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Article

The second find of a primate from the early Middle Pleistocene locality of Mauer (SW Germany): a molar of *Macaca* (Mammalia, Cercopithecidae)

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With 3 figures and 1 table

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Abstract: The Grafenrain sand pit N of Mauer near Heidelberg (SW Germany) became famous for the find 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 new preparation activities connected to the celebrations of the centenary of the hominid lower jaw discovery of *Homo heidelbergensis* produced samples of sediment (medium gravel) in which an isolated lower cheek tooth of a macaque has been found. The find adduces the presence of *Macaca sylvanus* in the faunal assemblage of Mauer and represents the second find of a primate from this Pleistocene hominid site.

Key words: Primates, Cercopithecidae, morphology, systematics, taxonomy, early Middle Pleistocene, locality of Mauer, Mauerer Sande.

1. Introduction

Beside the Hominidae (humans, apes), the Cercopithecidae (Old World monkeys), in particular the macaques, are a common element in the faunal assemblages from the Neogene of Europe. The Cercopithecidae are mainly represented by isolated teeth, fragments of upper and lower jaws, but also by cranial (e.g. Sénèze, France, Depéret 1929) and postcranial skeletal elements (e.g. Villafranca d'Asti, Italy, Rook et al. 2001, and Voigtstedt, Germany, Kahlke 1961). Table 1 shows the stratigraphical distribution of localities bearing fossils of *Macaca* in the Plio- and Pleistocene of Europe. Especially in the Western Mediterranean region *Macaca* is common, known since the early Pliocene with the finds from Montpellier, but more frequent within the Late Pliocene. In the Lower and Middle Pleistocene *Macaca* became more common, and widespread across southern Europe. The occurrence of *Macaca* in Upper Pleistocene localities of Italy (Grotta degli Orsi Volanti, Mazza et al. 2005) and Spain (Cova Negra and Solana del Zamborino, Ardito & Mottura 1987) shows that a continuity can be supposed from fossil populations up to the Recent ones, now decreased, and restricted to northwest Africa and Southeast Asia.

The Recent distribution of macaques in the region of the Atlas Mountains matches a residual area in North Africa, in Europe they are extinct. The origin of the population in Gibraltar (South of Iberian Peninsula) is very probably a result of multiple introductions of

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Table 1. Stratigraphically ordered list of Plio- and Pleistocene European fossil sites, which yielded the genus *Macaca* ([1]Rook et al. 2001, [2]Mazza et al. 2005, [3]Ardito & Mottura 1987, [4]Franzen 1973, [5]Gentili et al. 1998, [6]Fuentes Vidarte 1993, [7]Alba et al. 2008, [8]Lumley et al. 1988, [9]Szalay & Delson 1979, [10]Zapfe 2001).

Early Pliocene	Late Pliocene	Lower Pleistocene	Middle Pleistocene	Upper Pleistocene
Montpellier[1]	Balaruc 2[1]	Beremend 4[1]	Bristie 2[5]	Cova Negra[3]
	Costa San Giacomo[5]	Gombasek[9]	Capo Figari (Sardinien)[5]	Grotta degli Orsi Volanti[2]
	Csarnota 2[1]	Hohensülzen[3]	Cava Pompi[5]	Solana del Zamborino[3]
	Gundersheim[1]	Mluteni[4]	Colle Marino[5]	
	Orciano[5]	Monte Sacro[5]	Fluminimaggiori (Sard.)[5]	
	Steyl[3]	Mugello[5]	Fontana Ranuccio[5]	
	Villafranca d'Asti[1]	Pietrafitta[5]	Grays Thurrock[3]	
		Sandalja[3]	Heppenloch[3]	
		Sénèze[3]	Hoxne[3]	
		St. Vallier[3]	Monte Peglia (Orvieto)[5]	
		Tegelen[1]	Montsaunès[3]	
		Terrassa[7]	Mosbach 2[3]	
		Untermassfeld[10]	Orgnac-3[3]	
		Upper Valdarno[3]	San Vito di Leguzzano[5]	
		Val di Chiana[5]	St. Estève G[3]	
		Vallonet[8]	Swanscombe[3]	
		Voigtstedt[3]	Torralba-Ambrona[6]	
		Zlatý Ko H[9]	Torre in Pietra[5]	
		Zoppega 2[5]	Tourkobounja[3]	
			Valdemino[5]	
			West Runton[3]	

the animals by humans in historical times (van Hooff 1988; Mottura & Gentili 2006).

An assemblage of fossil macaque remains from two localities on Sardinia, Italy (Capo Figari and Fluminimaggiori, Gentili et al. 1998), introduced by Azzaroli (1946) as *Macaca majori*, represents an isolated island population of *Macaca*. The taxonomical status of the remains is still under discussion. In a recent study Mazza et al. (2005) described few moderate anatomical differences in the cheek teeth, and smaller sizes, but still inside the range of the statistical distribution of the genus. Mazza et al. dissented the species rank, and referred the material from Sardinia to a subspecies *Macaca sylvanus majori* according to Delson (1980). Because of the isolated situation of this population a separated taxonomical status can be legitimate.

In northwestern, central and eastern Europe *Macaca* is well represented in fossil sites as well. From West Runton in Great Britain (Ardito & Mottura 1987) to Măluşteni 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 v. Koenigswald 1997; Schreiber et al. 2007).

2. Short history of investigation

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'. In 1907, on the 21st October, the workman Daniel Hartmann found the lower jaw of *Homo heidelbergensis* in the pit. The lower jaw, and moreover a huge number of mammalian remains, made the locality of Mauer world famous as a rich and diverse Pleistocene mammalian fossil site.

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

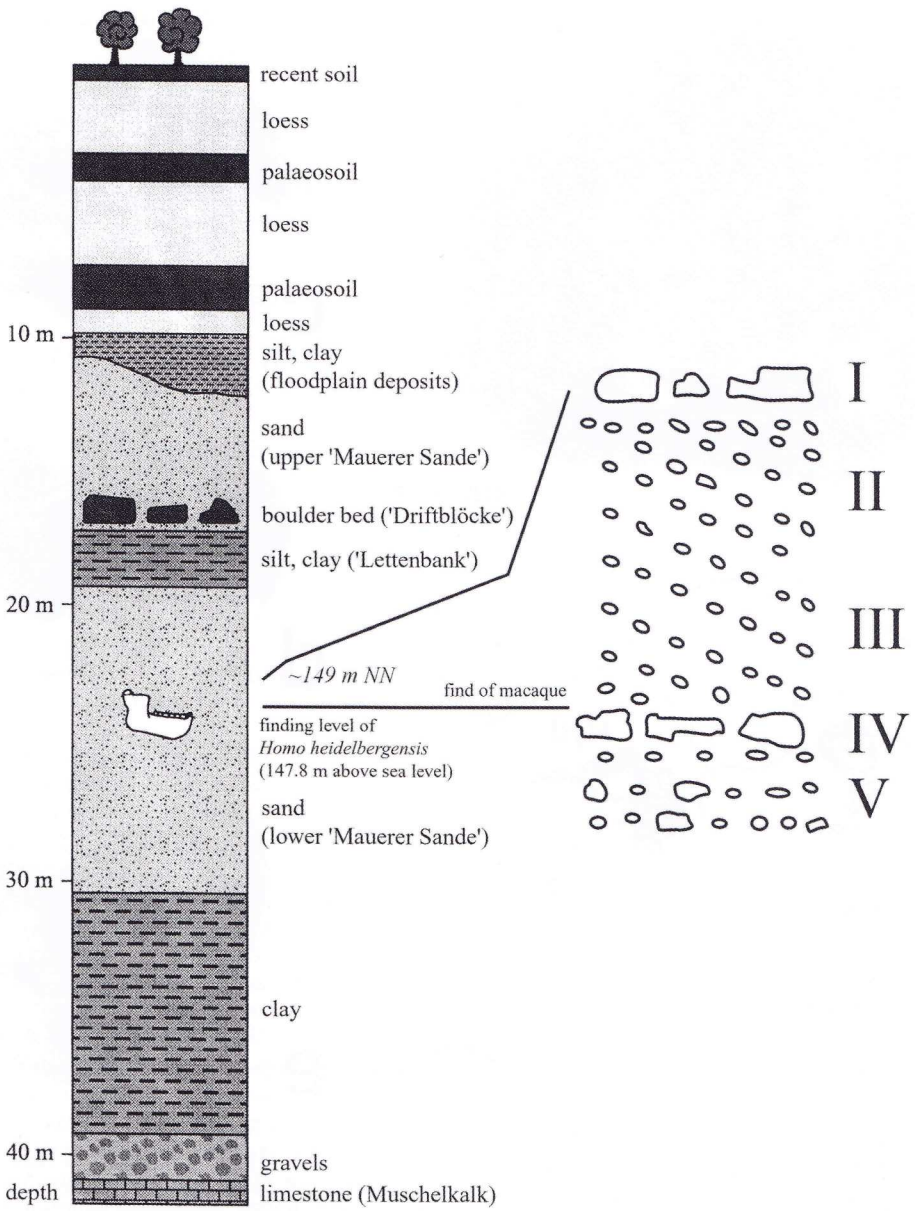

Fig. 1. The section shows the simplified sedimentary structures and assigned horizons for samples in the upper part of the lower 'Mauerer Sande' related to a geological section in the Grafenrain sand pit (modified after WAGNER & BEINHAUER 1997). The macaque remain occurred in sample-horizons II to III, directly above the level where *Homo heidelbergensis* was found.

for further macromammalian finds from the Mauer locality were limited. As a result, further investigations on micromammals, formerly described by HELLER (1934, 1939), seemed to be the most effective option to continue the research on Mauer for two reasons:

a) the biostratigraphical value of the micromammal remains, especially the molars of voles (Arvicolidae), increased in recent decades (see v. KOENIGSWALD & KOLFSCHOTEN 1996; MAUL et al. 2000), and

b) the extraction of sufficient sediment for micromammal studies is still possible in spite of the reduced amount of available material. Experience of fossiliferous horizons of the 'Mauerer Sande' shows that a volume of about 10 m^3 sediment will typically contains only one macromammal, but up to hundreds of micromammal remains, as well as additional small remains of macromammals (1-2 cm diameter, e.g. teeth of *Capreolus* and *Cervus*).

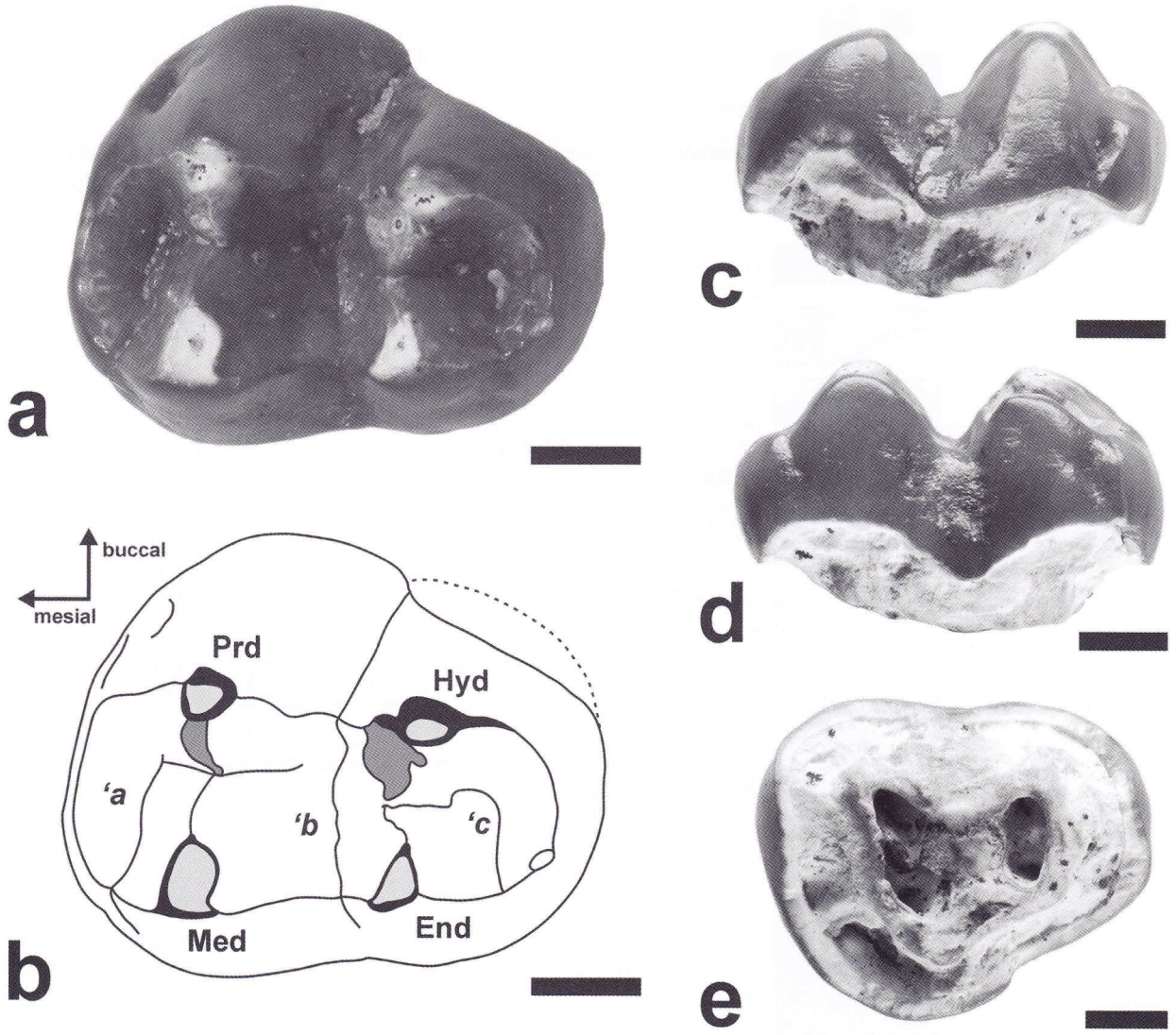

Fig. 2. *Macaca sylvanus* (Linneaus, 1758), isolated second lower jaw molar (m2), right, Mauer near Heidelberg, Grafenrain sand pit, 'Mauerer Sande' (SMNK-Pal 6602), **a**: occlusal, **b**: occlusal drawing, black areas: ages of enamel, light grey areas: dentine, dark grey areas: damage, **c**: buccal, **d**: lingual, **e**: ventral. Scale is 2 mm. Prd: protoconid, Med: metaconid, Hyd: hypoconid, End: entoconid, 'a: mesial fovea, 'b: talonid basin, 'c: distal fovea (nomenclature after Kay 1977; Szalay & Delson 1979).

Following a research campaign in the late 1980s, initiated by Dr Reinhard Kraatz (former curator at the Geologisch-Paläontologisches Institut of the University of Heidelberg) and Erich Mick (former mayor of Mauer), which focused on the stratigraphical position of the 'Mauerer Sande', the investigation of micromammals started in 1995 as a school project with the support of secondary school and university students. In the following decade a huge amount of sediment (about 50 m^3) has been extracted from the Grafenrain sand pit, dry sieved, and its fossil content has been picked. Micromammals were mainly found in the gravel grade, while small macromammals, e.g. teeth, were found in the fine pebble grade. The molar of a macaque was found in such a fine pebble grade from a sample from 148-149 m above sea level (Fig. 1), collected in February 2008. Since the find of the lower jaw of *Homo heidelbergensis* this molar is the second primate fossil recovered from the Mauer locality.

3. Systematic palaeontology

Systematic follows McKenna & Bell (1997).

Order Primates Linnaeus, 1758
Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Tribe Papionini Burnett, 1828
Subtribe Macacina Owen, 1843
Genus *Macaca* Lacépède, 1799

Macaca sylvanus (Linnaeus, 1758)
Fig. 2

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], ca. 145-164 m above sea level.

Horizon: 'Untere Mauerer Sande', the lower section of the 'Mauerer Sande'.

Collection: State Museum of Natural History Karlsruhe, inventory number: SMNK-Pal 6602.

Description. – The isolated tooth (Fig. 2) shows a bilophodont tooth pattern with four cusps, surrounding a trigon basin, respectively a talonid basin. The crests between the mesial, as well the distal cusps, are less prominent, making the principle bunodont character of the tooth still recognisable. Mesial and distal from each cusp arise crests, which are elongated, fused at their ends, and producing a circular crest on the rim of the crown. This crest is slightly incised lingually and buccally of the basin, forming a moderate shaped lingual and buccal notch. Mesial and distal of the tooth the circular crest limits a rectangular shaped mesial fovea, as well as a square shaped distal fovea (Fig. 2a, b). Down the cusps the convexity of the buccal and lingual longitudinal sides is weak, resulting in a low degree of the molar flare. The tooth measures 9.9 mm in mesiodistal length (MDL), 8 mm in mesial breadth (MB), and 7.6 mm in distal breadth (DB) (the last value is estimated, because of the buccodistal damage of the crown). The roots are broken off below the enamel rim (cervix), opening the dental pulp with four corresponding segments beneath the cusps (Fig. 2c-e), the edges on the dentine are smoothed by the process of transportation.

From the anatomy of this tooth its position within the molars can be considered as a right second lower molar (m2). The third lower molar (m3) can be excluded, in the macaques this tooth has an additional extension distally, composed of the hypoconulid and the tuberculum sextum (Szaley & Delson 1979), which does not exist in the tooth from Mauer. In comparison to the upper molars, the lower molars of the macaques are more slender in relation to their length, and the tooth from Mauer has a length-breadth-relation, which corresponds to a lower molar (Fig. 3). Furthermore the relatively longer distance between protoconid and metaconid (trigonid) in comparison to the distance between hypoconid and entoconid (talonid) indicates the mesial-distal orientation, additionally the different inclination of longitudinal sides indicates the buccal-lingual orientation (Fig. 2a, b). Summarising these anatomical features the specimen from Mauer presented here is assignable as a right lower molar, and according to its dimensions as a second molar (m2) (Fig. 3).

Around the basal rim of the enamel the specimen shows some damage, with edges smoothed to varying degrees, indicating different events, like its transportation after the breaking off of the roots. In particular, the buccodistal rim of the enamel is widely broken off, and shows well-rounded edges. These conditions indicate early damage, followed by transport in the current of a river. Other damaged parts of the rim are less rounded, suggesting a relation to younger events. Another kind of damage occurred on the mesial hypoconid, where the fracture surface suggests a possible accessory cusp that has been broken off (Fig. 2a).

Apical of all four cusps are plane traces of abrasion, which are identifiable as initial wear facets. On the lingual metaconid and entoconid the dentine is more open as on the both buccal cusps.

The enamel is white, but partially strong yellow-orange to reddish impregnated. Beside this the dentine is white but slightly yellowish coloured on the surface with few spots of manganese mineralisation. The preservation pattern of the specimen under study here matches the most common pattern seen in the fossils from the 'Mauerer Sande': a disarticulated, isolated, and in parts a fragmentary skeletal element, with primary white coloured substance of the bone, as well as the enamel, with intensive yellow, red to brown regions coloured by several iron mineralisations on the surfaces, and with manganese impregnations (Schreiber 2006).

4. Discussion

The bilophodont tooth pattern with talonid basin, mesial, and distal foveae characterise the specimen from Mauer as a tooth of a Cercopithecidae, and the low relief of the crown (low-crowned tooth) indicates the membership of the Papionini. The low degree of the molar flare (on the lingual and buccal side), and additionally the relative small-sized dimension indicates the tooth as one of the genus *Macaca* (see Szalay & Delson 1979).

In comparison to the fossil cercopithecid *Paradolichopithecus*, a Papionini from Puebla de Valverde, Spain (Ardito & Mottura 1987), *Macaca* is small- to medium-sized in dimension, and in comparison to *Macaca* the papionin *Theropithecus* from Cueva Victoria, Spain (Gilbert et al. 1995), has high-crowned teeth with three deep shaped-basins, and column-shaped 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 Colobinae (Layna, Perpignan, Ardito & Mottura 1987), differ from *Macaca* with their high-crowned dentition (Szalay & Delson 1979).

Szalay & Delson (1979) have proposed five biochronological subspecies of *Macaca sylvanus* for fossil and Recent macaques. But neither Szalay & Delson nor later authors (see Rook et al. 2001; Alba et al. 2008) discussing *Macaca*-fossils mentioned any diagnostic morphometric features for the assignment. Additionally Szalay & Delson (1979) note, that in the genus *Macaca* the Recent species show a wide variation of morphology and dimensions. Fooden (1980) distinguished 'species-groups' within the genus *Macaca* on the basis of soft tissue anatomy. But a sufficient correlation between Recent soft tissue, skeletal, and tooth morphology with fossil skeletal morphology, has not been described up to now. In the current paper these proposed subspecies are not considered, because of their insufficient diagnosis, and in general we suggest to not using them until a suitable diagnostic is available. In summary the specimen from the Grafenrain sand pit from the Mauer locality is assigned to the species *Macaca sylvanus* (Linnaeus, 1758).

5. Ecological evidence

The Recent geographical distribution of the genus *Macaca* in northwest Africa and southeast Asia implies that the fossil populations of macaques also preferred subtropical to tropical climate zones. With regard to the environment of *Homo heidelbergensis* it would mean a different climate signal as was recently proposed (see below). In fact Recent macaques live in 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 between arboreal and terrestrial locomotion (van Hoof 1988). 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 extended variety of its habitat might be a sufficient explanation 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 a recent ecomorphological study of Eronen & Rook (2004) on European Mio-Pliocene primate occurrences, showing

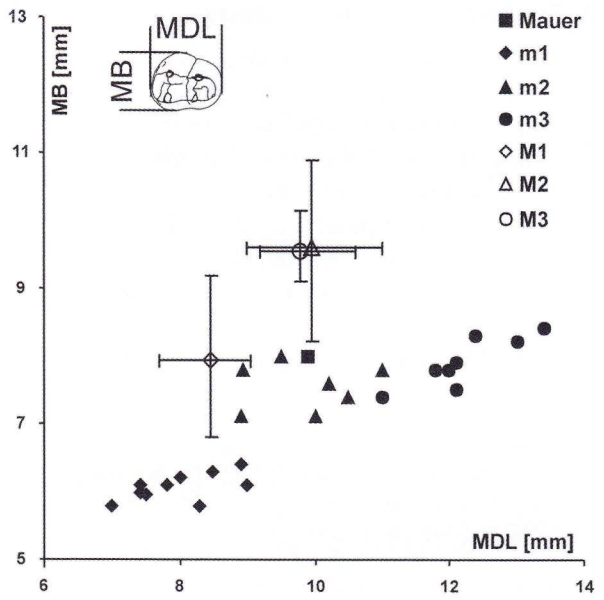

Fig. 3. Bivariate plot of mesodistal length (MDL) and the mesial width (MB) for *Macaca* from the Plio- and Pleistocene of Europe. Plotted are the length and width of the lower molar (m2) from Mauer (SMNK-Pal 6602), of the first, second, and third lower molars (m1, m2, m3) by Schreuder (1945), Franzen (1973), Penela (1983), Köhler et. al (2000), Zapfe (2001), Mazza et al. (2005), Alba et al. (2008), 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), Penela (1983), Rook et al. (2001), and Alba et al. (2008). The plot shows the different proportions of the slender lower cheek teeth in comparison to the relatively wide upper cheek teeth, and the increasing of size from the first to the third molars.

that the Cercopithecoidea, especially the *Macaca*, had occupied a variety of environmental conditions.

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). Moreover, with their mode of life, the macaques fit well inside the image of the landscape of the *Homo heidelbergensis*, which is currently described by Schreiber et al. (2007) as having 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.

6. Conclusions

The specimen of an isolated right second molar of the lower jaw (m2), 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 anatomical features like the low relief of the crown, the bunodont character of the tooth pattern, four cusps and three basins, the specimen is assigned to the species *Macaca sylvanus* (Linnaeus, 1758). The tooth represents the second record of a primate from the 'Mauerer Sande', after the find of the lower jaw of *Homo heidelbergensis*.

The presence of *Macaca* at Mauer confirms the previous expectation that macaques would be found in the faunal assemblage of the 'Mauerer Sande' (see v. Koenigswald 1997; Schreiber et al. 2007). In most other important mammalian fossil sites of Europe, like Mosbach, Upper Valdarno, Hoxne, Pietrafitta, Sénèze, Montpellier, Voigtstedt, Heppenloch, Tegelen, Untermassfeld, *Macaca* were present, but not in Mauer. With the new find an important gap in the list of the faunal assemblage of Mauer is now closed.

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