europe?”. The answer is “At least one” on the basis of the lower central incisor from Thannhausen previously identified as a suid second incisor, but here attributed to a large hominoid.

A lower central incisor of a large-bodied hominoid reported from the Middle Miocene (late MN 5 or basal MN 6) locality in the upper freshwater molasse at Thannhausen, Swabia, Germany was originally identified as a suid second lower incisor. The specimen is in fact a hominoid lower central incisor as shown by a suite of morphological features. This specimen is

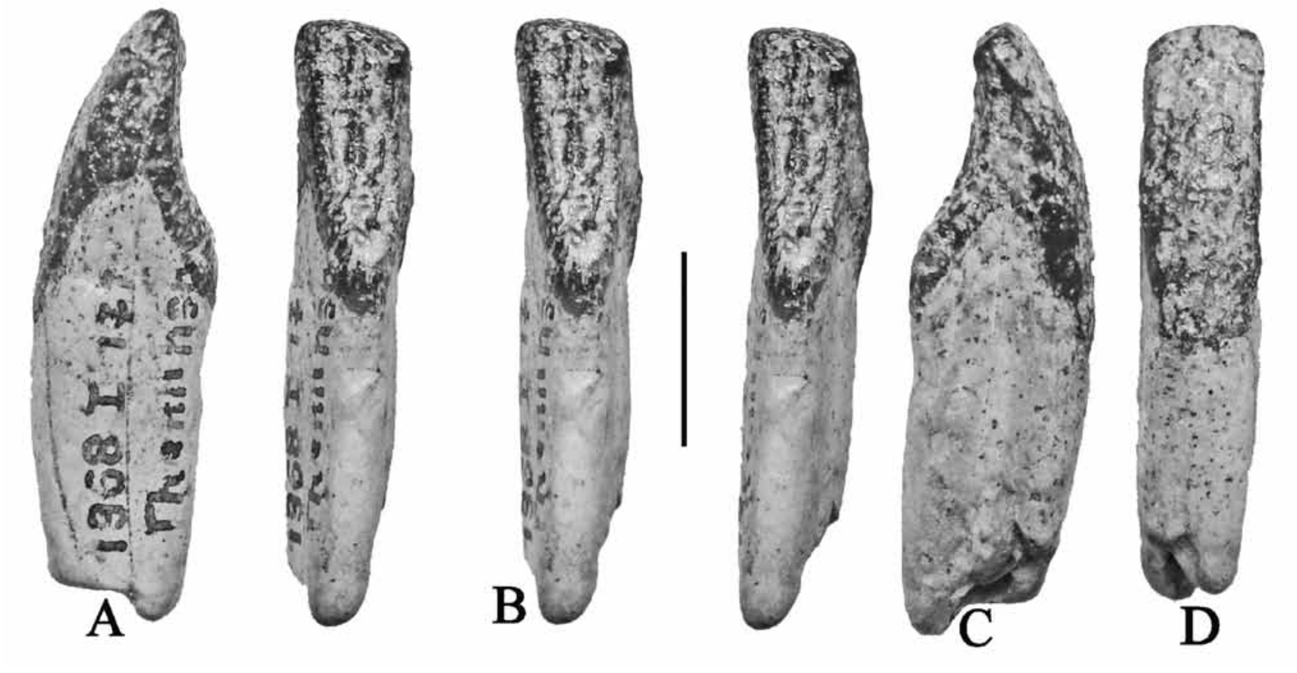

Figure 2: BSPG 1968 I 171, right i/1, large hominoid; **(A)** mesial, **(B)** stereo lingual, **(C)** distal and **(D)** labial views (scale: 10 mm).

the first large hominoid specimen to be recognised in late MN 5 or basal MN 6 deposits of Germany, and, as such, it helps to fill an important stratigraphic gap in the hominoid fossil record of the country, which used to extend between MN 5 at Engelswies, and MN 9 at various deposits in the Swabian Alb and the Rhine Graben. The affinities of the tooth appear to lie with *Griphopithecus suessi*, which suggests biogeographic links to the Paratethys (Austria, Slovakia and Turkey) rather than to the Franco-Iberian province.

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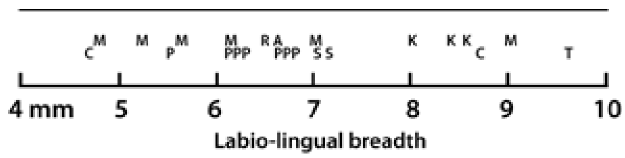

Figure 3: Metric comparison of labio-lingual breadth of lower central incisors of selected Miocene hominoids from Europe, Africa and Asia. Because the mesio-distal length varies enormously as the crown wears down, the most reliable measurement for comparison is the labio-lingual breadth. The Thannhausen tooth (T) is the broadest in the sample. (A – *Anoiapithecus brevirostris* from Spain, C – Unidentified taxon from Can Llobateres, Spain, K – *Afropithecus turkanensis* from Kalodirr, M – *Ugandapithecus major* from Kenya and Uganda, P – *Griphopithecus* and *Kenyapithecus* from Paşalar, R – *Rudapithecus hungaricus* from Rudabánya; S – *Sivapithecus indicus* from Siwaliks, T – *Griphopithecus* from Thannhausen) (Data from (A) Moyà-Solà et al. 2009; (C) Harrison pers. commun.; (K) Leakey et al. 1988; (M) Pickford et al. 2009; (P) Kelley et al. 2008; (R) Kordos 1991; (S) Preuss 1988).

References

Abdul-Aziz H, Böhme M, Rocholl A, Zwing A, Prieto J, Wijbrans J, Heissig K, Bachtadse V. 2010. Integrated stratigraphy and ^{40}AR/^{39}Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in Eastern Bavaria (Germany). International Journal of Earth Sciences 99, 115–134.

Abel O. 1902. Zwei fossile Menschenaffen aus den Leithakalkbildungen des Wiener Beckens. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse 111, 1171–1207.

Abel O. 1903. Zwei neue Menschenaffen aus den Leithakalkbildungen des Wiener Beckens. Centralblatt für Mineralogie, Geologie und Palaeontologie 1903, 176–182.

Alba DM, Fortuny J, Moyà-Solà S. 2010. Enamel thickness in the middle Miocene great apes *Anoiapithecus*, *Pierolapithecus*, and *Dryopithecus*. Proceedings of the Royal Society, Biological Sciences 1691, 2237–2245.

Alpagut B, Andrews P, Martin L. 1990. New hominoid specimens from the Middle Miocene site at Paşalar, Turkey. Journal of Human Evolution 19, 397–422.

Andrews P, Harrison T, Delson E, Bernor R, Martin L. 1996. Distribution and biochronology of European and Southwestern Asian Miocene Catarrhines. In: R Bernor, V Fahlbusch, HW Mittmann (Eds), The Evolution of Western Eurasian Neogene Mammal Faunas New York, Columbia University Press, 168–207.

Begun D. 2002. European hominoids, In: WC Hartwig (Ed.), The Primate Fossil Record. Cambridge, Cambridge University Press, 339–368.

Böhme M. 2007. The reconstruction of Early and Middle Miocene climate and vegetation in Southern Germany as determined from the fossil wood flora. Palaeogeography, Palaeoclimatology, Palaeoecology 253, 91–114

Böhme M, Aziz H, Prieto J, Bachtadse V, Schweigert G. 2011. Biomagnetostratigraphy and environment of the oldest Eurasian hominoid from the Early Miocene of Engelswies (Germany). Journal of Human Evolution 61, 332–339.

Böhme M, Ilg A, Ossig A, Küchenhoff H. 2006. New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. Geology 34, 425–428.

Böhme M, Ilg A, Winklhofer M. 2008. Late Miocene "Washhouse" climate in Europe. Earth and Planetary Science Letters 275, 393–401.

Casanovas-Vilar I, Alba D, Garcés M, Robles J, Moyà-Solà S. 2011. Updated chronology for the Miocene hominoid radiation in Western Europe. Proceedings of the National Academy of Sciences of the USA 108, 5554–5559.

Dehm R. 1980. Über ein neues *Hyotherium* (Suidae, Schweine-Verwandte) aus der Oberen Süsswassermolasse Südbayerns. Annalen des Naturhistorischen Museums Wien 83, 49–57.

Ehrenberg K. 1938. *Austriacopithecus*, ein neuer menschenaffenartiger Primat aus dem Miozän von Klein-Hadersdorf bei Poysdorf in Niederösterreich (Nieder-Donau). Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse, Abteilung 1, Biologie, Mineralogie, Erdkunde 147, 71–110

Eronen J, Rössner G. 2007. Wetland paradise lost, Miocene community dynamics in large herbivorous mammals from the German Molasse Basin. Evolutionary Ecology Research 9, 471–494.

Heissig K. 1989. Neue Ergebnisse zur Stratigraphie der mittleren Serie der oberen Süsswassermolasse Bayerns. Geologica Bavarica 94, 239–257.

Heissig K. 1997. Mammal faunas intermediate between the reference faunas of MN 4 and MN 6 from the Upper Freshwater Molasse of Bavaria. Actes du Congès BioChroM'97; Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier 21, 537–546.

Heissig K. 2006. Biostratigraphy of the « Main Bentonite Horizon » of the Upper Freshwater Molasse in Bavaria. Palaeontographica, Abt. A 277, 93–102.

Heizmann E, Begun D. 2001. The oldest Eurasian hominoid. Journal of Human Evolution 41, 463–481.

Holec P, Emry R. 2003. Another molar of the Miocene hominid *Griphopithecus suessi* from the type locality at Sandberg, Slovakia. In: LJ Flynn (Ed.), Vertebrate Fossils and their Context, Contributions in Honour of Richard H. Tedford. Bulletin of the American Museum of Natural History 279, 625–631.

Kälin D, Kempf O. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene northern Alpine Foreland Basin of Switzerland. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 254, 177–235.

Kelley J, Andrews P, Alpagut B. 2008. A new hominoid species from the middle Miocene site of Pasalar, Turkey. Journal of Human Evolution 54, 455–479.

Kordos L. 1991. Le *Rudapithecus hungaricus* de Rudabánya (Hongrie). L'Anthropologie 95, 343–362.

Leakey R, Leakey MG, Walker A. 1988. Morphology of *Afropithecus turkanensis* from Kenya. American Journal of Physical Anthropology 76, 289–307.

Moyà-Solà S, Alba D, Almécija S, Casanovas-Vilar I, Köhler M, Esteban-Trivigno S, Robles J, Galindo J, Fortuny J. 2009. A unique Middle Miocene European hominoid and the origins of the great ape and human clade. Proceedings of the National Academy of Sciences of the USA 106, 9601–9606.

Moyà-Solà S, Köhler M, Alba D, Casanovas-Vilar I, Galindo J. 2004. *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. Science 306, 1339–1344.

Pickford M. 2012. Hominoids from Neuhausen and other Bohnerz localities, Swabian Alb, Germany, evidence for a high diversity of apes in the Late Miocene of Germany. Estudios geologicos 68, 113–147.

Pickford M, Senut B, Gommery D, Musiime E. 2009. Distinctiveness of *Ugandapithecus* from *Proconsul*. Estudios geologicos 65, 183–241.

Preuss T. 1988. The face of *Sivapithecus indicus*: Description of a new, relatively complete specimen from the Siwaliks of Pakistan. Folia Primatologica 38, 141–157.

Rössner G. 2002. Miozäne Ruminantia Süddeutschlands: Taxonomie und Ökologie. Habilitationsschrift, Fakultät für Geowissenschaften, Ludwig-Maximilians Universität Munchen, 254 pp.

Schweigert G. 1992. Die Untermiozän Flora (Karpatium, MN 5) des Süsswasserkalks von Engelswies bei Messkirch (Baden-Würtemberg). Stuttgarter Beiträge zur Naturkunde B 188, 1–55.

Seehuber U. 2009. Litho- und biostratigraphische Untersuchungen in der Oberen Süsswassermolasse in der Umgebung von Kirchheim in Schwaben. Documenta naturae 175, 1–355.

Tekkaya I. 1974. A new species of Tortonian anthropoid (Primates, Mammalia) from Anatolia. Bulletin of the Mineral Research and Exploration Institute of Turkey 83, 148–165.

Ziegler R. 1995. Die Untermiozänen Kleinsäugerfaunen aus den Süsswasserkalken von Engelswies und Schellenfeld bei Sigmarigen (Baden-Württemberg). Stuttgarter Beiträge zur Naturkunde B 228, 1–53.