The fossil pig from the Late Miocene of Dorn-Dürkheim 1 in Germany

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Abstract:

The Early Turolian locality of Dorn-Dürkheim 1 (Rheinhessen, Germany) yielded a large collection of teeth of the fossil pig genus *Microstonyx*. This collection elucidates the phylogeny of this genus. Two species of *Microstonyx* occurred in Europe during the Turolian: *M. major* and *M. erymanthius*. Most authors considered these as just one species or as two subspecies. *M. major* is larger than *M. erymanthius*. M. erymanthius from Pikermi and Samos is more progressive than *M. major* in the clongation of the second and third upper incisors.

Microstonyx from Dorn-Dürkheim 1 is similar in size to M. erymanthius, but in the elongation of its I^2 and I^3 it is intermediate between M. major from Spain and M. erymanthius from Pikermi and Samos. Dorn-Dürkheim 1 is older than Pikermi and Samos and its suid represents therefore an earlier form of M. erymanthius.

The two sizes of *Microstonyx*, *M. major* or and *M. erymanthius*, were contemporaneous for a long period and display independent evolution in the incisors. This suggests that they were two species instead of subspecies. The suid from Dorn-Dürkheim 1 is named *M. erymanthius brevidens* n. ssp. because it differs from *M. erymanthius erymanthius* in its shorter incisors.

Keywords: Miocene, Turolian, Suidae, Europe, taxonomy, phylogeny

Kurzfassung:

Die unterturolische Wirbeltierfundstätte Dorn-Dürkheim 1 (Rheinhessen, Deutschland) hat unter anderem zahlreiches Material der fossilen Schweinegattung *Microstonyx* geliefert. Diese Sammlung ermöglicht nunmehr ein besseres Verständnis der Stammesgeschichte dieser Gattung. Während des Turoliums gab es demnach zwei Arten von *Microstonyx* in Europa, *M. major* und *M. erymanthius*. Die meisten Autoren betrachteten diese bislang als nur eine Art oder als zwei Unterarten. *M. major* ist größer als *M. erymanthius*. *M. erymanthius* von Pikermi und Samos ist dagegen progressiver als *M. major* hinsichtlich der Verlängerung der zweiten und dritten oberen Schneidezähne.

Microstonyx von Dorn-Dürkheim 1 hat die Größe von M. erymanthius, steht aber in bezug auf die Verlängerung seiner I^2 und I^3 in der Mitte zwischen M. major von Spanien und M. erymanthius von Pikermi und Samos. Dies wird so interpretiert, daß Dorn-Dürkheim 1 offenbar älter ist als Pikermi und Samos, und sein Suide eine frühe Form von M. erymanthius darstellt.

Da die zwei Größen von Microstonyx, M. major und M. erymanthius, lange Zeit nebeneinander auftraten, und die Evolution ihrer Schneidezähne unabhängig voneinander verlief, muß es sich bei ihnen um zwei verschiedene Arten anstelle von Unterarten handeln. Der Suide von Dorn-Dürkheim 1 wird dementsprechend M. erymanthius brevidens n. ssp. genannt. Er unterscheidet sich von M. erymanthius erymanthius durch seine kürzeren Inzisiven.

Schlüsselworte: Miozän, Turolium, Suidae, Europa, Taxonomie, Phylogenie

Introduction

Dorn-Dürkheim 1 is a Lower Turolian (Upper Miocene, MN 11)¹ locality in Rheinhessen (Germany). An introduction to the locality was given by FRANZEN and STORCH (1975), who also studied the carnivores, proboscideans and rodents discovered up to 1974. The insectivores were published by STORCH (1978). FRANZEN and SCHÄFER (1981) analysed the taphonomy of the site. The excavations were described by FRANZEN (1990), and in this volume.

Dorn-Dürkheim 1 yielded nearly 500 teeth of *Microstonyx*. This fossil pig occurs frequently in Vallesian and Turolian localities in Europe and Asia, but is little understood. There are different views of the taxonomy and stratigraphic range of the European *Microstonyx*.²

HÜNERMANN (1968), THENIUS (1972) and GINS-BURG (1988) recognised two species, Microstonyx antiquus (KAUP, 1833) and M. major (GERVAIS, 1848-1852), the latter including M. erymanthius (ROTH and WAGNER, 1854). Eumaiochoerus etruscus (= "Microstonyx choeroides"), a species that was endemic of Toscane (then an island), is later considered in the discussion. HÜNERMANN and THENIUS treated these two species as contemporaneous, suggesting that Microstonyx antiquus was a forest dwelling species, and M. major lived in the steppe or savannah environment. GINSBURG (1980) stated that Microstonyx antiquus was older (Vallesian, MN 9 - 10) than M. major (Early and Middle Turolian, MN 11 - 12).

1) MN = Neogene Mammal Unit (MEIN, 1990).

²⁾ Microstonyx PILGRIM, 1926 and Hippopotamodon LYDEKKER, 1877 are synonymus, but a discussion of the subject as well as the subgenus Limnostonyx GINSBURG, 1988 is beyond the scope of this paper, and the name Microstonyx will be used for the time being.

VAN DER MADE and MOYA-SOLA (1989) suggested that Microstonyx antiquus was Early Vallesian in age (MN 9), that M. major was Late Vallesian and Early and Middle Turolian (MN 10 - 12), and that M. erymanthius was either younger (later part of MN 12) or a geographical subspecies (identifying it at only three Greek localities: Pikermi, Samos and Kerassia). The MN 10 material that THENIUS placed in Microstonyx antiquus was assigned to M. major by us. Microstonyx antiquus is a large species (114 % linear measurements of the cheek teeth; VAN DER MADE, MONTOYA and ALCALÁ, 1992), M. major major is smaller (100 %) and M. erymanthius erymanthius is still smaller (93 %). M. major erymanthius displays also some morphological differences with M. major major.

The material from Dorn-Dürkheim 1 clarifies the relationship between M. major and M. erymanthius: two different species, and the latter species shows some evolutionary change.

The collection from Dorn-Dürkheim 1 includes many teeth that are not common. I^2 and I^3 are of special interest for the evolution of Microstonyx. Some teeth, such as I^3 , D^2 and D_2 might be confused with teeth of the smaller species Propotamochoerus palaeochoerus (MN 8 - 13/14?) and Propotamochoerus provincialis (MN 13 - 15). P. palaeochoerus is abundant in MN 8 and MN 9 (uppermost Aragonian and Lower Vallesian), and becomes rare after that, or may be replaced by another species of the same genus. All or some of the Propotamochoerus of MN 10 - 13/14 differ in a number of characters from P. palaeochoerus of MN 8 - 9: the premolars are smaller and the incisors differ morphologically. A comparison with Propotamochoerus from MN 10 - 13/14 is most interesting, but this is not possible here for practical reasons. Compa-

Measurements are given in mm. Teeth, measurements and indices of teeth are indicated with the following abbreviations:

 $Cf = Canine of a female; C_f and C^f indicate lower and upper canines.$

 $Cm = canine of a male; C_m and C^m indicate lower and upper canines.$

 $Cx = canine of a male or a female; C_x and C^x indicate lower and upper canines.$

DAP = length, measured as indicated by VAN DER MADE (1990).

DAP' = length of a tooth expressed as a percentage of



Figure 1. Two ways of measuring DMD in the I_3 . DMD is measured parallelly to the way it is measured in the first two incisors, but in isolated teeth this is difficult. DMD2 is therefore taken as another measurement which can easily be repeated in a constant way.

risons will be made with *P. palaeochoerus* from MN 8 and MN 9, *P. provincialis*, *Microstonyx major*, and *Microstonyx erymanthius*.

This study has two main aims:

- 1) to describe the material from Dorn-Dürkheim 1, with an emphasis on the infrequently recovered check teeth, and
- 2) to elucidate an obscure part of the evolution of *Microstonyx*.

Abbreviations and Definitions

the length of the first molar DAP' = (DAP / DAP MI) x 100% (for upper teeth the length of the M^1 is used as a standard, for lower teeth the length of the M_1). DAP' may be calculated on averages of populations or on teeth of one individual.

DLL = linguo-labial width, measured as indicated by VAN DER MADE and HAN (1994). See also text-fig. 1.

DLL' = linguo-labial width expressed as a percentage of the DT of the M1. Calculated on averages of populations or on teeth of one individual.

DMD = mesio-distal distance, measured as indicated by VAN DER MADE and HAN (1994). See also text-fig. 1.

Figure 2. Scatter diagram of the lower cheek teeth of *Microstonyx* and *Propotamochoerus*. Legend: triangles = *Microstonyx erymanthius*, black triangles from Dorn-Dürkheim 1 and open triangles from Pikermi; dots = *Microstonyx major* from Spanish localities (data from VAN DER MADE, MONTOYA and ALCALÁ, 1992); crosses = *Propota-mochoerus* from various localities, upright crosses = *P. palaeochoerus*, and oblique crosses = *P. provincialis*.

P. palaeochoerus is often found in the same locality as *P. steinheimensis*, and the molars are difficult to distinguish. Only M_1 and M_2 found associated with premolars are plotted. Only M_3 from Wissberg are plotted (one large sample). The same procedure is followed for the upper cheek teeth.



DMD' = mesio-distal distance expressed as a percentage of the DT of the M1. Calculated on averages of populations or on teeth of one individual.

DT = maximum width, either DTa or DTp, measured as indicated by VAN DER MADE (1991).

DTa = width of first lobe.

DTp = width of second lobe.

 $DTpp = width of third lobe (in M_3).$

DT' = width of a tooth expressed as a percentage of the maximum width of the first molar DT' = (DT / DT MI) x 100%. DT' is calculated on averages of populations or on teeth of one individual.

I = index (DAP / DT) x 100% or (DMD / DLL) x 100%.

La = width of the labial side of the C_m measured as indicated by GUAN JIAN and VAN DER MADE (1993).

La' = width of the labial side of the C_m as a percentage of the width of the M₁. Lá is calculated on averages of populations or on teeth of one individual.

Li = width of the lingual side of the C_m , measured as indicated by GUAN JIAN and VAN DER MADE (1993).

Li' = width of the lingual side of the C_m as a percentage of the width of the M_1 . Li' is calculated on averages of populations or on teeth of one individual.

Po = width of the posterior side of the C_m , measured as indicated by GUAN JIAN and VAN DER MADE (1993).

Po' = width of the posterior side of the C_m as a percentage of the width of the M₁. Po' is calculated onaverages of populations or on teeth of one individual.

SD = standard deviation.

V = coefficient of variation; 100 x (SD/mean).

V' = Measure of variability (FREUDENTHAL and CUENCA, 1984).

$$V' = \frac{200 \text{ x (maximum - minimum)}}{(\text{maximum + minimum})}$$

Material Studied

A total of 475 dental specimens, and 8 bones were studied from Dorn-Dürkheim 1 : 15 I₁, 29 I₂, 15 I₃, 7 C_f, 11 C_m, 2 P₁, 12 P₂, 16 P₃, 20 P₄, 16 M₁, 19 M₂, 46 M₃, 6 DI₁, 2 DI₂, 1 DI₃, 4 D₂, 3 D₃, 12 D₄, 25 I¹, 14 I², 11 I³, 9 C^m, 1 C^f, 9 P¹, 24 P², 24 P³, 25 P⁴, 19 M¹, 16 M², 42 M³, 5 DI¹, 4 DI², 4 D², 1 D³, 5 D⁴, 5 phalanges and 3 partial metapodials. These parts represent a minimum of 25 individuals, at least seven of which were males and six were females. All this material is housed in the Forschungs-Institut Senckenberg at Frankfurt am Main (SMF).

The suid fossils from Dorn-Dürkheim 1 are compared to fossils of other suids:

Propotamochoerus palaeochoerus from Eppelsheim (Hessisches Landesmuseum, Darmstadt - HLD), Wissberg near Gau-Weinheim (HLD; Naturhistorisches Museum, Mainz; Instituut voor Aardwetenschappen, Utrecht - IVAU), Johnsdorf (Steiermärkisches Landesmuseum, Graz), San Quirze (Institut Paleontològic Dr. M. Crusafont, Sabadell - IPS; Museo Geológico del Seminario Conciliar, Barcelona), Castell de Barberá (IPS), Hostalets (IPS, collection Villalta, Barcelona), Can Llobateres (IPS), Can Ponsic I (IPS), Ballestar (IPS) and the Münchener Flinz/Isarbett (Bayerische Staatssammlung für Paläontologie und Historische Geologie, München).

Propotamochoerus provincialis from Montpellier (Université Claude Bernard, Lyon; Naturhistorisches Museum, Basel - NMB), Venta del Moro (Museo Nacional de Ciencias Naturales, Madrid - MNCN), Casino (Accademia dei Fisocritici, Siena - AFS), Herbholzheim (casts in NMB), Roussillon (cast in NMB), Arenas del Rey (MNCN) and Ptolemais-Kardia (IVAU).

Microstonyx erymanthius from Samos (NMB; HLD) and Pikermi as described by PEARSON (1928).

Microstonyx major from 21 Spanish localities, described by VAN DER MADE, MONTOYA and ALCALÁ (1992).

Eumaiochoerus etruscus from Monte Bamboli (AFS; NMB; Museo Regionale di Scienze Naturali, Torino; Museo di Storia Naturale e del Territorio Universitá di Pisa; Dipartimento di Scienze della Terra, Universitá di Firenze; Dipartimento di Scienze della Terra, Universitá la Sapienza, Roma) and Baccinello (MBA).

Descriptions and Comparisons

Microstonyx is common in European upper Miocene localitics (GAUDRY, 1862 - 1867; GOLPE, 1978, 1979a, 1979b, 1980a, 1980b; HÜNERMANN, 1968; PAVLOW, 1913; THENIUS, 1972; TROFIMOV, 1954),. and a detailed description of the cheek teeth is avoided here. Instead I will emphasise descriptions of teeth that are rare or that have special importance for the phylogeny of this genus. For additional descriptions I will refer to VAN DER MADE and HUSSAIN (1989); VAN DER MADE, MONTOYA and ALCALÁ (1992); VAN DER MADE and The cheek teeth of *Microstonyx erymanthius* from Pikermi are 101% (values of molars from PEARSON, 1928) of the average size of the Dorn-Dürkheim 1 teeth, and those of *Microstonyx major* from Spain are 111% as large (values from VAN DER MADE, MONTOYA and ALCALÁ, 1992). Check teeth from Samos are similar in size to those from Pikermi. For Samos, averages could not be calculated because I did not have the opportunity to measure a large sample. The molars from Dorn-Dürkheim 1 cluster with those from Pikermi in the scatter diagrams (text-figs. 2 and 3). They are smaller than those of *M. major* from Spain, but overlap to some degree. The molars from Dorn-Dürkheim 1 are larger than those of *Propotamochoerus*, but overlap in Ml and M2 with the large *P. provincialis*. In the premolars (text-figs. 2 and 3) the overlap with this species is even greater and there is even some overlap with the smaller *Propotamochoerus palaeochoerus*. This is a consistent difference between the genera: *Microstonyx* has enlarged M3 and *Propotamochoerus* has large premolars. The individual check teeth are similar in morphology.

The third lobe of the M_3 may have one, two or three cusps, or it may have an irregular shape with many smaller cusps (DD 3041). The M^3 also shows variation in the structure of the talon. For a discussion on variability of the last lobes of the M3 in *Microstonyx*, see VAN DER MADE, MONTOYA and ALCALÁ (1992).

The M_1 and M_2 are similar, but the M_2 is larger (132%) and there is no overlap in size (Table 2). The D_4 is similar in morphology to M_1 , but has an extra lobe. The main roots are below the first and last lobe and there is no large root below the middle lobe. This allows identification of fragmentary teeth as D_4 , because there is a large root below both lobes in M_1 . The last lobe of the D_4 is approximately 15 % smaller than the last lobe of the M_1 and no overlap occurs.

The D^4 , M^1 and M^2 are similar, but increase in size in this order (Tables 3 - 4). There is no overlap. The D^4 has an oblique anterior side and is slightly more elongate than the permanent molars.

The D^3 has a very characteristic shape: there is one large cusp on the anterior lobe and the morphology of the second lobe is similar to that of the D_4 and the molars. There is no overlap in DTp between D^3 and D^4 .

The $\mathbf{P}_{\mathbf{l}}$ (Plate 1, figs. 25-26) and $\mathbf{P}^{\mathbf{l}}$ (Plate 1, figs. 31-32; Plate 2, figs. 57-60) are small. The $\mathbf{P}_{\mathbf{l}}$ is as

DAP 20 19 P 18 17 16 P3 15 14 13 12 D 9 10 11 12 13 14 15 16 17 19 DT 5 6 7 8 18

Figure 4. Scatter diagram for the P^2 (open), P^3 and D^2 (closed figures) of Microstonyx from Dorn-Dürkheim 1 (triangles) and Spain (circles), as well as Propotamochoerus palaeochoerus(diamonds) and Propotamochoerus provincialis from various localities

large as D_2 , but has one large flat root, whereas the D_2 has two roots. There is considerable variation in the morphology of the P¹ (see plates). The P¹ has two roots. *Microstonyx* shows an evolutionary trend to loose the P₁ by reduction and in later stages the P¹ also. Between the first stage of having the P₁ and the stage that the tooth is not formed there might be the stage in which the P₁ is lost early in life, or that it is formed only in a few individuals. There are 9 P¹ and only 2 P₁. This could be due to reduction of the P₁ or to taphonomy.

The P_2 (Plate 1, figs. 27-28), P_3 , D_2 (Plate 1, figs. 18-19) and D_3 are similar, but in the deciduous teeth the roots are more divergent. The D_2 is much smaller than the other teeth, but the P_2 and D_3 are "8" in occlusal view, whereas the D_3 shows a more bulky triangular outline.

The \mathbf{P}^2 (Plate 1, figs. 29-30; Plate 2, figs. 55-56), \mathbf{P}^3 and \mathbf{D}^2 are similar. The P² is more elongate and the P³ is more hypsodont (Tables 4, 6 and 7). It is striking that P³ of *Propotamochoerus* and similar in size (Tables 4 and 5). The P₂ has the shape of an *Microstonyx* form one cluster and P² and D² two other ones (text-fig. 4; although, within these clusters there are size differences between the species). This is caused by the relatively large premolars of the smaller species of *Propotamochoerus*, making them nearly as large as those of the larger *Microstonyx* (see also Tables 4 and 6). Isolated elements are not easily identified.

The C_f (Plate 1, figs. 13-17) has enamel all around (unlike the C_m which lacks posterior enamel). The crown section of a C_f of most individuals is triangular, but the lingual and labial sides are so convex as to give a section that is more or less oval with two posterior keels (which do not mark the widest point of the tooth). The tooth is small compared to body size (Table 8; DAP' = 45, DT' = 48). The crown is low and there is a nearly horizontal apical facet. An anterior dipping facet may be present (due to contact with the I³?). The

crown seems to be lower than in *M. major* from Spain (VAN DER MADE, MONTOYA and ALCALÁ, 1992, plate 2, fig. 5).

One fragmentary C^{f} is preserved. Its crown is low, narrow, and elongated. C^{f} of *Microstonyx* becomes clongated like the I² and I³.

The C_m (Plate 1, figs. 20-24) is small (Table 8) compared to body size. The genus *Microstonyx* was based on the character of reduced canines. The Li', La' and Po' have values of 95, 78 and 61. The Spanish canines might represent a size reduction in time, their values range between $\pm 76 - 112$, 80 - 94 and between 48 - 83 respectively. The canines of *Propolamochoerus* are as large as those



Figure 5. Scatter diagrams for the canines of *Microstonyx* erymanthius from Dorn-Dürkheim 1 (triangles), *Microstonyx* major from Spain (dots), *Propotamochoerus provincialis* (oblique crosses), and *Propotamochoerus palaeochoerus* from different European localities (crosses). For the C_m, the dot represents a canine of *M. major* from Montredon (data from GINSBURG, 1988).

of Microstonyx, despite its smaller size, and have a wider posterior side (text-fig. 5). The canines of Microstonvx are like those of Sus verrucosus, with a labial side that is wider than the posterior side, and the canines of Propotamochoerus are like those of S. scrofa, with a wider posterior side. The canines from Dorn-Dürkheim 1 have peculiar apical wear facets, which are caused by occlusion with the upper canines. The facets are flat and make an angle of approximately 45⁰ with the long axis of the tooth (at that place the tooth is curved). PAVLOW (1913, Plate 3, fig. 2) figured a mandible from Grebeniki, in which the canines display a horizontal apical wear facet. In other suids this angle is much smaller and the wear facet longer and often curved. This indicates a shift of position or orientation of at least one of the canines. The same type of facet can be seen on a canine in a mandible of Eumaiochoerus from Monte Bamboli (IGF 4002). In this mandible the lower canine was apparently rotated into a more horizontal position. The orientation of the canine is similar to that the incisors, and the canine is reduced to

The C^m (Plate 2, figs. 49-54) are very short and are not curved. Like the lower canines, they bear an apical facet that makes a large angle with the long axis of the tooth. Usually it is a single flat facet, but two facets at an angle of approximately 120° may also occur. This arrangement implies that the facet of the lower canine is angled too. Canines in more advanced suids are curved and have a horizontal orientation at the place of occlusion with the lower canine. The apical wear facet is oriented vertically. This was apparently not the case in the Dorn-Dürkheim animals. If both upper and lower canines are oriented in such a way that they occlude and that the wear striae are oriented transversely, the upper canine is directed forward and downward. In this case the lower canine is oriented forward, it curves a little upward and only a slightly outward. The orientation of the C_m must have been much like in the mandible of Eumaiochoerus. The canine of M. major is similar (GINSBURG, 1988, plate 1, fig. 1), but larger. The DAP' and DT' values of the Spanish canines are 107 and 85, for Dorn-Dürkheim 1 these values are 77 and 60. There are few Spanish canines so that I got only 1 value for the upper and 2 and 3 values for the lower canines. Probably there was a size reduction in the canines of M. major.

The I_1 , I_2 (Plate 1, figs. 1-3), DI_1 and DI_2 are similar, but the second incisors are more asymmetrical. The deciduous incisors are smaller (Table 9), approximately 60 % as large as the permanent incisors, and are equally hypsodont (i.e. similar in relative crown height). The deciduous incisors are also more rounded shape than the permanent incisors and morphological features are less pronounced. The permanent incisors are slightly larger than the incisors of *Propotamochoerus palaeochoerus* (text-fig. 6). The height of the crown could be measured only in a few specimens (Table 9) and no direct comparison can be made to *M. major* from Spain.

The I₃ (Plate 1, figs. 4-9) and DI₃ (Plate 1, figs. 10-12) are similar, but differ approximately 40 % in size (Table 9). The I₃ from Dorn-Dürkheim 1 has a relatively lower crown than the I_3 of *M. major* from Spain (VAN DER MADE, MONTOYA and ALCALÁ, 1992, text-fig. 5, number 3 and Plate 2, fig. 8). Measurements of the crown height of the incisors are given in Table 11, the crown height of the only specimen from Spain could not be measured. I^3 occludes with the distal side of the I_3 and I^2 respectively. The height of the I_3 are apparently related to the length of the I^3 but, at present, this cannot be substantiated by measurements. Increase of hypsodonty of the lower incisors (a progressive trait) would cause elongation of the upper incisors. A comparison between the lower incisors from Dorn-Dürkheim 1 and Pikermi or Samos would be very interesting.

The I^1 (Plate 2, figs. 43-48) and DI^1 (Plate 2, figs. 40-42) are similar in morphology, but the deciduous incisor is smaller (Table 10). The I^1 has a lingual cingulum that is developed as a horizontal crest. The cingulum of the DI^1 is a more vertically oriented structure.

tooth in *M. major* from Spain. *Propotamochoerus* incisors are similar in size (text-fig. 7), and are thus relatively larger. The I^{I} from Dorn-Dürkheim 1 is more hypsodont than in *P. palaeochoerus*, but resembles the other species of *Propotamochoerus* and *Microstonyx* in degree of hypsodonty.

The 1² (Plate 2, figs. 33-34), 1³ (Plate 2, figs. 35-38) and the DI² (Plate 2, fig. 39) arc more or less similar. The I^2 is larger and the I^3 and DI^2 are similar in size (Table 13; text-fig. 7). The two smaller incisors can be separated morphologically: the DI^2 is a small copy of the I^2 and has a lower, more elongated crown than the 1^3 , the tip of its crown is placed more forward. The occlusion with the lower canine causes a posterior facet on the I^3 ; the DI² and I² lack such a facet. The I³ occludes at its posterior side with the I_3 , whereas the I^2 and DI^2 occlude at the anterior side with the I_2 and DI_2 . The I^3 may also develop an anterior facet like the I^2 . It is possible that this was caused by contact with the I_3 but only, if the I^3 has an outward flare. Such an orientation is suggested by the orientation of the posterior wear facet and the striae. In M. erymanthius from Samos the 1^3 does not as much flare outward as the Dorn-Dürkheim 1 specimen, and it has a large anterior facet and no posterior facet (VAN DER MADE and MOYÀ-SOLÀ, 1989, Plate 1, fig. 13). In the material from Samos, there is a diastema between I^2 and I^3 , which may have caused also the area of occlusion with I_3 to move forward on the I^3 . The I^2 of *P. palaeochoe*rus and P. provincialis are similar to those of M. erymanthius (VAN DER MADE and MOYÀ-SOLÀ, 1989, Plate 1, figs. 11 and 8), the I^3 is shorter, with a higher crown, especially the I^3 of *P. palaeochoerus* (VAN DER MADE and MOYÀ-SOLÀ, 1989, Plate 1, figs. 9 and 10). The length of the I^2 of *P. provincialis* is the same as from Dorn-Dürkheim 1, but the I^3 is smaller (text-fig. 7). The I^3 from Samos has the same size as the I^2 from Dorn-Dürkheim 1 and these two teeth are indistinguishable. The I^2 of *P. palaeochoerus* is similar in size to the I^3 and DI^2 from Dorn-Dürkheim 1, but lacks the posterior facet of the I^3 and has thicker enamel than the DI^2 .

The I^2 of both *M. major* from Spain and *M. ery*manthius from Samos are larger. One incisor from Dorn-Dürkheim 1 is also that large. The I^2 from Samos are more elongate. In Table 12, the length and width of the incisors is expressed as the length of the first upper molar (DMD' and DLL'). Although these DMD' and DLL' values are in some cases calculated on the basis of small samples they suggest that the main differences in the relative size of the incisors is in the DMD' of the I^2 and I^3 . These incisors are elongated in all *Micro*stonyx. This apparently follows a trend of elongation starting with the I^2 and affecting the I^3 less or in a later stage. The form of Samos is most advanced, the other two have similar values for the I^2 , but Dorn-Dürkheim 1 is more advanced in the I^3 than Spain.

The phalanges and metapodials are morphologically similar to *Sus*, but they are larger (Table 13).



Figure 6. Scatter diagrams for the lower incisors of Microstonyx erymanthius from Dorn-Dürkheim 1 (triangles), Microstonyx



Figure 7. Three scatter diagrams for the I^1 , I^2 and I^3 of Microstonyx erymanthius from Dorn-Dürkheim 1 (black triangles), Microstonyx erymanthius from Samos (open triangles), Microstonyx major from Spain (dot) as well as Propotamochoerus palaeochoerus (crosses) and Propotamochoerus provincialis from various European localities (oblique crosses). The I^3 of Microstonyx major may have been slightly longer (1 mm?).

The fourth scatter diagram shows three incisors with the same morphology of *Microstonyx erymanthius* from Dorn-Dürkheim 1 $(I^2 \text{ big black triangles; } I^3 \text{ small black triangles and } DI^2 \text{ big black triangle with the point downward}) and the I^3 of$ *Microstonyx erymanthius*from Samos (open triangle) and the I² of*Propotamochoerus palaeochoerus*from various European localities

Discussion

VAN DER MADE and MOYÀ-SOLÀ (1989) recognised two subspecies, *Microstonyx major major* and *Microstonyx major erymanthius*: these taxa differ in two dental characters:

1) Size.

The check teeth of M. erymanthius are 93 % as large the check teeth of M. major (in linear measurements).

- 2) Morphology.
 - The I^2 , I^3 and C^f of M.

and have a relatively long crown (or great DMD' value). Elongation of the incisors is interpreted as a progressive character (VAN DER MADE and MOYÀ-SOLÀ, 1989).

From the decription it follows that:

- 1) The linear sizes of the cheek teeth of *Microstonyx* from Dorn-Dürkheim 1 (100%) and those of *M. ery-manthius* from Pikermi (101%) are similar, and those of *M. major* from Spain are larger (111%; whereas those from Dorn-Dürkheim 1 are 91% as large as teeth from Spain).
- 2) The relative length of the 1^3 from Dorn-Dürkheim 1 (DMD' = 78) is much advanced over the length in *M. major* from Spain (56 < DMD' < 60), but not yet as much as in *M. erymanthius* from Samos (99). The DMD' of the 1^2 from Samos and Pikermi (127 and 136) are advanced over Dorn-Dürkheim 1 and Spain (Table 12).

The taxon from Dorn-Dürkheim 1 differs from M. major from Spain in size, and it is more progressive

in the elongation of the I^3 . It is similar to *M. erymanthius* from Pikermi and Samos in size and in its more progressive elongation of the incisors. The taxon from Dorn-Dürkheim 1 (MN 11) belongs to the same lineage as *M. erymanthius* from Pikermi (MN 12), but is not yet as advanced in the elongation of the incisors. *M. major* apparently remains more conservative in the degree of elongation of the incisors.

A cast of a large M₃ from Polgardi (in the NMB), indicates that M. major still existed in MN 13. M. erymanthius occurs in Tudurovo and this species may have evolved into the Pleistocene Chinese M. ultimus (HAN, 1987). The size difference between the lineages of M. major (MN 10 - 13) and M. erymanthius (MN 11 - Pleistocene) existed for several millions of years. It seems likely that these taxa represented two different species, rather than subspecies, as indicated by VAN DER MADE and MOYÀ-SOLÀ (1989). Differences in body size, were probably important in separating these species. Body weights are estimated as 225 kg for M. erymanthius from Dorn-Dürkheim 1 and 217 kg from Pikermi, 298 for M. major from Spain and 402 kg for M. antiquus from Eppelsheim on the basis of LE-GENDRE's (1986) method.

There is a difference between the Dorn-Dürkheim I and Pikermi forms, and this is potentially of stratigraphic use. This difference should be reflected in taxonomy. The difference is only small and based on infrequently found incisors. Thus it is best reflected at the subspecies level.

Microstonyx erymanthius brevidens n. ssp.

Holotype: a left I^2 (Plate 2, figs. 33-34) housed in the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF DD 4132).

Paratypes: all other suid fossils from Dorn-Dürkheim 1, described here, stored in the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Type locality: Dorn-Dürkheim 1, Rheinhessen, Germany.

Type layer: Dorn-Dürkheim Formation.

Age: Early Turolian (MN 11), Late Miocene.

Diagnosis: a *Microstonyx erymanthius* with relatively short I^{2-3} and probably also with short C^{f} (DAP).

Derivatio nominis: the subspecies differs from the M. erymanthius erymanthius in its shorter I^2 and I^3 .

The snout of *Microstonyx* from Pikermi is elongated with respect to *Microstonyx* from Stratzing and Terrassa. THENIUS (1972) used the distance $C_x - P_3$ to show this. Elongation of the snout also occurred in *M. erymanthius*, but the character is very difficult to interpret from a single skull or mandible. The variation of distances between premolars and canines in a sample of 1991). The distance $C_x - P_2$ in this sample is for the adult females 71 % of that for the adult males, the V' is 74 for the females, 49 for the males and 85 for all adults. The female cheek teeth are 97 % as large (linearly) as the males. In this study no incisors were measured, but V' for the I^2 and I^3 from Dorn-Dürkheim 1 have much smaller values (22 and 16 for the DMD) than the distance $C_x - P_2$ in the Sus scrofa sample (85). Although elongation of the snout occurred in *M. erymanthius*, the degree of elongation of the incisors separates different evolutionary stages in this lineage better.

VAN DER MADE and MOYÀ-SOLÀ (1989) suggested that *Eumaiochoerus etruscus* is a descendant from *Microstonyx major* and that the species evolved in the earlier part of MN 12. The timing of the separation of the lineages was estimated on the basis of the state of reduction of the P^I. However, it is now recognised that there are two contemporaneous species of *Microstonyx*, and the evolutionary scenario has to be modified. The DMD' of the I² and I³ of *Eumaiochoerus* have values above those of *M. major* and intermediate between Samos on the other. The argument concerning the premolars, used by VAN DER MADE and MOYÀ-SOLÀ remains valid, but weak. Both arguments indicate that *Eumaiochoerus* evolved from *M. erymanthius* late in MN 11 or early in MN 12. This indicates that (the lower part or all of) the Baccinello V2 level is as old as the earlier part of MN 12.

The small canines were probably not very dangerous weapons. The orientation of the wear facets makes the canines blunt and indicates that the canines did not project out of the mouth as in other suids. THENIUS (1972) deduced from the wide parietal and occipital region of the skull of *Microstonyx* that the males did not fight each other like in *S. scrofa*, but instead as in *Phacochoerus*. In *Sus scrofa* the males push each of their sides, and when one has to give way, the other has the opportunity to deal a dangerous blow with the canines. In *Phacochoerus* the males push the heads against each other and dangerous situations are much less frequent. According to THENIUS, this way of competition is less dangerous and better for the species. The morphology of the canines is consistent with THENIUS' interpretation.

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PLATE 1 🗲

Microstonyx erymanthius brevidens n. ssp. from the Turolian of Dorn-Dürkheim 1.

Figure 1. I_2d (DD 3045), mesial view. Figure 2. I₂d (DD 3045), lingual view. Figure 3. I₂d (DD 3045), distal view. Figure 4. I₃s (DD 4236), lingual view. Figure 5. I₃d (DD 4236), labial view. Figure 6. I₃d (DD 882), distal view. Figure 7. I₃d (DD 882), mesial view. Figure 8. $I_{3}s$ (DD 532), mesial view. Figure 9. I₃s (DD 532), lingual view. Figure 10. DI₃ (DD 1002), distal view. 11. DI₃ (DD 1002), lingual view. Figure Figure 12. DI₃ (DD 1002), mesial view. Figure 13. Cfd (DD 3080), lingual view. Figure 14. Cfd (DD 3080), posterior view. Figure 15. Cfd (DD 3080), labial view. Figure 16. C_fd (DD 2891), labial view. Figure 17. C_fd (DD 2891), apical view. Figure 18. D_2d (DD 979), buccal view. Figure 19. D₂d (DD 979), lingual view. Figure 20. C_ms (DD 1011), labial view. Figure 21. C_ms (DD 1011), posterior view. Figure 22. C_ms (DD 1011), lingual view. Figure 23. C_ms (DD 5494), labial view. Figure 24. C_ms (DD 5494), posterior view. Figure 25. P₁d (DD 969), buccal view. Figure 26. P₁d (DD 969), lingual view. Figure 27. P₂s (DD 3025), buccal view. Figure 28. P₂s (DD 3025), lingual view. 29. P²d (DD 2967), buccal view. Figure 30. P^2d (DD 2967), lingual view. Figure 31. $P^{1}d$ (DD 981), lingual view. Figure 32. P^1d (DD 981), buccal view. Figure

All specimens coated with Ammoniumchloride (NH₄Cl). Figures 1-9, 13-17 and 20-28 ca. x 1.5, figures 10-12, 18-19 and 29-32 ca. x 2.- Photos by Forschungsinstitut Senckenberg, Elke Pantak-Wein.



PLATE 2

Microstonyx erymanthius brevidens n. ssp. from the Turolian of Dorn-Dürkheim 1.

- Figure 33. I²s (DD 4132), holotype, occlusal view.
- Figure 34. I^2 s (DD 4132), holotype, lingual view.
- Figure 35. $I^3 d$ (DD 552), lingual view.
- Figure 36. $I^3 d$ (DD 552), labial view.
- Figure 37. 1³d (DD 528), lingual view.
- Figure 38. $I^3 d$ (DD 528), buccal view.
- Figure 39. DI²s (DD 880), labial view.
- Figure 40. DI¹s (DD 4378), labial view.
- Figure 41. DI¹s (DD 4378), mesial view.
- Figure 42. $DI^{1}s$ (DD 4378), lingual view.
- Figure 43. I¹d (DD 2992), mesio-lingual view.
- Figure 44. $I^1 d$ (DD 2992), labial view.
- Figure 45. I¹d (DD 2992), lingual view.
- Figure 46. I's (DD 5486), labial view.
- Figure 47. I¹s (DD 5486), lingual view.
- Figure 48. I¹s (DD 5486), mesio-lingual view.
- Figure 49. C^md (DD 883), anterior view.
- Figure 50. C^md (DD 883), posterior view.
- Figure 51. C^md (DD 883), apical view.
- Figure 52. C^md (DD 5532), apical view.
- Figure 53. C^md (DD 5532), labial view.
- Figure 54. C^md (DD 5532), posterior view.
- Figure 55. P²d (DD 862), buccal view.
- Figure 56. P²d (DD 862), lingual view.
- Figure 57. P¹d (DD 988), buccal view.
- Figure 58. P¹d (DD 988), lingual view.
- Figure 59. P¹d (DD 980), buccal view.
- Figure 60. P¹d (DD 980), lingual view.

All specimens coated with Ammoniumchloride (NH₄Cl). Figures 33-54 ca. x 1.5, figures 55-60 ca. x 2. Photos by Forschungsinstitut Senckenberg, Elke Pantak-Wein.



	I ₁	1	2		I ₃		Cf		Cm	
	DMD	DMD	DLL	DMD	DMD2	DLL	DT	Li	La	Po
mean	8.4	8.8	15.3	10.3	9.3	8.5	7.2	14.1	11.6	9.1
n	14	25	8	10	10	9	6	10	11	10
SD	0.4	0.5	0.8	1.0	1.1	0.7	0.8	0.7	1.2	1.3
V	4.8	5.7	5.1	9.3	11.9	8.7	10.9	4.9	10.3	14.2
V′	19	23	16	32	46	27	26	18	41	46
	P ₂		P ₃		46	P ₄		D ₄	DI ₁	
	DTa	DAP	DTa	DTp	DAP	DTa	DTp	DTp	DMD	
mean	7.0	18.7	9.4	9.4	20.1	12.2	14.0	12.1	5.1	
n	11	7	12	8	12	14	16	5	6	
SD	0.7	1.1	0.9	0.8	0.8	0.8	1.1	0.9	0.3	
v	10.4	5.9	9.4	8.5	4.2	6.3	8.0	7.7	6.5	
V	32	18	28	22	15	18	34	19	20	
		м ₁			M ₂			N	13	
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
mean	22.2	14.0	14.9	27.9	19.5	19.5	44.9	21.8	20.0	16.8
n	8	9	12	9	11	13	13	20	18	30
SD	0.8	1.1	0.6	1.1	1.1	1.0	1.4	0.8	1.1	1.2
v	3.8	7.5	4.0	3.9	5.6	5.1	3.2	3.6	5.6	7.2
V'	11	29	17	12	17	14	11	13	26	33
	1	[1	I	2	I	3	Cm			
	DMD	DLL	DMD	DLL	DMD	DLL	DAP			
mean	16.8	9.9	22.6	8.8	17.7	6.7	17.4			
n	14	17	7	11	7	9	6			
SD	1.0	0.7	1.7	0.9	0.9	0.6	0.4			
v	5.7	7.1	7.8	1.0	5.3	8.9	2.4			
V	23	30	22	38	16	29	7			
	F	5 1		P ²			р3		F	•4
	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT
mean	5.6	5.8	17.4	8.0	9.9	17.3	11.4	16.0	16.6	18.5
n	7	8	7	15	14	12	16	11	21'	19
SD	0.5	0.5	0.6	0.6	0.8	0.8	0.6	0.8	0.6	0.8
v	8.8	8.3	3.2	4.7	8.3	4.6	4.9	5.0	3.6	4.6
V	25	25	8	16	23	13	17	15	16	16
		M ¹			M ²			N	A ³	
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
mean	22.6	19.6	19.2	28.3	24.9	23.0	41.1	26.9	23.8	14.9
n	12	12	11	8	10	10	19	27	23	27
SD	1.3	0.8	1.0	0.9	1.2	0.5	1.5	1.0	1.0	1.4
V	5.7	4.3	5.1	3.2	4.7	2.1	3.7	3.6	4.3	9.4
V'	19	13	18	10	14	8	12	12	18	44

Table 1. Mean number of measured specimens (n), standard deviation (SD), coefficient of variation (V) and V' of the suid teeth from Dorn-Dürkheim 1. Based on five or more measured specimens.

L

Ml	no.	pos.	DAP	DTa	DTp
DD	598	1			14.7
DD	868	1	23.0		15.5
DD	959	1	21.7	≥14.8	14.8
DD	960	1		14.2	
DD	961	1	21.8	13.7	13.9
DD	962	1	22.1	≥14.0	≥14.7
DD	963	r			14.9
DD	964	г			14.8
DD	965	r		13.8	
DD	966	1	0	14.2	
DD	967	1	22.4	13.7	14.7
DD	968	r	23.1	14.1	14.8
DD	3079	1		14.5	15.2
DD	4125	1			14.6
DD	4320	r	20.7	≥14.7	14.9
DD	5522	1		12.0	
DD	5554	1	23.1	16.1	16.4

M ₂	no.	pos.	DAP	DTa	DTp
DD	3066	1	29.4	19.7	21.0
DD	3067	1		()	18.8
DD	3068	1	28.5	18.0	18.3
DD	3069	1	-		20.0
DD	3070	r		≥19.4	
DD	3071	r		21.4	
DD	3072	1		20.3	
DD	3073	1			21.1
DD	3074	1		20.2	
DD	3075	1	28.8	20.4	21.0
DD	3076	1	28.0	19.7	19.2
DD	3948	1	26.9	18.7	18.5
DD	4673	r	26.1	18.3	18.9
DD	5487	r			19.2
DD	5506	r	26.8	19.2	19.5
DD	5525	1			19.5
DD	5541	r	27.9	18.1	18.5
DD	5552	1	28.5		

M ₃	no.	pos.	DAP	DTa	DTp	DTpp
DD	3026	1	44.5	21.3	20.5	15.4
DD	3028	r		22.0		
DD	3029	1			20.2	17.1
DD	3030	r		21.6	19.8	
DD	3031	r	44.5	-		17.3
DD	3032	r		101	>20.2	16.6
DD	3033	r		10		17.0
DD	3034	r		10		17.8
DD	3035	1	43.4	20.4	19.3	16.2
DD	3037	1		≥22.4		
DD	3038	r	44.8	>19.8	19.5	15.7
DD	3039	r	46.0	22.3	20.2	16.9
DD	3040	1		20.8		
DD	3041	r			>21.5	17.9
DD	3042	1	44.3	21.9	19.8	16.4
DD	3078	1		_		15.0
DD	3091	r			20.9	
DD	3935	r		>20.5	>17.8	
DD	3976	r	-	24 <u>-</u>		15.7
DD	4087	r	42.6	21.6	19.6	15.9
DD	4290	1	·	22.0		
DD	4316	1	47.7		>22.5	17.2
DD	4388	1		-	-	16.4
DD	4556	r	45.0	22.5	21.0	20.9
DD	4632	1		22.3		
DD	4781	1	46.1	22.7	20.3	17.5
DD	5490	r		21.0		
DD	5492	1				167

M ₃	no.	pos.	DAP	DTa	DTp	DTpp
DD	5504	r	46.2	21.7	20.3	18.0
DD	5507	r				16.0
DD	5512	1				17.6
DD	5519	r			20.3	17.7
DD	5523	r		21.4		
DD	5524	r				17.3
DD	5528	r			≥19.6	
DD	5534	1	>49.3	22.7	20.2	15.1
DD	5543	1	43.1	20.4	18.7	15.5
DD	5548	1				17.5
DD	5549	т			21.1	
DD	5549	r		≥23.6		
DD	5552	1	45.8	22.8	21.1	18.1
DD	5578	1		23.2	- 2	
DD	5579	1				16.1
DD	5584	r		22.1		
DD	5588	1			16.3	
DD	5594	1				15.5

Table 2. Measurements of the lower molars in mm.

"--" means that a measurement could not be taken because of damage; ".." means that data were not recorded for any other reason, for instance because a part of a tooth was covered by sediment or bone.

Table 3. Measurements of the upper molars in mm.

M ¹	no.		DAP	DTa	DTp
DD	37	r	>21.5		
DD	872	1	23.0	18.3	17.0
DD	874	1			>16.6
DD	877	г	20.0	19.2	
DD	2956	1	23.8	20.6	19.5
DD	2958	r	21.9		20.2
DD	2959	r	23.2	20.1	19.3
DD	2960	1	22.6	≥19.5	19.6
DD	2961	1	22.9	18.3	18.1
DD	2962	r	22.6	20.1	20.0
DD	3950	1	21.8	20.3	19.6
DD	4074	r		>18.1	
DD	4128	1	24.2	20.9	
DD	4732	r			20.3
DD	4740	r	24.0	19.4	19.0
DD	5483	1		19.2	
DD	5500	r	20.7	>17.3	18.6
DD	5527	r		19.1	
DD	5604	1		19.9	

M ²	no.	8	DAP	DTa	DTp
DD	873	1			≥26.0
DD	2940	r			
DD	2951	r	27.6	24.1	23.2
DD	2953	1	≤27.8	26.4	≤25.0
DD	2954	r	28.1	24.0	22.7
DD	2956	r	30.1	24.7	23.1
DD	2957	1	27.9	24.9	23.2
DD	2958	r			22.9
DD	2962	r	>28.0	25.0	
DD	4555	1	±32.3	27.4	±27.0
DD	4635	1	28.2	24.3	22.3
DD	4762	1	28.1	24.2	23.3
DD	5480	1	9	≥24.9	
DD	5533	r	29.0	23.7	22.9
DD	5235	1	27.2	≥22.4	22.6
DD	5559	1			24.1

M ³	no.		DAP	DTa	DTP	DTpp
DD	870	r			23.0	11.4
DD	871	r			>20.9	
DD	876	1				13.1
DD	2934	r		≥24.7	22.5	
DD	2935	r		27.4	23.9	
DD	2936	r				16.5
DD	2937	1		26.4	23.9	
DD	2938	1	40.7	28.4	24.2	13.7
DD	2939	1		26.5		
DD	2941	r	43.3	28.0	24.9	15.4
DD	2942	r		26.9		
DD	2943	r	42.0			16.1
DD	2944	1	42.7	27.9	24.5	13.1
DD	2945	r	40.9	26.0	23.4	14.0
DD	2946	1	43.2	26.7	23.3	14.4
DD	2947	r	40.5	26.3	23.6	14.9
DD	2948	r	40.1	25.4	22.6	14.0
DD	2949	r	42.0	27.5	25.1	16.4
DD	2950	г	40.2	26.3	23.2	14.1
DD	2983	r		27.9		
DD	2985	r	39.8	25.7	22.7	15.8
DD	3027	1				15.7
DD	3036	1				16.6
DD	3821	1	40.1	26.6	>22.8	>13.5
DD	3838	1	41.5	26.5	23.8	15.2
DD	3935	1				
DD	4063	г		27.8		
DD	4542	1	38.6	28.5	24.8	15.4
DD	4548	1				≥15.1
DD	4716	r	38.6	26.1	22.7	15.0
DD	5508	r			>21.0	>13.8
DD	5529			26.1		
DD	5531	r				13.9
DD	5531a	1	43.7			14.6
DD	5535	r	42.0	26.2	23.5	17.8
DD	5538	r	42.1	28.3	24.4	16.0
DD	5542	r	39.4	25.4	22.8	13.6
DD	5551	r		28.3	23.1	
DD	5556	r	≤43.7	26.9	26.9	16.5
DD	5576	1		28.5		
DD	5580	r			23.9	13.5
DD	5582	1				15.8

		D ₂					D3					Ľ	94		
no.	Π	DAP	DTa	DTp	no.		DAP	DTa	DTp	no.		DAP	DTa	DTm	DTp
DD 979	r	12.9	4.4	≥5.7	DD 976	r		-	6.3	DD 994	r		-	11.6	
DD 984	1	13.0	4.6	5.3	DD 978	1	8	5.8		DD 995	1		2		13.0
DD 987	1			4.6	DD 991	1	13.6	6.1	7.3	DD 996	r	-			12.9
DD 4490	1			5.8	2 1 2 1		12	2		DD 996	1	2 <u>-</u> 0			
	T				3 2	T	18	2		DD 997	r	- 5	-		10.7
	T									DD 998	r	-	9.1		11.9
										DD 999	r				11.9
	T							20	20 C	DD 999	r	-	10.4		-
	T									DD 1000	1	-	≥9.6		
	T					T				DD 4065	1			10.4	
					2 2	T		g	1 1 2	DD 4782	r		≥9.1		
	T					T				DD 5544	1				>11.4
	-	D ²		-			D ³		5 2	2.13	-	I) 4	1	
no.	Γ	DAP	DTa	DTp	no.	Γ	DAP	DTa	DTp	no.	Γ	DAP	DTa	DP	
DD 881	1	13.5	6.2	8.5	DD 4554	r	15.8	8.3	12.6	DD 3070	r		-	>15.8	
DD 2929	r	13.7	6.4	8.4	6 6 .			<u>a</u> [DD 5482	?	>16.2	18	16.4	
DD 4419	r			7.6		T				DD 5514	r		16.0		
DD 5502	1			8.8		T				DD 5563	r			15.6	
	T							8		DD 5569	1	_		15.9	

Table 4. Measurements of the deciduous cheek teeth in mm.

Table 5. Measurements of the lower premolars in mm.

		Pl					P ₂					P ₃					P4		
		DAP	DTa	DTP	по.		DAP	DTa	DTp	no.		DAP	DTa	DTP	no.		DAP	DTa	DTP
696	-	12.9	6.1	6.1	DD 3015	1	16.5	6.5		DD 979	ы	I	1	8.6	DD 973	-	20.0	11.9	14.0
4642	-	>11.5	5.3	5.2	DD 3018	1	1	6.4		DD 990	L	16.7	8.2	8.5	DD 974	1	1	11.5	1
					DD 3021	1	1	7.1		DD 3010	1	I	I	9.5	DD 975		19.8	11.4	13.5
					DD 3024	L	15.9	1	7.1	DD 3017	1	20.0	10.9	1	DD 975	1	20.4	11.4	13.9
					DD 3025	-	17.2	7.6	8.0	DD 3020	1	19.3	10.6	10.6	DD 982	-	18.8	12.3	14.2
					DD 4525	5	15.5	6.0	7.2	DD 3024	t	18.6	9.3	9.8	DD 983	-	1	12.9	1
					DD 5537	5	15.7	6.3	6.9	DD 4395	1	19.4	8.8	000 	DD 990	-	20.2	11.2	12.9
					DD 5567	1		1 1 1 1	6.7	DD 4681	r	17.8	8.8	8.8	DD 3016	-	equ	1	14.6
					DD 5591	r	1	7.7	1	DD 5540	1	18.8	9.2	10.2	DD 3019	-	1	11.7	1
					DD 5597	1	I	7.7	1	DD 5546	1	19.6	≥9.8	10.8	DD 3022	-	21.0	13.0	14.4
					DD 5601	-	1	8.3	1	DD 5565	r	I	8.7	1	DD 3858	-	19.8	12.3	14.9
					DD 5598	ч	ı	7.2	ı	DD 5581	r	1	ı	8.8	DD 3931	ч	20.2	13.4	15.3
					DD 5599	5	1	6.4	1	DD 5582	r	I	9.2	1	DD 4326	1	1	1	14.4
					DD 5605	-	1	7.3	I	DD 5593	1	1	9.2	-1	DD 4398	1	20.2	12.0	13.1
							and se			DD 5596	1	1	9.4	1	DD 4764	L	18.9	12.9	14.0
							ola i								DD 5484	1	1	1	15.2
															DD 5513	ы	1	1	13.8
															DD 5546	L	1	10.9	I
															DD 5547	r	21.9	13.4	15.3
															DD 5550	1	1	1	≥15.1

				-		-	-					-	-	_	-		-	_								
	DT	17.6	17.8	17.7	>18.3	18.4	>18.2	18.2	17.4	20.5	1	18.5	18.4	20.1	18.7	18.9	19.2	17.7	19.3	1	17.7	18.3	±19.8	19.0	1	18.2
P4	DAP	16.4	16.8	16.3	1	15.8	15.9	16.5	15.7	16.7	>15.2	16.3	16.3	16.7	17.1	16.6	17.1	16.6	18.5	1	16.3	16.4	16.6	1	17.2	17.1
		-	-	-	-	-	ы	L	-	L	1	-	ı	r	-	-	r	-	-	-		-		-	-	-
	no.	DD 851	DD 852	DD 852	DD 854	DD 855	DD 856	DD 857	DD 858	DD 863	DD 864	DD 865	DD 2962	DD 2963	DD 2964	DD 2969	DD 2973	DD 2976	DD 2984	DD 3791	DD 4430	DD 4639	DD 4680	DD 5501	DD 5526	DD5558
	DTp	15.2	1	1	1	16.8	16.5	16.4	16.0	1	15.6	1	15.0	1	1	16.2	17.5	15.2	1	15.3	1	1	ı	ı	1	
	DTa	11.2	>10.7	11.0	10.6	10.9	12.6	1	11.6	1	1	11.4	1	,	10.7	12.2	11.8	10.7	1	1.11	11.2	11.7	1	11.6	11.5	
p3	DAP	16.6	16.1	16.5	18.1	16.4	17.9	1	17.0	1	1	1	1	18.4	1	17.0	18.3	17.5	>16.5	17.4	1	1	I	1	ı	
		r	1	L	-	-	-	1	r	1	-			-	L	L	1	1	1	1	1		1	L	1	
	no.	DD 859	DD 860	DD 866	DD 2965	DD 2966	DD 2970	DD 2971	DD 2974	DD 2975	DD 2978	DD 2981	DD 4430	DD 4500	DD 4646	DD 4676	DD 4714	DD 4750	DD 5479	DD 5539	DD 5592	DD 5555	DD 5560	DD 5602	DD 5603	
	DTp	9.7	9.9	9.8	1	ı	10.4	10.5	9.6	I	1	9.7	10.1	9.2	1	1	11.6	0	10.5	10.3	I	1	≥9.8	9.3		
	DTa	8.2	7.8	7.8	8.7	8.0	8.3	8.4	1	8.0	8.0	7.4	1	1	8.3	8.0	1	7.4	1	1	≥8.3	7.6	1	1		
\mathbf{p}^2	DAP	17.7	17.8	17.7	1	I	16.7	18.1	1	1	1	16.7	1	1	1	1	1	1	1	1	1	1	1	I		
		r	r	r		1		L	1	1	1	1	1	r	1	ы	L	1	-	-	1	1		-		
	no.	DD 861	DD 862	DD 867	DD 964	DD 2927	DD 2967	DD 2968	DD 2972	DD 3014	DD 3023	DD 4362	DD 5530	DD 5568	DD 5571	DD 5572	DD 5574	DD 5577	DD 5585	DD 5586	DD 5587	DD 5590	DD 5595	DD 5600		
	DTp	≥5.2	5.2	5.8	5.0	6.4	5.8	5.7	6.3	6.3			0.01	241					-							
	DTa	5.0	I	5.9	5.0	5.7	5.7	5.6	6.4	1			100	00												
Pl	DAP	≥11.5	I	12.6	>10.3	>12.5	10.8	12.1	>12.9	1																
		-		-	L			-	-	-																
		971	972	<i>LL6</i>	980	186	988	4628	4822	5573				_						-		-				

Table 6. Measurements of the upper premolars in mm.

	Pl		31.8	Pl HIi HI 977 ≥7.1 ≥7 988 5.7 7. 988 5.7 7. 4628 6.7 8. 4822 6.6 7. $P2$ 862 11 2968 11 ±12 $P3$ 2965 15 2970 14 5539 15	
	Hli	Hla			Hla
DD 969	8.7	8.2	DD 977	≥7.1	≥7.9
			DD 988	5.7	7.2
			DD 4628	6.7	8.3
			DD 4822	6.6	7.2
	P ₂		8 8 8	P2	3 8
DD 3024	10.6		DD 862		11.6
DD 5537	9.8	10.3	DD 2968		11.6
			DD 3014		±12.0
	P ₃			р3	
DD 3020	14.5	15.1	DD 2965		15.1
DD 5540	15.3	15.9	DD 2970		14.8
			DD 5539	-	15.4

Table 7. Measurements of the height of the crowns of the premolars in mm.

		Cm			18 19	C	f		1.0	С	m	316	1.81	(⊡ f	
no.		Li	La	Po	no.		DAP	DT	no.		DAP	DT	no.		DAP	DT
DD 1009	r		13.3		DD 2891	r	9.5	6.3	DD 883	r	17.3	- 1	DD 3011	1	>>13.0	>7.9
DD 1010	r	14.1	10.7	9.0	DD 3077	1		6.8	DD 884	r	18.0	15.2				
DD 1011	1	12.8	8.8	10.2	DD 3080	r	9.9	8.2	DD 885	r		-	12			
DD 1012	1	14.7	12.7	11.3	DD 3081	r		≥7.7	DD 886	r			1			
DD 1014	r	14.1	11.2	9.9	DD 3082	r		6.4	DD 888	1	17.6	13.7				
DD 1015	1	15.3	12.5	8.7	DD 5536	r	10.4	7.8	DD 889	r	17.2	14.2				
DD 1016		14.4	12.3	7.6	DD 5510	r	9.9	7.5	DD 3926	1	16.8	12.2				
DD 1017	1	14.0	11.3	9.8					DD 5532	r	>17.5	13.4				
DD 2986	r	14.6	11.6	9.6					DD 5478	r	17.7	-				
DD 4662	r	13.6	11.7	8.0								2	1			
DD 5494	1	13.7	11.4	7.1												
											-					

		I ₁			I ₂					I3				
no.		DMD	DLL	no.		DMD	DLL	no.		DMD	DMD2	DLL		
DD 3051	r	9.2		DD 2980	1	9.2	>13.4	DD 482	r	11.5	11.4	9.2		
DD 3059	1	8.7	>11.6	DD 3043	1	8.5		DD 521	1	9.5	9.3	7.6		
DD 3063	1	8.1	13.1	DD 3044	r	≥8.3		DD 522	1	11.3	9.4	9.0		
DD 3047	r	8.2	>11.6	DD 3045	r	9.7	16.8	DD 523	1	10.8	9.8	8.8		
DD 3054	1	8.3	-	DD 3046	1	8.9	>12.6	DD 527	r	10.6	8.3	≥9.3		
DD 3055	1	8.7		DD 3048	r	9.2	-	DD 532	1	10.6	9.4	7.5		
DD 3058	r	8.4		DD 3049	1	8.9		DD 551	r	10.7	9.9	8.2		
DD 3060	r	8.3		DD 3050	1	8.5		DD 849	r	≥10.6	≥8.8			
DD 3062	1	8.4		DD 3052	r	8.7	15.4	DD 882	r	8.3	7.1	9.8		
DD 4237	r			DD 3053	r	8.7	15.6	DD 1008	1					
DD 4396	1	8.9		DD 3056	1	8.4	14.4	DD 2925	1	-				
DD 4547	1	8.0		DD 3057	r	8.8	>13.0	DD 2930	1	9.7	9.2	8.4		
DD 4550	r	7.6		DD 3060	1	8.6		DD 2933	r	-				
DD 4636	r	8.3	12.3	DD 3061	r			DD 3830	r	-				
DD 5557	1	8.2		DD 3064	r	9.4	>14.9	DD 4236	1	9.8	9.1	8.4		
				DD 3065	1	8.2	15.1		100					
				DD 3065	r	8.1		0.000	1115					
				DD 3083	r	8.5								
				DD 3803	r	8.5	14.3			1.1				
				DD 3943	r	9.1								
				DD 4039	1	9.3	15.2			3.4				
				DD 4088	1	>6.8								
				DD 4348	1	8.7								
				DD 4405	1	10.0								
				DD 4638	1	8.9								
				DD 4791	1	8.2								
				DD 5491	1	7.9								
				DD 5545	1		15.5							
				DD 5589	1	8.4								
		DI ₁				DI ₂	-115			DI ₃				
no.		DMD	DLL	no.		DMD	DLL	no.	100	DMD	DLL			
DD 1001	r	5.1		DD 1003	1	5.6	≥7.5	DD 1002	1	4.0	4.4			
DD 1004	r	5.5		DD 1007	1	5.7	≥8.7	00	00					
DD 1005	1	5.2				17	9-81 L.	7.410	00					
DD 1006	r	5.2	>6.8			22	ET< 1	195	00					
DD 1013	г	4.5	≥6.3											
DD 4475	1	5.2												

Table 9. Measurements of the permanent and deciduous lower incisors in mm.

Table. 10. Measurements of the permanent and deciduous upper incisors in mm.

	I	1	111/00	- Sell	I	2	926	9.00	I	3	
no.		DMD	DLL	no.		DMD	DLL	no.		DMD	DLL
DD 39	1			DD 525	r		≥7.5	DD 524	1	17.5	6.8
DD 526	r		-	DD 538	1		≥8.4	DD 528	1	17.1	5.8
DD 534	1			DD 539	1	-	7.9	DD 529	1	18.9	6.7
DD 537	r		-	DD 850		>18.2	6.9	DD 531	1	17.5	7.3
DD 2979	r	17.0	11.7	DD 2987	1	21.6	8.6	DD 535	1	16.1	6.6
DD 2990	r	16.4	10.4	DD 2987	1	>>17.6	8.6	DD 536	r		7.8
DD 2991	r		- 08.	DD 2988	1	21.0	8.4	DD 552	r	18.5	7.0
DD 2992	r	17.2	9.8	DD 2988	r	23.6	9.0	DD 986	r		6.3
DD 2993	r		9.4	DD 2991	r	22.3	8.9	DD 2926	r		≥6.0
DD 2994	1	16.2	10.9	DD 2997	1	22.5	9.9	DD 2989	r		≥6.1
DD 2995	r	>15.1	8.6	DD 2998	r	>22.6	8.8	DD 3905	1	18.0	6.2
DD 2996	r	16.7	9.5	DD 4132	1	26.1	10.1				
DD 2999	1	17.6	9.1	DD 5499	1	21.4	9.5		-		
DD 3789	1	17.6	9.8	DD 5562			≥7.8	and the			
DD 3897	1							and of the			
DD 3937	1	18.2	9.8					EDME CIEL			
DD 4111	1	16.6	10.1					Gev: 09			
DD 4346	1	17.1	10.4				2	000-00			
DD 4689	r	17.8						ages and			
DD 4713	1							840-66			
DD 4719	r	14.5	10.1			0	21 .	DD 4405			
DD 4802	1	15.5	9.7				1	NEAR GO			
DD 5486	1	16.9	9.7				2	1951 0 0-1			
DD 5497	r		10.0					LANG CITE			
DD 5498	1	>16.3	9.5								
	1		1	DI	2		DI3				
no.		DMD	DLL	no.		DMD	DLL	no.		DMD	DLL
DD 530	1	10.1	5.7	DD 880	1		≥4.0	coor data			
DD 548	1		≥6.4	DD 970	1		6.0	001 012			
DD 549	1	11.8	6.1	DD 3837	1	16.9	7.1				
DD 2932	r	-	6.3	DD 5493	1	>13.2	5.9				
DD 4378	1	9.5	5.6								

		I ₁		
	Hli	Hla	Hmes	Hdist
DD 3047		h3	16.3	18.2
DD 3055			±17.9	>20.5
DD 4547			16.5	16.7
DD 4636	31.7		17.6	18.1
		I ₂		811
DD 3045	>>30.5	>>34.5	>14.6	>25.0
DD 3057		-	17.2	
DD 3060		-	±20.4	(D)(d)
DD 3064			18.1	> 21.8
		I ₃	8	0.0
DD 521	16.8	17.3	7.7	16.7
DD 522			>6.2	>14.3
DD 527	>10.2		6.0	
DD 532			>6.3	>12.6
DD 551	>14.1	>13.8	>6.1	>11.9
DD 882	>18.4	>17.9	7.4	17.7
DD 1008			7.9	
DD 2925			6.2	\$ 80 <u></u> 5
DD 2930		13.8	6.4	0.05
DD 4236	14.1	14.9	7.4	15.1
		DI ₂		3.34
DD 1003			10.2	2.01 2
		DI ₃		1.01
DD 1002	>7.2	>7.2	>4.0	>4.9
		I ³		232
DD 552	8.9	10.4		2.15

Table 11. Height of the crowns of the incisors in mm.

	M ¹		1	1			MIMT 1	[2		-	I	3	
	n	n	DMD'	n	DLL'	n	DMD'	n	DLL'	n	DMD'	n	DLL'
Pikermi	1					1	136						
Samos	1	0		0		2	136	2	45	1	106	1	37
Dorn-Dürkheim 1	12	14	86	17	57	7	115	11	45	7	90	9	34
Spain	11	3	89	3	56	2	118	3	45	1	>62	1	31
Monte Bamboli	27	5	88	1	52	2	117	3	40	1	86	1	29
	M ₁		I	1			1	2		I ₃			
	n	n	DMD	n	DLL'	n	DMD'	n	DLL'	n	DMD'	n	DLL'
Dorn-Dürkheim 1	12	14	56	2	85	25	59	8	103	10	69	9	57
Spain	15	8	58	5	93	5	60	2	98	1	43	1	65

Table 12. DMD' and DLL' values for the incisors. Data on one individual from Pikermi from GAUDRY (1862 - 1867).

Table 13. Measurements of the phalanges and metapodials in mm.

	no.		DAPp	DTp	L	DAPd	DTd
Phalange 1, III or IV	DD 5518	1	24.5	26.4	44.7	14.8	20.0
Phalange 1, II or V	DD 5489	r	16.1	14.0	23.5	9.7	≥11.4
Phalange 2	DD 5521	r		19.9	27.1	15.2	16.6
Phalange 2, II or V	DD 878	1	14.2	11.5	20.2	±11.8	>10.7
"	DD 4147	1	14.0	11.7	18.0	11.1	10.1
Metapodial	DD 3086	1				-	23.3
	DD 3087	r				23.3	23.9
"	DD 3088	r				22.2	21.5