

Fossil remains of *Macaca sylvanus* (Mammalia, Cercopithecidae) from the early Middle Pleistocene locality of Mauer (SW Germany)

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Abstract

The Grafenrain sand pit to the North of Mauer near Heidelberg (SW Germany) became famous for the discovery of the lower jaw of *Homo heidelbergensis* in October 1907 (SCHOETENSACK 1908). Until the termination of the extractions in 1962 the sand pit yielded a rich and diverse mammalian faunal assemblage. In 2007 and the following years new preparation activities connected to the celebrations of the centenary of the hominid lower jaw discovery of *H. heidelbergensis* produced samples of sediment (medium gravel to fine pebble) in which at least two isolated lower cheek teeth of macaques have been found. The finds demonstrate the presence of *Macaca sylvanus* in the Mauer faunal assemblage and represent the occurrence of a second primate species in this Pleistocene hominid site.

Kurzfassung

Fossilien von *Macaca sylvanus* (Mammalia, Cercopithecidae) aus dem Mittelpleistozän von Mauer bei Heidelberg (SW Deutschland)

Die Sandgrube Grafenrain nördlich von Mauer wurde mit dem Fund des Unterkiefers von *Homo heidelbergensis* im Oktober 1907 (SCHOETENSACK 1908) weltbekannt. Bis zum Ende des Sandabbaus 1962 hat die Sandgrube eine umfangreiche und vielfältige Säugetierfauna geliefert. Im Rahmen der Vorbereitungs- und Folgearbeiten am Profil in der Sandgrube Grafenrain anlässlich der 100-Jahr-Feier des Fundes von *H. heidelbergensis* konnten aus der Mittelkiesfraktion von Proben der Unteren Mauerer Sande bisher zwei isolierte Unterkiefermolare von Makaken geborgen werden. Diese Funde belegen die Präsenz von *Macaca sylvanus* in der Faunenassoziation der Lokalität Mauer und damit die Anwesenheit eines zweiten Primaten in der frühmittelpleistozänen Hominiden-Fundstelle Mauer.

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Introduction

Shortly after the publication of the first find of a macaque molar (SCHREIBER & LÖSCHER 2011), the

finder, M. LÖSCHER (Sandhausen), inventoried a second molar of *Macaca* from a sample taken in 2010. This molar was first mentioned and illustrated in publications by LÖSCHER & LÖSCHER (2012), SCHREIBER (2012), and SCHREIBER et al. (2018) but without a sufficiently detailed description. Because of its relevance as supporting evidence for the occurrence of the macaques as a new faunal element in the early Middle Pleistocene locality of Mauer and its contribution to morphometrical features in the dentition of the macaques, it is necessary to introduce this second find to the scientific community.

Besides the Hominidae (humans, apes), the Cercopithecidae (Old World monkeys), in particular the macaques, are a regular element in the faunal assemblages from the Neogene and Pleistocene of Europe and North Africa, especially in the periphery of the Mediterranean Sea. In Europe the Cercopithecidae are mainly represented by isolated teeth, fragments of upper and lower jaws, but also by cranial [e.g. Sénéze, France (DEPÉRET 1929), and Is Oleris, Sardinia, Italy (ZOBOLI et al. 2016)] and postcranial skeletal elements [e.g. Voigtstedt, Germany (KAHLKE 1961), Villafranca d'Asti, Italy (ROOK et al. 2001), and Quibas, Spain (ALBA et al. 2011)]. Table 1 shows the stratigraphical distribution of localities bearing fossils of *Macaca* in Europe. Especially in the Western Mediterranean region *Macaca* is common, known since the late Miocene (Moncucco Torinese), and early Pliocene (Montpellier), but more frequent within the late Pliocene. In the Lower and Middle Pleistocene *Macaca* became much more common and widespread across Europe. The occurrence of *Macaca* in Upper Pleistocene localities of Italy (Grotta degli Orsi Volanti), Spain (Cova Negra and Solana del Zamborino), and the Netherlands (North Sea) shows a continuous presence in Europe up until the recent restriction to northwest Africa (*Macaca sylvanus*) and Southeast Asia (*M. silenus*, *M. mulata*, etc.).

Table 1. Stratigraphically and geographically ordered list of Mio-, Plio- and Pleistocene European fossil sites, which yielded the genus *Macaca* (¹ROOK et al. 2001, ²ALBA et al. 2014, ³GENTILI et al. 1998, ⁴ZAPPE 2001, ⁵ARDITO & MOTTURA 1987, ⁶FRANZEN 1973, ⁷ROOK et al. 2013, ⁸SZALAY & DELSON 1979, ⁹LUMLEY et al. 1988, ¹⁰ALBA et al. 2008, ¹¹ALBA et al. 2016, ¹²ALBA et al. 2011, ¹³SCHREIBER & LÖSCHER 2011, ¹⁴FUENTES VIDARTE 1993, ¹⁵BONA et al. 2016, ¹⁶MAZZA et al. 2005, ¹⁷REUMER et al. 2018).

	W-Mediterranean	Central-Europe	E-Europe	E-Mediterranean	NW-Europe
Late Miocene	Almenara-Casablanca M ¹ Moncucco Torinese ²				
Early Pliocene	Montpellier ¹				
Late Pliocene	RDB quarry ¹ Costa San Giacomo ³ Villafranca d'Asti ³ Balaruc 2 ¹	Gundersheim ¹	Csarnota 2 ¹		
Lower Pleistocene	Inferno di Sotto ⁴ Strette ⁴ Upper Valdarno ⁷ Mugello ³ Val di Chiana ³ Pietrafitta ³ Monte Zoppega 2 ³ Monte Sacro ³ Orciano ³ Sénèze ⁵ St. Vallier ⁵ Vallonet ⁹ Terrassa ¹⁰ Incarcal I ¹¹ Quibas ¹²	Untermassfeld ⁴ Tegelen ¹ Steyl ⁵ Hohensülzen ⁵ Voigtstedt ⁵	Beremend 4 ¹ Mălușteni ⁶ Gombasek ⁸ Zlatý Kůň ⁸	Sandalja ⁵	
Middle Pleistocene	Montsaunès ⁵ St. Estève G ⁵ Orgnac-3 ⁵ Aldène ⁵ Capo Figari ³ San Vito di Leguzzano ³ Monte Peglia ³ Colle Marino ³ Valdemino ³ Cava Pompei ³ Fontana Ranuccio ³ Bristie ³ Torre in Pietra ³ Torralba-Ambrona ¹⁴ Quecchia quarry ¹⁵	Mauer ¹³ Mosbach 2 ⁵ Heppenloch ⁵		Tourkobounja ⁵	Grays Thurrock ⁵ West Runton ⁵ Hoxne ⁵ Swanscombe ⁵
Upper Pleistocene	Grotta degli Orsi Volanti ¹⁶ Solana del Zamborino ⁵ Cova Negra ⁵				North Sea ¹⁷

The recent distribution of macaques in the region of the Atlas Mountains matches a residual area in North Africa, whereas in Europe they became extinct within the Holocene. The origin of the population in Gibraltar (South of the Iberian Peninsula) is very probably the result of multiple intro-

ductions of the animals by humans in historical times (VAN HOOFF 1988, MOTTURA & GENTILI 2006). Fossil macaque remains from to date three localities on Sardinia, Italy – Capo Figari, Is Oleris, and Monte Tuttavista (ZOBOLI et al. 2016), described by AZZAROLI (1946) as *Macaca majori*, represent an

isolated island population of *Macaca*. For a considerable time the remains were considered to be distinct only at the subspecies level, i.e. *Macaca sylvanus majori* (DELSON 1980, MAZZA et al. 2005). Based on a recent find from Is Oreris (ZOBOLI et al. 2016) and an earlier comparative study (ROOK & O'HIGGINS 2005), the macaque remains from Sardinia are clearly referable to a distinct species, which formed an isolated, dwarfed insular population in the Plio-Pleistocene of Sardinia. *M. majori* is characterized by smaller cranial dimensions and a shorter anteroposterior palatal length compared to extant species, and a dentition of smaller dimensions (ZOBOLI et al. 2016). In north western, central and eastern Europe *Macaca* is well represented in fossil sites as well. From West Runton in Great Britain (ARDITO & MOTTURA 1987) to Mălușteni in Romania (FRANZEN 1973) the genus occurs in many faunal assemblages. In particular, a find in the locality of Mosbach near Wiesbaden [SW Germany (KAHLKE 1961, 1967, ARDITO & MOTTURA 1987)], similar in age to Mauer, gave rise to the idea that an occurrence of *Macaca* in Mauer might be expected (see KOENIGSWALD 1997, SCHREIBER et al. 2007).

Material

The Grafenrain sand pit (north of Mauer) is situated in a former meander of the Neckar River, exposing its early Middle Pleistocene sediments, the so-called 'Mauerer Sande' (Mauer sands). On October 21, 1907 the palaeontological workman DANIEL HARTMANN (1854-1952) found the lower jaw of *H. heidelbergensis* in the pit (SCHOETENSACK 1908). The lower jaw, and moreover a huge number of fossil remains, made the locality of Mauer world famous as a rich and diverse Pleistocene mammalian fossil site (see SCHREIBER et al. 2007, WAGNER et al. 2011).

The area of the Grafenrain sand pit is the last remaining outcrop of the 'Mauerer Sande' available for scientific purposes. After the termination of sand extraction from the pit in 1962 the possibilities for further macromammalian finds from the Mauer locality were limited. As a result, further investigations on micromammalian, first described by HELLER (1934, 1939), seemed to be the most effective option to continue the research on the fossil site. Since 1995 a huge amount of sediment (about 50 m³) has been extracted from the section in the Grafenrain sand pit, and analysed by M. LÖSCHER and collaborators. The number and diversity of the micromammalian fossils increased remarkably (see MAUL et al. 2015). The

remains derived mainly from the gravel grade, while small macromammalian fossils, e.g. teeth, came from the fine pebble grade. Both macaque molars were found in such fine pebble grade samples, made between 148 and 149 m above sea level (see SCHREIBER & LÖSCHER 2011: 299, Fig. 1), the first one collected in February 2008, the second one in August to October 2010.

The new find (Fig. 1)

Systematic Palaeontology

(after MCKENNA & BELL 1997, VAN HOOFF 1988):

Order Primates LINNAEUS, 1758
 Superfamily Cercopithecoidea GRAY, 1821
 Family Cercopithecidae GRAY, 1821
 Tribe Papionini BURNETT, 1828
 Subtribe Macacina OWEN, 1843
 Genus *Macaca* LACÉPÈDE, 1799
 Species *Macaca sylvanus* (LINNAEUS, 1758)

Locality: Grafenrain sand pit, Mauer, SE of Heidelberg, Germany, 08° 48' 08" E – 49° 20' 82" N, 485 550 E – 5466 100 N [UTM-coordinates (zone32), referred to WGS84/ETRS89].

Horizon: 'Untere Mauerer Sande', the lower section of the 'Mauerer Sande', ca. 140-164 m above sea level.

Collection: State Museum of Natural History Karlsruhe (SMNK)

Inventory number: SMNK-PAL 6630.

Description

The isolated tooth (Fig. 1) is a right third lower molar (m3), according to its bilophodont tooth pattern with four cusps and its additional distal extension, composed of the hypoconulid and the tuberculum sextum, typical in the macaques (SZALAY & DELSON 1979). The crests between the mesial cusps and between the distal cusps are prominent, but do not mar the overall bunodont character of the tooth. Mesial and distal from each cusp arise crests, which are elongated, fused at their ends, and form a circular crest on the rim of the crown. In the distal portion the hypoconulid and the tuberculum sextum, the latter separated into two distinct parts or cusps (Fig. 1, b), complete the circular crest. This crest is slightly incised on the lingual and buccal margins of the talonid basin, forming moderate lingual and buccal notches. Mesially the circular crest limits a small mesial fovea, whereas distally the crown shows a triangular distal fovea because of the additional distal extension. Basally, the convexi-

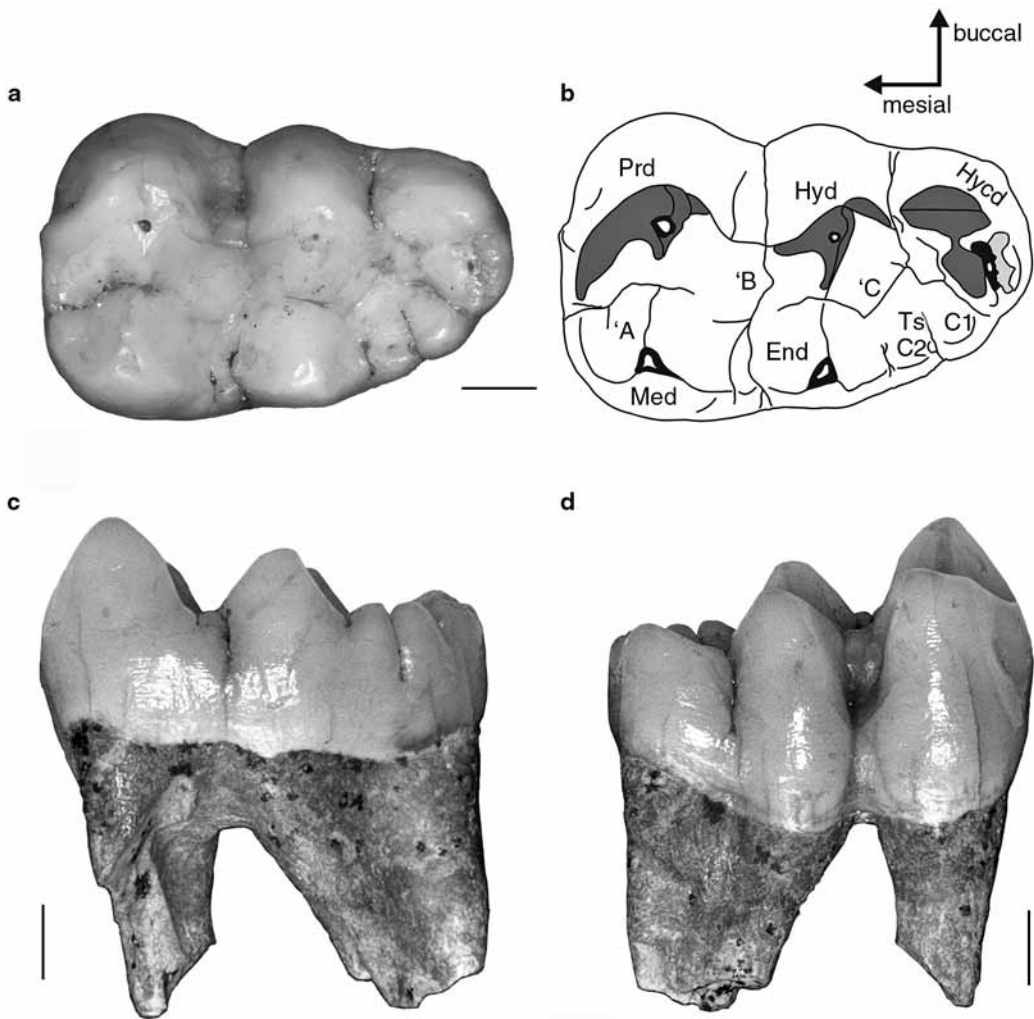


Figure 1. *Macaca sylvanus* (LINNEAUS, 1758), isolated third lower molar (m3), right, from Mauer near Heidelberg, Grafenrain sand pit, 'Mauerer Sande' (SMNK-PAL 6630), a) occlusal, b) occlusal drawing, black areas: ages of enamel, dark grey areas: facets caused by attrition, light grey area: damage, c) buccal, d) lingual. Scale is 2 mm. Prd=protoconid, Med=metaconid, Hyd=hypoconid, End=entoconid, Hycd=hypoconulid and the Ts=tuberculum sextum with C1, C2 cusp1, 2, 'A'=mesial fovea, 'B'=talonid basin, 'C'=distal fovea (nomenclature after KAY 1977, SZALAY & DELSON 1979, pictures were made with Kenyence VHX 5000).

ty of the buccal and lingual longitudinal sides is weak, resulting in a low degree of molar flare. The m3 from Mauer measures 12.5 mm in mesiodistal length (MDL), 8.2 mm in mesial breadth (MB), and 7.7 mm in distal breadth (DB). The roots are largely preserved; only their distal tips are broken off. Apically of all four cusps are slight planes of attrition, which are identifiable as

initial wear facets. On the protoconid and (to a lesser extent) on the hypoconid small patches of the dentine are exposed; these are not present on the lingual cusps.

The enamel is white, slightly off white. The dentine is white to yellow-orange in surface colour, with a few black spots of manganese mineralization. The preservation of the specimen under

study here is quite different to that of the m2 (SMNK-PAL 6602, Fig. 2 [MDL 9.9 mm, MB 8.0 mm, DB 7.6 mm], described by SCHREIBER & LÖSCHER 2011), but it matches a very common pattern seen in the fossils from the 'Mauerer Sande': a disarticulated, isolated, and partly fragmentary skeletal element, with primary white-coloured substances, like the enamel, in parts slightly yellow, and the dentine with intensive yellow, red to brown areas coloured by several iron mineralisations on the surfaces, and with manganese impregnations (see SCHREIBER 2006).

As mentioned above, from the anatomy of this tooth its position within the molars can be clearly considered as a right third lower molar (m3), because of its additional extension distally, composed of the hypoconulid and the tuberculum sextum. In comparison to the upper molars, the lower molars of the macaques are more slender in relation to their length, and both teeth from Mauer have a length-breadth-relation, which corresponds to lower molars (Fig. 3).

Considering only count data, both specimens (m2 and m3) could match the posterior part of a right lower cheek dentition from the same individual. But the two teeth come from levels separated by nearly one meter in the fluvial section (pers. comm. M. LÖSCHER), and their quiet different preservation patterns (Fig. 2) imply distinct diagenetic histories. In conclusion it is more probable that the specimens come from different individuals.

Discussion: systematics and taxonomy

The bilophodont tooth pattern of the new Mauer specimen – with talonid basin, mesial, and distal foveae, its distal extension – is characteristic of Cercopithecidae, and the low relief of the crown (low-crowned tooth) indicates membership of the Papionini. The low degree of the molar flare (on the lingual and buccal side), and the relatively small size permit the reference to the genus *Macaca* (see SZALAY & DELSON 1979).

The fossil cercopithecid *Paradolichopithecus*, a papionin from Puebla de Valverde, Spain (ARDITO & MOTTURA 1987), is larger than *Macaca*. The papionin *Theropithecus* from Cueva Victoria, Spain (GILBERT et al. 1995), has high-crowned teeth with three deep shaped basins and columnar cusps. Other fossil cercopithecids from localities in Europe like *Mesopithecus* [Villafranca d'Asti (GENTILI et al. 1998), Perpignan, Celleneuve, Pikermi, Saloniki, Titov Veles, Eppelsheim, Mollon (ARDITO & MOTTURA 1987)], and *Dolichopithecus*, a colobine [Layna, Perpignan (ARDITO & MOTTURA 1987)], differ from *Macaca* in their high-crowned teeth (SZALAY & DELSON 1979).

Beside *M. s. sylvanus* and "*M. ? s. majori*" (provisory treated as subspecies) SZALAY & DELSON (1979) additionally proposed three biochronological subspecies of *M. sylvanus* for the fossil macaques, of which *M. s. prisca*, *M. s. florentina*, and *M. s. pliocena* are still under discussion for the Plio-Pleistocene fossil record (ROOK et al.



Figure 2. Comparative picture of the lower right molars m2 (SMNK-PAL 6602) and m3 (SMNK-PAL 6630) from Mauer, and a mandible with the tooth row (shown [p4], m1, m2, m3) of an extant macaque (SMNK 5492, *M. sylvanus*), scale is 10 mm.

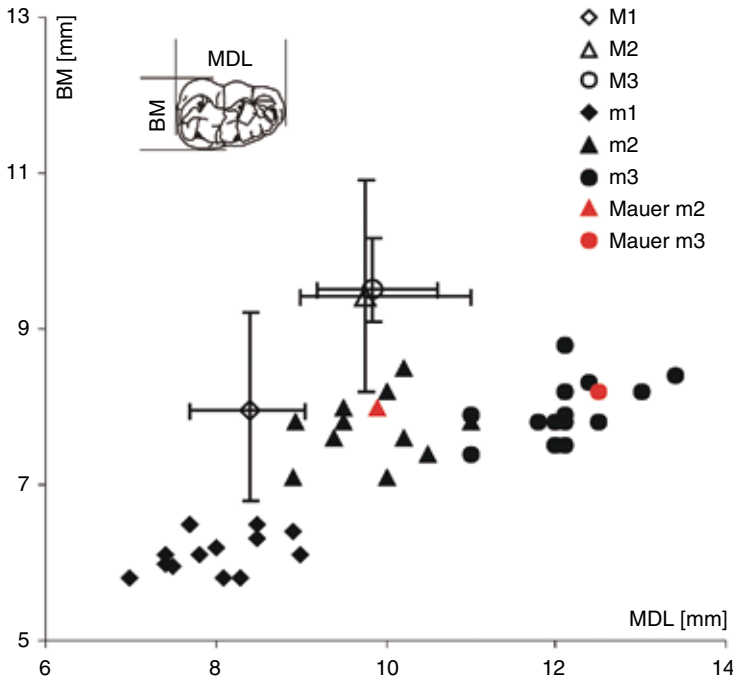


Figure 3. Bivariate plot of mesiodistal length (MDL) and the mesial breadth (MB) for *Macaca* from the Mio-, Plio- and Pleistocene of Europe. Plotted are the length and breadth of the lower molars m2 (SMNK-PAL 6602), m3 (SMNK-PAL 6630) from Mauer, of the first, second, and third lower molars (m1, m2, m3) by SCHREUDER (1945), FRANZEN (1973), MARTIN PENELA (1983), KÖHLER et al. (2000), ROOK et al. (2001), ZAPFE (2001), MAZZA et al. (2005), ALBA et al. (2008, 2011, 2014), BONA et al. (2016), REUMER et al. (2018), in comparison to the variation range (values for the mean, minimum, and maximum) of the first, second, and third upper molars (M1, M2, M3) by ADAM (1975), SINGER et al. (1982), MARTIN PENELA (1983), ROOK et al. (2001), and ALBA et al. (2008, 2011, 2016), BONA et al. (2016). The plot shows the different proportions of the slender lower cheek teeth in comparison to the relatively wider upper cheek teeth, and the increasing in size from the first to the third molars.

2001, ALBA et al. 2008, 2011, 2016). But neither SZALAY and DELSON, nor later authors mentioned any diagnostic morphological character for the assignments. The proportional differences given to distinguish them by ALBA et al. (2011, 2016) fall within the range of variation of MDL and MB, as illustrated in the bivariate plot in figure 3, which shows the close length-breadth relations across the tooth positions in the *Macaca* dentition.

In the current paper, these proposed subspecies are not accepted, because the diagnoses are still inadequate. The presence of two distinct cusps at the tuberculum sextum (Fig. 1, b) on the distal extension of the m3 from Mauer could be a possible distinctive morphological feature for a separation of fossil *Macaca* specimens on the species level. It distinguishes the Mauer specimen from the holotype (the lower jaw IGF10034), found in the Lower Pleistocene Upper Valdarno Basin (Le Forre), with one cusp at the tuberculum sextum on the left and right m3 (see ROOK et al. 2013: 112, Fig. 12), originally described as "*Aulaxinuus florentinus*" by COCCHI (1872). Future investigations on the phylogenetic history of the genus *Macaca* in the Plio-Pleistocene of

Europe may include this feature. For example, the different morphology of the m3 may separate the Middle Pleistocene *Macaca* from the Lower Pleistocene ones at the species level.

In summary the second specimen (m3) from the Grafenrain sand pit from the Mauer locality is assigned to the species *Macaca sylvanus* (LINNAEUS, 1758).

Ecological evidence

The recent geographical distribution of the genus *Macaca* in Northwest Africa and Southeast Asia suggests that the fossil populations of macaques similarly may have preferred subtropical and tropical climate zones.

With regard to the environment of *H. heidelbergensis*, *Macaca* might suggest a different climate signal than recently proposed (see below). In fact recent macaques live in many different kinds of habitats, which show their variability and wide range of ecological requirements. They appear in tropical rain forests, monsoon- and mangrove forests, in forests of high mountains, humid forests of highlands, and also in open grass- and scrublands. Their mode of life varies from arbore-

al to terrestrial (see VAN HOOFF 1988). The North African macaques are most abundant in tall, mixed cedar and evergreen oak forests (MASSETI & BRUNER 2009). On the one hand the ecological preference of a recent mammal should not be directly projected onto its fossil ancestors, but on the other hand the great variation of its extant habitat might be a sufficient explanation as to why *Macaca* occurred repeatedly in several faunal assemblages of the temperate zone of Europe during the warm ages of the Plio- and Pleistocene. This is supported by the ecomorphological study of ERONEN & ROOK (2004) on European Mio-Pliocene primate occurrences, and by ELTON & O'REGAN (2014), showing that the Cercopithecoidea, especially the *Macaca*, had occupied a variety of environmental conditions, including the North West of Europe in the Middle Pleistocene. Therefore the occurrence of *Macaca* in the Mauer locality does not contradict the current climate reconstruction, based on the faunal assemblage from the 'Mauerer Sande' (SCHREIBER et al. 2007, WAGNER et al. 2011). Moreover, with regard to their mode of life, the macaques fit well inside the reconstructed landscape of the *H. heidelbergensis*, with floodplain forests along the river, meandering in the wide valley, forests on the slopes, and open forests on the hills, with grass- and scrubland areas. Because of the fissure water system in the Triassic basement (Buntsandstein and Muschelkalk) the hill sites would probably have been dry habitats. In summary the diversity of forest and open land habitats that appear in the locality of Mauer made an ideal environment for the versatile macaques.

Conclusions

The specimen of an isolated right third molar of the lower jaw (m3), which was found in the fine pebble grade of a sample from the lower 'Mauerer Sande' of the Grafenrain sand pit north of Mauer, is described. Because of its low relief of the crown, the bilophodont yet overall bunodont character of the tooth pattern, with the four cusps and three basins, and its additional distal elongation, the specimen is assigned to the species *Macaca sylvanus* (LINNAEUS, 1758). This second specimen implies the presence of a second *Macaca* individual from the 'Mauerer Sande'. Additionally, its distinctive feature - the two separated cusps on the tuberculum sextum - may enable the morphological differentiation of species for *Macaca* in the fossil record of Europe.

The presence of *Macaca* at Mauer confirms the previous expectation that macaques would be found in the faunal assemblage of the 'Mauerer Sande' (see KOENIGSWALD 1997, SCHREIBER et al. 2007). *Macaca* were previously documented in most other important mammalian fossil sites in the Plio-Pleistocene of Europe, like Tegelen, Upper Valdarno, S  n  ze, Untermassfeld, Voigtstedt, West Runton, Mosbach 2, Hoxne, Swanscombe, and Heppenloch, but not in Mauer. With the two finds an important gap in the list of the faunal assemblage of Mauer is now closed.

Acknowledgements

Without the enthusiastic engagement of MANFRED L  SCHER (Sandhausen) for extracting sediment samples from the Mauer locality during the last two decades the increase of the micromammalian diversity in the faunal assemblage from Mauer would not be archived as it is now. As a side effect some finds of macromammals and especially the primate remains completed his work. Additionally the author likes to thank KRISTER T. SMITH (Forschungsinstitut Senckenberg Frankfurt) for critical comments and the correction of the manuscript.

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